Terrestrische Arthropoden-Assoziationen als ökologische Indikatoren von Umweltveränderungen

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Inhaltsverzeichnis

1. Einleitung

Arthropoden besetzen als artenreichste Organismengruppe eine Vielzahl von funktionellen Nischen und Mikrohabitaten in terrestrischen Ökosystemen (Kremen et al. 1993, Odegaard 2000). So sind sie beispielsweise als Herbivore, Pollinatoren, Detritivore, Mutualisten, Prädatoren, Parasiten oder als Nahrungsgrundlage für viele Wirbeltiere in den meisten Ökosystemen von essentieller Bedeutung (u.a. Curry 1994, Samways 1994, Tscharntke & Greiler 1995, Price 1997). Daraus lässt sich die potentielle Eignung dieser Tiergruppe als Indikatoren von Umweltveränderungen über ein weites Spektrum räumlich-zeitlicher Skalen hinweg ableiten (Kremen et al. 1993, Harrington & Stork 1995, McGeoch 1998). Hinzu kommen das große Kolonisationspotential und die kurzen Generationszeiten vieler Arthropoden-Taxa, die mitunter enorme Populationsfluktuationen als unmittelbare Reaktion auf Veränderungen in der Habitatqualität bewirken (Brown & Southwood 1983, Williams 1993, Harrington & Stork 1995, Price 1997). Des Weiteren weisen Arthropoden im Vergleich zu anderen Tiergruppen (z.B. Wirbeltieren) viel größere Populationsdichten auf, die einerseits wiederholte Stichprobennahmen ermöglichen ohne dadurch erhebliche Veränderungen in der Populationsdynamik hervorzurufen (Southwood et al. 1979, Kremen et al. 1993, Williams 1993) und andererseits numerisch „verwertbare Zahlen" liefern und damit statistische Auswertungen zulassen (Dent & Walton 1997, Duelli et al. 1999).

Auf die besondere Eignung von terrestrischen Arthropoden und insbesondere Insekten als Bioindikatoren macht McGeoch (1998) aufmerksam. Am Beispiel dieser Tiergruppe stellt sie heraus, dass das Konzept der Bioindikation bisher meist unspezifisch und für ein sehr breites Spektrum verschiedenster Fragestellungen verwendet wurde. Ausgehend von den drei Hauptanwendungen der Bioindikation reklassifiziert McGeoch (1998) drei Kategorien. Danach werden als (i) Umwelt-Indikatoren (*environmental indicators*) Arten oder Artengruppen charakterisiert, die den aktuellen Zustand der Umweltbedingungen messbar widerspiegeln, somit vorhersagbar (z.B. im Sinne von Zeigerarten) auf abiotische (oder auch biotische) Umweltveränderungen reagieren. Demgegenüber werden Arten oder Artengruppen als (ii) ökologische Indikatoren (*ecological indicators*) bezeichnet, die die Auswirkungen von (globalen) Umweltveränderungen auf biotische Systeme demonstrieren. Ökologische Indikatoren fungieren hier als Surrogate. Ihre Reaktion auf direkt meist schwer messbare komplexe Veränderungen (z.B. globaler Klimawandel) wird als repräsentativ für eine Biozönose (*community*) oder ein ganzes Ökosystem angesehen. Aussagen auf der Grundlage von ökologischen Indikatoren setzten dabei in der Regel wiederholte Datenerhebungen voraus (Lawton & Gaston 2001). (iii) Biodiversitäts-Indikatoren (*biodiversity indicators*) sind Artengruppen, deren Diversität (z.B. Artenvielfalt, Anzahl seltener Arten, Anzahl von Endemiten) stellvertretend die Diversität anderer Artengruppen, ganzer Biozönosen (*communies*) oder geografischer Regionen widerspiegelt. Folgt man dieser allgemein akzeptierten Klassifikation (u.a. Lawton & Gaston 2001) so ist festzustellen, dass die Verwendung von Arthropoden (Arten oder Artengruppen) als Umwelt-Indikatoren relativ verbreitet ist (u.a. Spellerberg 1991, Paoletti & Bressan 1996, Hoffmann et al. 2000), wobei hier Anwendungen im aquatischen Bereich überwiegen (Orendt 1998, Scrimgeour et al. 1998, Figueroa et al. 2003). Die Verwendung von Arthopoden als Biodiversitäts-Indikatoren hat sich besonders im Zusammenhang mit der Identifikation von vorrangig zu schützenden Lebensräumen (Noss 1990, Flather et al. 1997, Prendergast 1997, Reid 1998) und Fragestellungen des Naturschutzes in subtropischen und tropischen Ökosystemen im vergangenen Jahrzehnt etabliert (Kremen et al. 1994, Kitching et al. 2001). Bei der Nutzung von Arthropoden als ökologische Indikatoren dominieren Untersuchungen mit agrarökologischem Bezug (Duelli et al. 1999, Wardle et al. 1999). Aber auch im Zusammenhang mit Studien zum Restaurationsmanagement bzw. -monitoring, wo sich bisherige Arbeiten vorrangig auf die ablaufenden Regenerationsmechanismen der Vegetation als Basis für die Interpretation des Systemwandels beschränkten, werden zunehmend Arthropoden-Taxa als ökologische Indikatoren diskutiert und deren Vorteile gegenüber einem „reinen“ Vegetations-Monitoring herausgestellt (Madden & Fox 1997, Williams 1997, Topp 1998). Aufgrund der gegenwärtig dominierenden Probleme im Zusammenhang mit globalen Umweltveränderungen (u.a. Nutzungsänderungen, Klimawandel und CO_2-Anstieg, Abnahme der Artendiversität, Arteninvasionen exotischer Arten) ist jedoch die Verwendung und das Einsatzspektrum von Arthropoden als ökologische Indikatoren bisher weit weniger verbreitet, als erwartet.

Der Begriff „Assoziation“ wird in der vorliegenden Arbeit im Sinn des englischsprachigen Terms *assemblage* verwendet und nicht wie in der (deutschen) Pflanzensoziologie üblich, im Sinn einer definierten und hierarchisch angeordneten Organismeneinheit. Eine Assoziation (*assemblage*) umfasst somit eine Gruppe von Arten, ohne explizit Interaktionen zwischen diesen Arten anzunehmen, was (streng genommen) durch den Begriff *community* beschrieben wird (Calow 1998, Perner & Köhler 1998).

In Anlehnung an den in der englischsprachigen Literatur etwas „großzügigeren Umgang“ mit dem Begriff „Abundanz“ (*abundance*) wird auch dieser Term hier vielfach verwendet, obwohl es sich, methodisch bedingt, meist nur um Fang- oder Individuenzahlen bzw. Aktivitäts-Abundanzen handelt (u.a. Müller-Motzfeld, 1989).

Für die Beschreibung ökologischer Artengruppen wurden in den letzten beiden Jahrzehnten mehrere unterschiedliche Begriffe beschrieben, die aufgrund inkonsistenter Bezüge zu den ursprünglichen Konzepten teilweise synonym oder falsch verwendet wurden. Terminologische Klarheit verbunden mit einer Klassifikation der Konzepte brachten hier Arbeiten von Hawkins & Mac Mahon (1989) und Simberloff & Dayan (1991), sowie später die Arbeiten von Wilson (1999) und Blondel (2003). Gegenwärtig dominieren diesbezüglich drei Konzepte. Danach sind mit „Gilden" (*guilds*) Arten-Aggregationen definiert, welche ähnliche Ressourcen auf ähnliche Weise nutzen (Root 2001, Blondel 2003). Als „funktionelle Gruppen" (*functional groups*) werden hingegen Arten zusammengefasst, die einzelne (wichtige) ökologische Merkmale gemeinsam haben bzw. einzelne äquivalente Funktionen in Ökosystemen erfüllen (Smith et al. 1997, Steneck 2001, Blondel 2003). Demgegenüber werden unter „funktionellen Typen" (*functional types*) Artengruppen verstanden, die sich in Bezug auf ganze ökologische Merkmalskomplexe ähnlich sind (Smith et al. 1997, Wilson 1999, Semenova & van der Maarel 2000, Colasanti et al. 2001). Beispielsweise zählen dazu die für Pflanzen verwendeten CSR-Typen (Grime 2001).

Im Zusammenhang mit den aktuellen Debatten über die Effekte von globalen Umweltveränderungen auf die Ökosystemfunktionen hat in den letzten Jahren besonders das Interesse am Konzept der funktionellen Gruppen zugenommen (z.B. Bengtsson 1998, Blondel 2003). Dahinter steht die Erwartung, mit diesem Ansatz einerseits eine Verbindung zwischen Arten bzw. Artengruppen und einem breiten Spektrum verschiedenster Ökosystemfunktionen herzustellen (z.B. bio-geo-chemische Zyklen, Resistenz gegen Arteninvasionen, Herbivorie, Bestäubungsaktivitäten, Ökosystem-*Engineering*). Andererseits ermöglicht dieses Konzept aber auch die Aggregation von Arten-Assoziationen zu handhabbaren, funktionellen Einheiten, die als Werkzeug zur Vorhersage von Ökosystemveränderungen verwendet werden können (Körner 1993, Bengtsson 1998, Steneck 2001). Jede Art weist eine Vielzahl von morphologischen und physiologischen Eigenschaften sowie Verhaltensmustern auf, die sich auf ihre Populationsdichte auswirken und potentiell auch Ökosystemfunktionen beeinflussen können. Nach Chapin et al. (1997) sollten dabei die Eigenschaften von Arten die größten Effekte auf Ökosystemfunktionen haben, die (a) die Verfügbarkeit und Nutzung von limitierten Ressourcen steuern, (b) die Strukturen von Nahrungsnetzen modifizieren oder (c) das Auftreten und die Stärke von Störungen beeinflussen. Bezug nehmend auf Chapin et al. (1997) schlägt Tilman (2001) daher vor, vorrangig solche Eigenschaften von Arten zu identifizieren, die mit großer Wahrscheinlichkeit für die Beeinflussung von Ökosystemprozessen verantwortlich sind, und genau diese Eigenschaften für die Klassifizierung von Organismen in funktionelle Gruppen zu verwenden. Als Beispiel führt Tilman (2001) die Klassifizierung von Arten einer Assoziation (*assemblage*) auf der Grundlage ihrer Position im Nahrungsnetz an (Pflanzen, Herbivore, Prädatoren, Parasiten, Parasitoide, Detritivore). In einem zweiten Schritt, beispielsweise auf der Grundlage zeitlich oder räumlich unterschiedlicher Aktivitätsmuster oder auf der Grundlage physiologischer Eigenschaften, können diese dann weiter unterteilt werden. Bei der Verwendung dieses Konzeptes geht man davon aus, dass sich Arten innerhalb einer funktionellen Gruppe in Bezug auf eine Ökosystemfunktion einheitlicher verhalten, als Arten unterschiedlicher funktioneller Gruppen (Tilman 2001). Insbesondere für sehr artenreiche Gruppen wie terrestrische Arthropoden wird diese *a priori*-Klassifikation als ein „erster Schritt" in Richtung einer funktionellen Analyse empfohlen (Bengtsson 1998), da hier vielfach detaillierte Informationen zur Physiologie bzw. zur *life history* fehlen, die eine numerische Klassifikation zu funktionellen Gruppen ermöglichen würden. Im Gegensatz zu pflanzenökologischen (Symstad 2000, Reich et al. 2001, Tilman 2001) oder aquatischen Studien (Usseglio-Polatera et al. 2000, Pearson 2001), wo funktionellen Gruppen schon häufiger und erfolgreich Verwendung gefunden haben, wurde dieses Konzept für terrestrische Arthropoden bisher vergleichsweise wenig angewandt.

Die Berücksichtigung einer größeren taxonomischen und funktionellen Vielfalt und die damit im Zusammenhang stehende größere Vielfalt an Reaktionen auf Umweltveränderungen werden als hauptsächliche Argumente für die Verwendung von Artengruppen (z.B. funktionellen Gruppen) als Bioindikatoren anstatt der Nutzung einzelner Indikatorarten angeführt (Cousins 1991, Williams 1996, McGeoch 1998). Davon wird abgeleitet, dass mit diesem Ansatz eine bessere Abstufung bzw. Auflösung der Resultate im Rahmen von Bioindikationsstudien möglich ist (Kremen 1994). Dies betätigen beispielsweise Ergebnisse von Langzeituntersuchungen zu Auswirkungen von Störungen und Umweltveränderungen in aquatischen Ökosystemen, die zeigten, dass besonders Assoziationsparameter wie beispielsweise Diversitätsindizes, Nahrungskettenlängen, Anzahl von r-Strategen und Körpergrößenspektren, aber auch Veränderungen in den Interaktionsmustern zwischen Arten und Artengruppen sehr sensitive und indikativ verwertbare Parameter darstellen (Schindler 1990, Sugden 1992). Inwiefern diese Argumente bzw. Erkenntnisse auch auf terrestrische Arthropodengruppen übertragbar sind, wurde bisher nur unzureichend untersucht.

Im Mittelpunkt der vorliegenden Habilitationsschrift steht, anhand von verschiedenen Fallbeispielen im Zusammenhang mit komplexen Umweltveränderungen auf das Informationspotenzial aufmerksam zu machen, was Arthropoden-Assoziationen als ökologische Indikatoren bieten. In 11 Manuskripten werden die Reaktionen von Arthropoden-Assoziationen auf (i) Störungen durch landwirtschaftliche Nutzung oder Schadstoffimmissionen und auf die damit verbundenen Regenerations- und Sukzessionsprozesse analysiert, sowie (ii) deren Sensitivität gegenüber Klimadynamik und Arten-Invasionen untersucht. Außerdem werden (iii) das Konzept der funktionellen Gruppen und dessen Verwendbarkeit im Zusammenhang mit Bioindikation überprüft sowie (iv) methodische Aspekte bezüglich der Erhebung und insbesondere der Analyse von komplexen Freilanddaten beleuchtet.

Manuskript I widmet sich der Thematik der Stichprobengröße und der damit im Zusammenhang stehenden Genauigkeit von Ergebnissen, die bei Freilandstudien an Arthropoden zu erwarten sind. Einerseits steigt mit zunehmender Stichprobengröße die Zuverlässigkeit einer Analyse. Andererseits sind aus (zeitlichen/ finanziellen) Gründen Beschränkungen auf das „notwendige Maß” erforderlich. Besonders bei Untersuchungen von wirbellosen Tiergruppen, deren Erhebung im Freiland und vor allem deren Aufarbeitung im Labor mit großem zeitlichen Aufwand verbunden ist, spielt diese Optimierungsfunktion eine wesentliche Rolle (Duelli et al. 1999). Bioindikative Ableitungen sind dabei entweder anhand von Veränderungen im Vorkommen einzelner (Indikator-) Arten oder auf der Grundlage von Artengruppen (z.B. durch Verwendung komplexer Biodiversitätsmaße) möglich. Eine erfolgreiche Analyse setzt in jedem Fall voraus, dass Unterschiede zwischen verschiedenen Varianten (*between variability*) über das „Datenrauschen“ innerhalb einer Variante (*within variability*) hinaus indizierbar sind. Auf der Grundlage einer allgemein bekannten, jedoch selten konsequent angewandten Schätzprozedur wird im *Manuskript I* die Relation zwischen Stichprobengröße und der zu erwartenden Genauigkeit einer Analyse am Beispiel von Freilanddaten (Bodenfallendaten) für Arten- und Artengruppen-Parameter dargestellt.

Im *Manuskript II* stehen mit der Abundanzschätzung von epigäisch-aktiven Arthropoden ebenfalls methodische Aspekte im Vordergrund. Die bisher bekannten direkten Verfahren (z.B. Saugsammler, Emmergenzfallen) sind sehr zeitaufwendig und erfordern oft hohe Stichprobenzahlen, um verlässliche Dichteangaben zu ermöglichen (Dent & Walton 1997, Ekschmitt et al. 1997, Southwood & Henderson 2000), was ihre Nutzung vielfach limitiert. Auch die bekannten indirekten Methoden zur Abundanzschätzung von epigäischen Arthropoden (z.B. Fang-Wiederfang in Verbindung mit netz- oder gitterförmig angeordneten Bodenfallen-Arrangements) sind ausgesprochen zeitaufwendig (Parmenter et al. 2003, Parmenter et al. 1989). Darüber hinaus sind die in Verbindung mit der Dichteschätzung notwendigen mathematischen Modelle oftmals empfindlich gegenüber verletzten Grundannahmen (z.B. demografisch geschlossene Populationen, stabile Bewegungsmuster, hohe Fang-Wiederfang-Wahrscheinlichkeit; siehe dazu u.a. Schumacher et al. 2000, Parmenter et al. 2003), weshalb auch diese Methoden in der Praxis nur wenig angewandt werden. Im *Manuskript II* wird mit dem *Nested-Cross-Array* ein neues und einfach zu handhabendes Bodenfallenmuster vorgestellt, was in Verbindung mit der Anpassung einer hyperbolischen Funktion die Schätzung von Abundanzen epigäisch-aktiver Arthropoden ermöglicht. Mittels individuenbasierten Simulationen werden verschiedene Modelparameter variiert (u.a. Populationsdiche, Bewegungsmuster, Fangdauer, Verteilungsmuster) und Angaben zur Güte der Dichteschätzung in Abhängigkeit von der Parameterkonstellation präsentiert.

In Kulturlandschaften gehören Landnutzungsänderungen auf lokaler sowie regionaler Ebene zu den Einflussgrößen mit der größten Bedeutung für die Artendiversität. Eine Möglichkeit zur Reduktion des Verlustes von Artendiversität wird dabei u.a. in einer weniger intensiven Landnutzung gesehen (Duelli 1997, Van der Putten et al. 2000). Im *Manuskript III* werden drei verschiedene Arten-Assoziationen (Pflanzen, Coleoptera, Araneae) als ökologische Indikatoren zur Analyse landwirtschaftlich unterschiedlich intensiv bewirtschafteter Standorte verwendet. Auf der Grundlage von verschiedenen einfachen Assoziations-Parametern (Artenvielfalt, Camargo's Evenness) und multivariaten Analysen wird dabei deutlich, dass beachtliche Unterschiede in der Reaktion auf Nutzungsunterschiede zwischen den untersuchten Pflanzen- und Arthropoden-Assoziationen festzustellen sind. Daraus werden entsprechende Schlussfolgerungen für ein aussagekräftiges Monitoring von Restaurationsprojekten gezogen.

Seit Ende der 80ger Jahre wird der Bedeutung der Biodiversität für verschiedene Ökosystemfunktionen intensiv diskutiert (Überblick u.a. bei Loreau et al. 2002). Die meisten Arbeiten konzentrierten sich dabei auf die ökosystemaren Auswirkungen, die durch Veränderungen der Artendiversität auf der Produzentenebene hervorgerufen werden können. Obwohl entsprechende Effekte veränderter Pflanzendiversität auf die Artenvielfalt und Abundanz höheren trophischer Ebenen schon vor einigen Jahren Eingang in verschiedene Modelle und Hypothesen gefunden haben (Überblick siehe Rosenzweig 1995), liegen bisher vergleichsweise wenige empirischer Studien, und darüber hinaus mit teilweise widersprüchlichen Ergebnissen, zu dieser Thematik vor. Dies ist auf die komplexen und teilweise überlagerten Wirkungsmuster biotischer und abiotischer Faktoren zurückzuführen. *Manuskript IV* präsentiert eine empirische Studie, in der der Versuch unternommen wird, diese komplexen Wirkungen durch Variablen-Dekomposition statistisch aufzutrennen. Auf der Grundlage von Daten aus 71 verschiedenen Grünlandstandorten wird untersucht, ob (i) die Abundanzmuster verschiedener funktioneller Arthopodengruppen durch Unterschiede im Management bzw. Unterschieden in den Standortbedingungen signifikant beeinflusst werden, (ii) die Abundanzmuster der Arthropoden einen belastbaren Zusammenhang zur Diversität, Produktivität bzw. der Artenzusammensetzung der Vegetation aufweisen, auch wenn die potenziellen Wirkungen der unter Punkt (i) genannten Variablen statistisch kontrolliert werden und (iii) Unterschiede in den Abundanzmustern der verschiedenen funktionellen Gruppen in Abhängigkeit von ihrer trophischen Zuordnung festzustellen sind. Die Ergebnisse der Studie werden auch im Zusammenhang mit zwei von (Root 1973) vorgeschlagenen und vielfach zitierten Hypothesen diskutiert. Diese besagen, dass die Populationsdichten von Herbivoren in artenreicheren Pflanzengesellschaften niedriger sein sollten als in artenärmeren, entweder aufgrund von niedrigeren Konzentrationen der relevanten Wirtspflanzen (*resource concentration hypothesis*) oder aufgrund höherer Prädatoren-, oder Parasitoiden-Dichten (*natural enemies hypothesis*) in artenreicheren Pflanzengesellschaften.

Auch im *Manuskript V* steht die Frage im Mittelpunkt, ob sich Veränderungen in der Diversität auf der Produzentenebene kaskadenartig auf die Diversitätsmuster der Artengruppen höherer trophischer Ebenen übertragen, womit ebenfalls die beiden o.g. Hypothesen von Root (1973) berührt werden. Dies wird anhand eines umfangreichen Datensatzes aus einem ehemaligen Immissionsgebiet eines Düngemittelwerkes analysiert. Direkt nach Schließung des Werkes war mit dem Rückgang der Schadstoffwirkungen eine rapide Zunahme der Artendiversität (Artenvielfalt und Evenness) auf Produzentenebene verbunden. Daraufhin wurden im Zeitraum von 10 Jahren verschiedene, vorrangig hypergäisch lebende funktionelle Gruppen von Arthropoden erfasst, um deren Reaktionen auf die sich schnell ändernden Vegetationsmuster zu analysieren. Ähnlich wie im *Manuskript IV* wird in dieser Arbeit außerdem der Frage nachgegangen, ob Unterschiede in den Reaktionsmustern in Abhängigkeit von den verschiedenen trophischen Ebenen zu verzeichnen sind.

Die Beziehungen zwischen der mittlerer Körpergröße und der Struktur von Tierassoziationen waren schon vielfach Gegenstand ökologischer Studien. Hintergrund dieses Untersuchungsansatzes ist, dass die Körpergröße von Tieren mit einer Vielzahl von *life history-* Aspekten korreliert, wie z.B. der metabolischen Effizienz, der Generationszeit, der Reproduktionsrate oder dem Dispersal von Tieren (Peters 1983, Brown 1995). Daher wird die Verwendung von Körpergrößenklassen als Surrogat für funktionell unterschiedliche ökophysiologische Typen innerhalb von Artengruppen der gleichen trophischen Ebene als plausibler Kompromiss angesehen (Bengtsson 1998, Bradford et al. 2002). Im *Manuskript VI* wird am Beispiel von Carabidendaten des o.g. Immisionsgebietes (siehe *Manuskript V*) dieser Ansatz verwendet, um zu prüfen, ob ein Zusammenhang zwischen der mittleren Körpergröße von Carabiden-Assoziationen und den in diesem Fall sehr dynamischen Umweltbedingungen feststellbar ist. Dieser Zusammenhang wird im Rahmen von zwei unterschiedlichen Hypothesen postuliert: (i) der *efficiency-specialization hypothesis* (Siemann et al. 1999), die besagt, dass während der Sukzession (Regeneration) von Ökosystemen die mittlere Körpergröße von Konsumenten-Assoziationen abnimmt und (ii) der Hypothese von Blake et al. (1994), nach der mit abnehmender Störungsintensität in Ökosystemen die mittlere Körpergröße der Konsumenten zunimmt. Beide Thesen werden anhand der Ergebnisse aus dem untersuchten Immissionsgebiet diskutiert und daraus Schlussfolgerungen für die Verwendbarkeit von Größenklassen bei der Klassifizierung von funktionellen Gruppen im Rahmen der ökologischen Indikation gezogen.

Klima beeinflusst nicht nur die geografische Verbreitung und *life history* von Organismen und damit deren Populationsdynamik sowie die Zusammensetzungen von Artengemeinschaften (Harrington & Stork 1995, Lawton 2000). Klima wirkt sich indirekt auch auf Ökosystemfunktionen und die davon abzuleitenden „Serviceleistungen“ von Ökosystemen (*ecosystem services*) aus, von denen der Mensch profitiert (Tilman et al. 2001). Folglich ist die Abschätzung der Reaktionen von Arten und Artengemeinschaften auf Klimaveränderungen und deren Auswirkungen auf die Ökosystemleistungen eines der zentralen Forschungsthemen auf dem Gebiet der *global change*- Ökologie. Während auf der Ebene einzelner Arten eine Reihe von Studien aus Labor- und Mesokosmos-Experimenten vorliegen (u.a. Harrington & Stork 1995, Lawton 1995, Davis et al. 1998), gibt es vergleichsweise wenige empirische Studien, in denen der Versuch unternommen wird, die Populationsdynamik in Abhängigkeit von Witterungsparametern (zumindest teilweise) nachzuzeichnen. Anhand von Langzeitdaten aus Trockenrasen wird im *Manuskript VII* die Populationsdynamik von drei dominanten Heuschreckenarten unter Verwendung ausgewählter Witterungsparameter modelliert. Trotz des relativ einfachen Verfahrens der multiplen linearen Regression, was in dieser Studie angewandt wurde, können die spezifischen Unterschiede in den Populationsdichten der Arten in Abhängigkeit von Witterungsunterschieden der verschiedenen Untersuchungsjahre hinreichend genau modelliert werden, woraus Schlussfolgerungen für die Verwendung derartiger Techniken im Rahmen von Bioindikations- und Biomonitoring- Projekten abgeleitet werden.

Es ist unumstritten, dass Arten sehr spezifisch auf Klimaänderungen reagieren können (Lawton 2000, Thomas et al. 2001, Bale et al. 2002). Folglich besteht Grund zu der Annahme, dass unterschiedliche Reaktionen der Arten auf diese Änderungen zwangsläufig zu Störungen in den Arten-Interaktionen führen und damit die Funktionalität von Artengemeinschaften (*communities*) maßgeblich beeinflussen können (Harrington et al. 1999, Visser & Holleman 2001). Dabei sind besonders starke Störungen in den Arteninteraktionen dann zu erwarten, wenn sich die Sensitivität von Arten gegenüber Klimaänderungen systematisch zwischen den trophischen Ebenen unterscheiden sollten. Experimente an einzelnen, verschiedenen trophischen Ebenen zuzuordnenden Arten lassen vermuten, dass solche Unterschiede existieren könnten (Jones et al. 1998, Petchey et al. 1999). In diesem Fall würden größere Klimaänderungen zu fundamentalen Veränderungen in ganzen Artengemeinschaften bzw. Ökosystemen führen. Diese Form der „systematischen" Unterschiede in der klimatischen Sensitivität zwischen Arten verschiedener trophischer Ebenen konnte bisher jedoch anhand von Freilanddaten nicht belegt werden. Im *Manuskript VIII* werden umfangreiche Langzeitdatensätze von unterschiedlichen funktionellen Gruppen aus drei trophischen Ebenen (Produzenten, Herbivore, Karnivore) und aus zwei unterschiedlichen Grassland-Ökosystemen diesbezüglich analysiert.

Komplexität ist eine inhärente Eigenschaft von Artengemeinschaften, die im einfachsten Fall indirekt über Artenzahlen, oder, etwas detaillierter, direkt über die Anzahl von existierenden Arten-Interaktionen bzw. die mittlere Interaktionsstärke zwischen Arten einer Artengemeinschaft beschrieben werden kann (Forbes 1998). Ein sehr hilfreiches Konzept zur Beschreibung der Komplexität von Artengemeinschaften auf der Grundlage von trophischen Interaktionen sind dabei Nahrungsnetze (*food webs*; Pimm et al. 1991, Berlow et al. 2004). Jedoch gibt es neben den trophischen Beziehungen zwischen Arten eine Vielzahl anderer Interaktionstypen, die sich direkt oder indirekt auf die Komplexität von Artengemeinschaften auswirken können. Daher favorisiert Price (2002) die Verwendung des Begriffs „Interaktionsnetze" (*interaction webs*) für eine umfassendere Beschreibung der Komplexität von Artengemeinschaften. Interaktionsnetze sind jedoch mit den klassischen Methoden der Nahrungsnetzanalysen nur schwer zu charakterisieren, weshalb derartige Analysen bisher weitgehend fehlen. Im *Manuskript IX* wird eine Methode vorgestellt, mit der die Analyse von Interaktionsnetzen möglich ist. Auf der Grundlage von Freilanddaten für Pflanzen und Arthropoden aus einem naturnahen und einem gestörten Grasland-Ökosystem wird die vertikale Komplexität (kalkuliert als *vertical connectance*) zwischen funktionellen Gruppen verschiedener trophischer Ebenen (Produzenten, Herbivore, Karnivore) analysiert. In diesem Zusammenhang wird eine von Nahrungsnetzanalysen abgeleitet Hypothese überprüft, die besagt, dass sich gestörte Ökosysteme im Vergleich zu ungestörten Ökosysteme durch eine geringere Komplexität auszeichnen (O'Neill et al. 1986 Townsend et al. 1998).

Manuskript X baut direkt auf der Methodik und den Ergebnissen von *Manuskript IX* auf. In dieser Studie wird unter Verwendung desselben Datenmaterials (wie in *Manuskript IX*) geprüft, wie zuverlässig bzw. stabil Interaktionsnetze in Abhängigkeit von ihrer Struktur sind (*reliability-* Konzept). Mit dem Begriff *reliability* wird die Wahrscheinlichkeit beschrieben, mit der bei Ausfall eines oder mehrerer Netz-Elemente (*nodes*, in diesem Fall funktionelle Gruppen) die Funktionalität (z.B. Verbindung der Karnivoren mit den Produzenten) erhalten bleibt (Aggarwal 1993, Jordan & Molnar 1999). Es wird in dieser Arbeit untersucht, ob sich die *reliabilities* von Interaktionsnetzen auf der Basis von funktionellen Gruppen wesentlich von denen auf der Grundlage von Nahrungsnetzen (*food webs*) unterscheiden. Außerdem wird analysiert, in welchem Verhältnis die *reliability* zu anderen Netzparametern steht und ob sich diese Relationen wesentlich von denen aus Nahrungsnetzen abgeleiteten Zusammenhängen unterscheiden.

Die Komplexität von Artengemeinschaften bzw. Ökosystemen ist eng verknüpft mit der Invasibilität. Dieser grundlegende Zusammenhang wurde bereits von (Elton 1958) beschrieben und später durch die *resource-competition* - Theorie untermauert (MacArthur & Wilson 1967, Pimm 1991). Danach sollten artenreichere Gemeinschaften (*communities*) wesentlich resistenter gegenüber Invasoren sein, als (vergleichbare) artenarme Gemeinschaften (*diversity-resistance hypothesis*). Während theoretische und experimentelle Studien mit kleinräumigem Bezug diesen Zusammenhang weitgehend bestätigten konnten, ergaben andere experimentelle und empirische Studien, meist bezogen auf größere räumliche Skalen, hingegen widersprüchliche Ergebnisse. Dieser Widerspruch wird auf die Wirkung extrinsischer Faktoren (z.B. Klima, Boden, Störungen) zurückgeführt, die mit der Diversität von autochthonen und invasiven Arten (positiv oder negativ) korrelieren und somit die durch die *diversity-resistance hypothesis* vorausgesagten Effekte überlagern können (Naeem et al. 2000, Shea & Chesson 2002). Darauf aufbauend wird im *Manuskript XI* ein einfaches konzeptionelles Modell vorgeschlagen, welches postuliert, dass unabhängig von der Wirkung extrinsischer Faktoren, der Anteil invasiver Arten am Gesamtartenpool negativ zum Vorkommen autochthoner Arten korreliert sein sollte, falls o.g. *diversity-resistance hypothesis* wirklich zutrifft. Diese Hypothese wird am Beispiel von epigäisch aktiven Arthropoden unterschiedlicher funktioneller Gruppen aus Lorbeerwäldern verschiedener Kanarischer Inseln überprüft.

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2. Manuskript I

Perner, J. (2003)
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Sample size and quality of indication—a case study using ground-dwelling arthropods as indicators in agricultural ecosystems

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Abstract

A frequently cited but rarely used procedure for estimating sample size was tested on the level of both species and community parameters. The analysed field data resulted from a pitfall trap study dealing with the effects of changing agricultural land use on ground-dwelling arthropods. The relation between level of precision (LOP) and required sample size (RSS) showed significant differences between species and community parameters. For most species parameters a high precision level (5–10%) would require an unaffordable large sample size. For species that are habitat generalists realistic sample sizes around 10 allow an LOP between 25 and 50%, whereas the same sample sizes leads to a much lower LOP between 50 and 90% for selected habitat specialists. In general, the LOP–RSS relation was more favourable for the two tested community parameters (richness and evenness) than for the mean number of individuals of a species. For purposes of bioindication or comparisons of communities, the results presented herein favour the use of community parameters above species parameters. Finally, as a rule of thumb the RSSs for precision levels of 5, 10, 25 and 50% were given for both, level of species and for community parameters.

Keywords: Sample size; Level of precision; Coefficient of variation; Bioindication; Arthropods

1. Introduction

In agricultural ecology, invertebrate groups have been increasingly used as indicators for changes in agricultural land use (Duelli et al., 1999). Indicative deductions are possible on the basis of indices for (indicator-) species or for complex community parameters (e.g., measures of diversity). In all cases, successful indication requires that, e.g., differences at species- or community-level between various management practices (between group variability) are recognizable beyond the data noise within single management types (within group variability). Therefore, the precision of the sampled data has to be estimated, which is directly related to the variance of the data and thus, is a mathematical function of sample size (Tokeshi, 1993).

It is well known, that increasing sample size improves the validity and reliability of the data in question. However, personnel, temporal and financial limits apply for every study. To find a balance between these needs is particularly important for investigations of invertebrate groups that involve time-consuming field sampling, high skills and much time for species identification as well as a large amount of data processing.

A frequently cited (e.g., Manly, 1992; Motulsky, 1995; Krebs, 1999) but rarely used procedure for estimating sample size was tested on the level of both

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species and community parameters in order to investigate the relationship between sample size and precision. In addition, attempts to offer suggestions for a cost-benefit balance between financial constraints and precision needs.

2. Material and methods

2.1. Statistical procedure and terminology

The precision of an arithmetical mean of a sample is usually described by the confidence interval:

$$\left(\bar{x} - t_{n-1,\alpha}\frac{s}{\sqrt{n}}, \bar{x} + t_{n-1,\alpha}\frac{s}{\sqrt{n}}\right) \qquad (1)$$

where $\bar{x}$ is the arithmetical mean of the sample, s the standard deviation of the sample, $t_{n-1,\alpha}$ the student's t value for $n-1$ degrees of freedom for $1-\alpha$ level of confidence, n the sample size (for this study: the number of pitfall traps).

The half-width of this confidence interval, $d = t_{n-1,\alpha}s/\sqrt{n}$, gives an absolute measure of precision. More conveniently, the precision is expressed as a percentage proportion of the parameter in question (here: $\bar{x}$)

$$r = t_{n-1,\alpha}\frac{s}{\bar{x}\sqrt{n}}100\% \qquad (2)$$

and gives a relative measure of precision. This measure is directly linked to a common measure of relative variability, the coefficient of variation $\mathrm{CV} = s/\bar{x}$. Assuming a 95% confidence level and exploiting the fact that $t_{n-1,\alpha=5\%} \approx 2$ the formula for relative precision can be rearranged, giving

$$n \approx \left(\frac{200\mathrm{CV}}{r}\right)^2 \qquad (3)$$

as an approximate formula for the sample size required for a specified level r of relative precision. Note that *low* %-values correspond to *high* levels of relative precision. A detailed derivation of the formula for estimating necessary sample sizes is given by Manly (1992) and Krebs (1999). The required sample size (RSS) is the one needed to achieve a certain level of precision (LOP).

2.2. Study sites and analysed data

The study was carried out between 1996 and 1998 in the central Unstrut floodplain (Thuringia, Germany;

Table 1
Numbers of individuals for selected species of beetles sampled in seven different sites from 1996 to 1998 (group 1: habitat generalists of agricultural ecosystems, group 2: habitat specialists with a high preference for arable land and particularly young sown grassland sites, group 3: habitat specialists with high preference for re-wetted grassland sites)

	Site type (site abbreviations)							Total
	Arable land (A3)	Young sown grassland (A2)	Sown grassland (A1)	Permanent grassland (3-cut) (C)	Permanent grassland (1-cut) (B2)	Embankment grassland (AD)	Re-wetted grassland (fallow) (B1)	
Group 1								
P. melanarius	8802	9018	1328	4296	107	1753	1429	22437
B. obtusum	981	407	131	1860	51	101	359	2030
Group 2								
Calathus erratus	132	38	0	0	0	0	0	170
Hypera postica	26	33	1	0	0	3	0	63
Lesteva longoelytrata	54	3	0	1	0	0	0	57
Ocypus ophthalmicus	163	5	1	0	0	0	0	169
Group 3								
Bembidion lunulatum	0	0	0	0	0	3	17	20
Chlaenius nigricornis	0	0	0	0	0	7	149	156
O. helopioides	0	0	0	0	0	1	25	26
Stenus pusillus	0	0	0	0	0	1	14	15

51°08′N, 10°40′E). Seven sites of different management regimes (arable land, young sown grassland used by mowing and grazing, sown grassland with extensive cattle grazing, permanent grassland mowing 3-cuts per year, permanent grassland mowed with 1-cut per year, embankment grassland, re-wetted fallow land) were sampled by pitfall trapping. Two lines 20 m apart from each other, each consisting of five traps (4 m apart) were sampled the year around at every site. In total, these 70 traps yielded 502 species of beetles with 77,684 individuals and 120 species of spiders with 56,067 adult individuals (Malt and Perner, 2002; Perner and Malt, 2002).

Eq. (3) was used to estimate the LOP–RSS relation on species level based on numbers of individuals for selected species of beetles. Using a TWINSPAN-analysis (two-way-indicator-species-analysis; compare Hill, 1979; McCune and Mefford, 1997), three ecological groups of species were selected (Table 1). The first group includes habitat generalists, which are widespread in agricultural ecosystems and occurred in all investigated sampling sites. The second and third group was represented by habitat specialists. Species of group 2 had a high preference for arable land and partly also for young sown grassland sites (*Hypera postica*), whereas the species of group 3 were limited to re-wetted grassland and embankment grassland sites. Species of group 1 can be regarded as quantitative indicators with a fuzzy preference for certain environmental conditions (e.g., habitats). However, an

Table 2
Mean CV ±S.E. for beetles, carabids only and spiders calculated for species richness, Smith–Wilson evenness and mean numbers of individuals (see also Table 1)[a]

Taxon/parameter	Mean CV ±S.E.		
	Between sites	Between years	Total
Beetles/richness	0.143 ± 0.035	0.146 ± 0.009	0.146 ± 0.039
Beetles/Smith–Wilson evenness	0.114 ± 0.029	0.115 ± 0.022	0.115 ± 0.038
Carbids/richness	0.196 ± 0.076	0.192 ± 0.028	0.193 ± 0.083
Carabids/Smith–Wilson evenness	0.178 ± 0.071	0.183 ± 0.033	0.182 ± 0.092
Spiders/richness	0.128 ± 0.024	0.133 ± 0.026	0.132 ± 0.032
Spiders/Smith–Wilson evenness	0.105 ± 0.028	0.107 ± 0.021	0.106 ± 0.035
Beetles species/number of individuals			
Group 1			
P. melanarius	0.433 ± 0.150	0.398 ± 0.076	0.411 ± 0.172
B. obtusum	0.832 ± 0.467	0.731 ± 0.130	0.768 ± 0.478
Group 2			
Calathus erratus		1.473 ± 0.713	1.473 ± 0.713
Hypera postica[b]	0.848 ± 0.770	0.848 ± 0.199	0.848 ± 0.718
Lesteva longoelytrata		1.833 ± 1.155	1.833 ± 1.155
Ocypus ophthalmicus		1.211 ± 0.780	1.211 ± 0.780
Group 3			
Bembidion lunulatum		1.256 ± 0.307	1.256 ± 0.307
Chlaenius nigricornis		1.118 ± 0.101	1.118 ± 0.101
O. helopioides		0.943 ± 0.898	0.943 ± 0.898
Stenus pusillus		1.329 ± 0.066	1.329 ± 0.066
Mean			1.119

[a] For both community parameters and the species of group 1 the calculation of the mean CVs were performed regarding variation of the CVs between the seven sampling sites, between the 3 years and between all sites and years (total). For the species of groups 2 and 3 only the CVs of the preferred sites (A3, respectively, B1; see Table 1) were analysed. Therefore only the variation of the CVs between the 3 years within the preferred sites was calculated. Please note, that for this reason the values of those groups in columns "years" and "total" are identical.

[b] Because of a comparable number of individuals sampled in A3 and A2 (see Table 1) also a mean CV (between A3 and A2) were calculated for *H. postica*.

indication is possible if based on density changes for these species. The species of groups 2 and 3 belong to the category of qualitative indicators (indicator species in the narrower sense) and show a strong linkage to certain environmental conditions (see Müller-Motzfeld, 1989; McGeoch, 1998 for reviews).

Beside the numbers of individuals for the three selected species groups, two community parameters were analysed: the species richness and the Smith–Wilson evenness index (E_{var}). The latter index is independent of species richness and is sensitive to both rare and common species in the community (Krebs, 1999). The analysis was carried out separately for (i) all ground-dwelling beetles, (ii) for the carabids only, and (iii) the ground-dwelling spiders. The comparison of (i) and (ii) allows to validate the almost exclusive use of carabids in bioindication studies (e.g., Müller-Motzfeld, 1989) whereas (i) and (iii) compares the two most abundant taxa of ground-dwelling arthropods.

The coefficient of variation (CV) was calculated for the community parameters and the numbers of individuals recorded for the 10 traps per site and year separately. For both community parameters and the species of group 1 the calculation of the mean CVs were performed regarding variation of the CVs between the seven sampling sites (pooling CVs of different years per site), between the 3 years (pooling CVs of different sites per year) and between all sites and years (Table 2). For the species of groups 2 and 3 only the CVs of the preferred sites (A3, respectively, B1; see Table 1) were analysed. Therefore only the variation of the CVs between the 3 years within the preferred sites was calculated. Please note, that for this reason the values of those species groups in columns "years" and "total" are identical (Table 2).

In a second step, the mean CVs listed in column "total" of Table 2 were included in Eq. (3) to estimate the LOP–RSS relations for the selected species and the both community parameters.

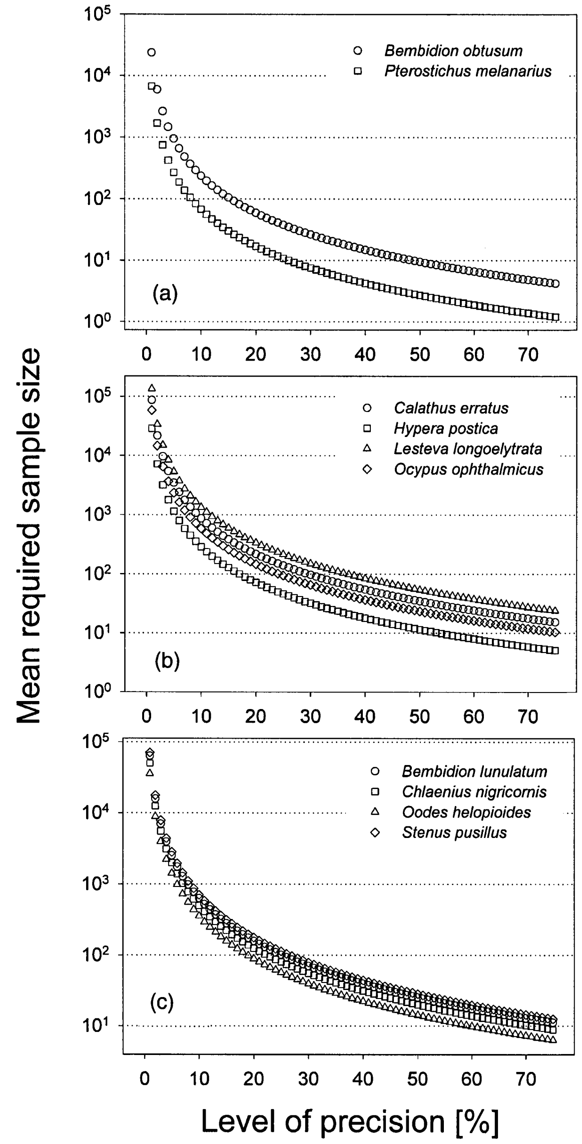

Fig. 1. Relation between LOP and RSS for ecological groups of beetles (a—group 1, habitat generalists; b—group 2, habitat specialists with a high preference for arable land; c—group 3, habitat specialists with high preference for re-wetted grassland).

3. Results

3.1. Species comparisons

With lower LOP, the RSS needed declines exponentially for all three ecological groups (Fig. 1; Table 1). There were considerable differences between the LOP–RSS relations for habitat generalists (Fig. 1a) and specialists (Fig. 1b and c). Whereas sample sizes of about 10 gave an LOP between 25 (*Pterostichus melanarius*) and 50% (*Bembidion obtusum*) for habitat generalists, the same sample size would yield only

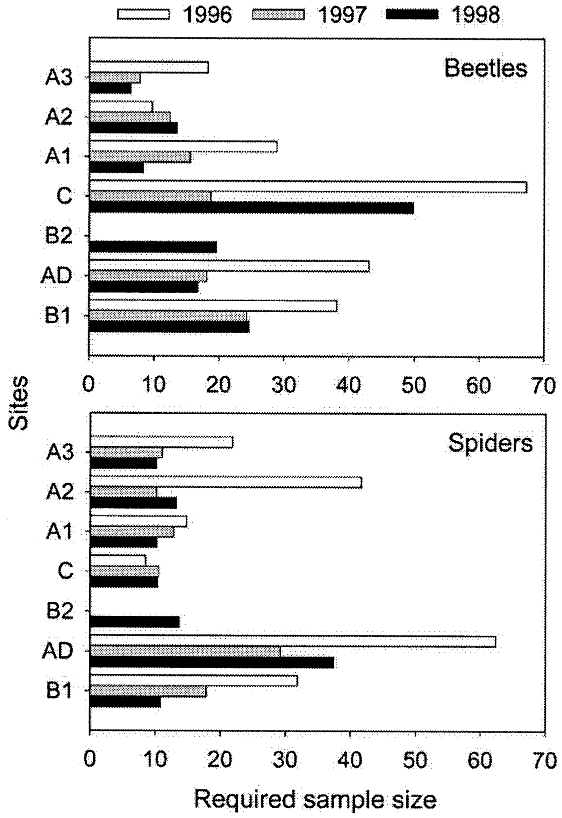

Fig. 2. Calculations for RSSs for a precision level (LOP) of 5% for beetles and spiders based on the CV caused by the Smith–Wilson evenness. Shown are the values for each of the 3 years of investigation and for each sample site.

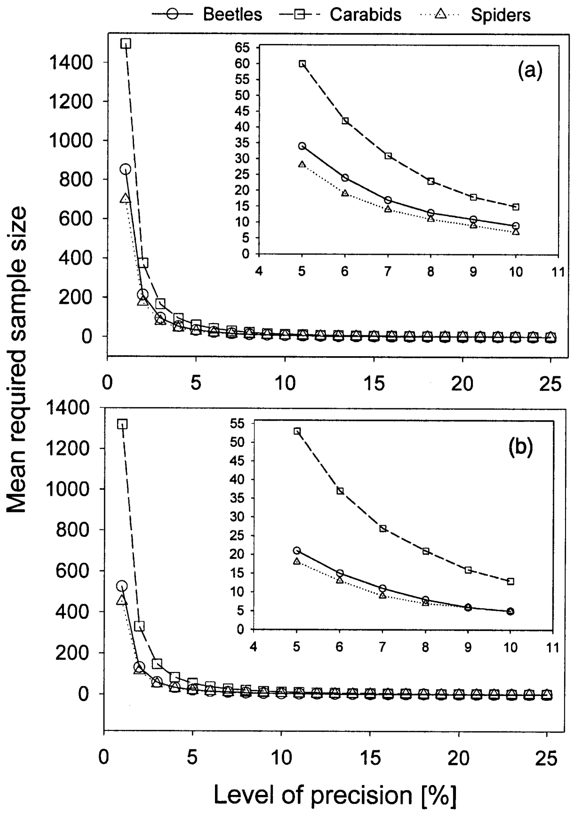

Fig. 3. Relation between LOP and mean RSS for beetles, carabids only and spiders on the basis of species richness (a) and Smith–Wilson evenness (b). Inset: enlarged plots for a range of the LOP between 5 and 10%.

an LOP between 60 and 100% for habitat specialists. On average, CV-values are very high (Table 2; mean: 1.119).

3.2. *Community parameters*

CV values for the two tested community parameters (richness and evenness) were distinctly smaller than those for mean numbers of individuals (Table 2). For an LOP of 5%, the RSS for both richness and evenness varies considerably within sampling sites, sampling years and taxonomic groups (Fig. 2). Despite this spatial and temporal variability, values for RSS were most often between 15 and 25 for an LOP of 5%. For all three taxonomic groups, RSS increases exponentially with LOP for both richness and evenness (Fig. 3). Whereas the plots for beetles and spider are nearly identical, carabids alone need a considerably higher RSS to reach the same LOP. In general, higher sample sizes were required for assessments on the basis of species richness than on the basis of evenness values.

4. Discussion

A procedure was tested to describe the LOP–RSS relation for abundances of selected (indicator) species and for two community parameters. The calculation used (Eq. (3)) allows to estimate the RSS necessary to obtain a specified LOP for one (!) mean of a parameter (here: numbers of individuals sampled, richness or evenness) or to assess the quality of sampled data for a given sample size. The data analysed in this study are the result of a 3-year study of sites subjected to different management regimes.

Strictly speaking, for such cases a more complicated calculation procedure should be applied to compare two or more means of a parameter (Motulsky, 1995). Beside the estimated standard deviation (s) and the minimum difference (d) between means of the parameter in question, the power index $(z_\alpha + z_\beta)^2$ has to be considered for this formula, with α as the probability of a type I error and β as the probability of a type II error (compare Krebs, 1999). However, from two reasons this procedure is hard to apply for field data. First, the procedure aims on the RSS necessary to detect a priori significant differences (with a given probability) between two means of a parameter (and to test its significance, e.g., by a Student's test). In studies like the one presented here it is not the priority to calculate the sample size that is needed to find significant differences at any cost, but to perform a cost (RSS)–benefit (LOP) analysis. To plan field studies like the one shown in this paper it is most important to have a rough idea about the quality of results (means of parameters) for a given sample size or to estimate the RSS needed for a given LOP. Second, the procedure explained above assumes that the two data sets have nearly equal standard deviations for the parameter in question, a condition hardly fulfilled for most field studies. As shown in Fig. 2, in most cases the temporal variability of the CVs within sites was higher than the spatial variability between sites. Hence it was regarded as sufficient to use Eq. (3) knowing that this procedure is not a precise calculation but a rough estimation of the LOP–RSS relation.

The results show significant differences in the LOP–RSS relations for species and community parameters. For mean numbers of individuals, affordable sample sizes between 10 and 30 cause low values of LOP, whereas for community parameters the same sample sizes would give clearly higher LOP values. For instance, if at a sample size of 10 five individuals of *Oodes helopioides* were caught at site B1, a mean LOP of 60% has to be accepted (see Fig. 1). This translates to a mean value of 5 ± 3 individuals. In contrast, the mean evenness for site B1 is 0.46, and the same sample size produces an LOP of about 7%, resulting in a much more precise evenness value of 0.46 ± 0.03.

Furthermore, the procedure presented herein can be helpful for the selection of trustworthy indicator species. Beside a high degree of habitat preference (or preference to specific conditions) a good indicator species should have a low CV for the mean number of individuals per site to allow an LOP as high as possible. The demonstrated procedure could function as a tool to select the best candidates from a pool of potential indicator species and would therefore complement the well-established TWINSPAN-analysis (Hill, 1979) or the newer and more efficient Indicator Value method after Dufrene and Legendre (1997). Occasionally, generalists of agricultural habitats (quantitative indicators; see above) were used as management intensity indicators (Büchs et al., 1999). In this study, the two generalists *P. melanarius* and *Bembidion obtusum* have indeed lower CV values than the habitat specialists and therefore a more favourable LOP–RSS relation (Fig. 1). This underlines the importance of generalists as indicator species (e.g., in the context of changes in land use) due to their better pattern of variance.

For the two analysed community parameters, three points seem to be worth of mention. First, species richness possesses a more unfavourable LOP–RSS relation than the Smith–Wilson evenness (Fig. 3). This means, e.g., that at a given sample size of 10, the LOP for mean evenness of beetles and spiders was as low as 7%, whereas the LOP for the species richness of the same groups was about 9%. This demonstrates the usefulness of this parameter for purposes of indication. As a detailed analysis of the data set demonstrated (Perner and Malt, 2003), the differences of evenness between the sites were precise enough to allow the discrimination of four sufficiently homogeneous subsets of sites. Currently the relation between productivity and evenness of a community (as one component of diversity) is under intensive (and controversial) discussion (e.g., Drobner et al., 1998; Wilsey and Potvin, 2000). In this context, a trustworthy estimation of the evenness parameter seems to be of particular importance.

Second, Fig. 3 shows approximately the same LOP–RSS relations for beetles and spiders, which makes both groups equally suitable as indicators when regarding their patterns of variance. Third, the more unfavourable LOP–RSS relation for carabids alone in comparison to beetles as a whole or spiders was unexpected (for the same LOP higher sample sizes needed!). In the light of these results, a sample size of about 15 would be necessary to obtain a mean species richness or evenness estimation with a precision of 10% if solely carabids would be used for indication. Consequently, sample sizes of about 5, as often used in practice for carabids, should be carefully evaluated.

5. Conclusions

The procedure tested herein allows a rough estimation of the LOP–RSS relation and is therefore a suitable tool to assess the quality of sampled data for a given sample size or to estimate the RSS for a given confidence level (LOP), e.g., in the context of preliminary investigations. The equation used is applicable for abundances of indicator species only as well as for community parameters. It could be demonstrated, that LOP–RSS relations are significantly better at the community level (richness, evenness) than at the species level (mean number of individuals). As a rule of thumb, RSS for LOP values of 5, 10, 25 and 50% are given for both species and community parameters in Table 3.

From the view of variance, the results recommend the utilization of community parameters to assess changes in agricultural land use. Furthermore, the procedure can be used as a tool for the selection of trustworthy indicator species from a pool of potentially usable species.

Table 3
Rules of thumb for RSSs corresponding with precision levels (LOP) of 5, 10, 25 and 50% for species and community parameters[a]

LOP (%)	RSSs			
	5	10	25	50
Species level (habitat generalists)	250–1000	50–250	10–50	3–10
Species level (habitat specialists)	1000–5000	250–1000	50–250	10–50
Community parameters	15–60	5–15	1–2	–

[a] Shown are the values for mean numbers of individuals for habitat generalists (as examples for quantitative indicators) and habitat specialists (examples for qualitative indicators) and for the two community parameters species richness and Smith–Wilson evenness.

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3. Manuskript II

Perner, J. & Schueler, S. (2004)
Estimating the density of ground-dwelling arthropods
with pitfall traps using a Nested-Cross array.
Journal of Animal Ecology, 73, 469-477

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73, 469–477

Estimating the density of ground-dwelling arthropods with pitfall traps using a nested-cross array

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Summary

1. A new procedure for estimating the population densities of ground-dwelling arthropods with pitfall trapping is described. It couples the fitting of single hyperbolic functions to trap data with the use of a 'nested-cross array', a cross-shaped trap arrangement with distances between traps doubling with increasing distance from the central trap.
2. We used individual-based simulation modelling to test the method's reliability given changes in population density, turning rate, trapping period, beetle distribution and intertrap distance.
3. Simulations show that function fits are more likely, and density estimates more accurate, with greater body size and therefore with net displacement, increasing population density, decreasing aggregation and increased turning rate.
4. Simulation indicates that the method is a promising procedure for density estimation that is worth testing in the field. Reliable density estimates are possible if the traps contain a neutral preservative, arrays are established in nearly homogeneous parts of habitat and the arms of the nested-cross array are distant from habitat edges.

Key-words: density estimation, hyperbolic function fit, pitfall trapping, simulation modelling, trap pattern.

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Introduction

Pitfall trapping is a standard method for collecting ground-dwelling arthropods (Dent & Walton 1997; Ekschmitt, Wolters & Weber 1997) but the numbers trapped depend not only on the population density of a species but also on its locomotory activity, as well as on other factors (Luff 1975; Adis 1979; Topping & Sunderland 1992; Spence & Niemelä 1994). Therefore, numbers caught do not allow direct estimation of population density but only of activity-density (Thiele 1977). If standardized sampling procedures are used, pitfall trapping yields results that can be compared between species (relative differences) sufficient for most studies of differences in population size or community structure in time or space (e.g. Duelli, Obrist & Schmatz 1999). However, for some approaches (e.g. pest control or population viability analyses in nature conservation) estimation of true density is indispensable and requires removal sampling, suction sampling, emergence traps or litter and soil extraction techniques (e.g. Dent & Walton 1997; Ekschmitt, Wolters & Weber 1997; Southwood & Henderson 2000). The major drawbacks of these methods are their difficulty and expense, which often result in their allowing only small sample sizes. Indirect estimation of the density of ground-dwelling arthropods using pitfall traps is possible using several sampling designs and mathematical models (Sunderland *et al.* 1995; Powell, Walton & Jervis 1996; Southwood & Henderson 2000). The most popular and widely used of these require mark–recapture or removal-sampling data and traps on grids (Crist & Wiens 1995; Raworth & Choi 2001; Parmenter *et al.* 2003) or trapping webs in combination with distance measure analysis (Parmenter, MacMahon & Anderson 1989; Parmenter *et al.* 2003). They are thus very time-consuming and often sensitive to violations of their basic assumptions (e.g. demographic closure, stability of animal movement, probability of capture or recapture and home-range behaviour; see Seber 1986; Schumacher, Klingelhöfer & Poethke 2000; Parmenter *et al.* 2003). Other methods of density estimation from pitfall trap data, as yet scarce in the literature, require movement parameters to be known (Fechtner 1977; Kuschka, Lehmann & Meyer 1987; Stoyan & Kuschka 2001). These parameters must be estimated beforehand for all species under study but

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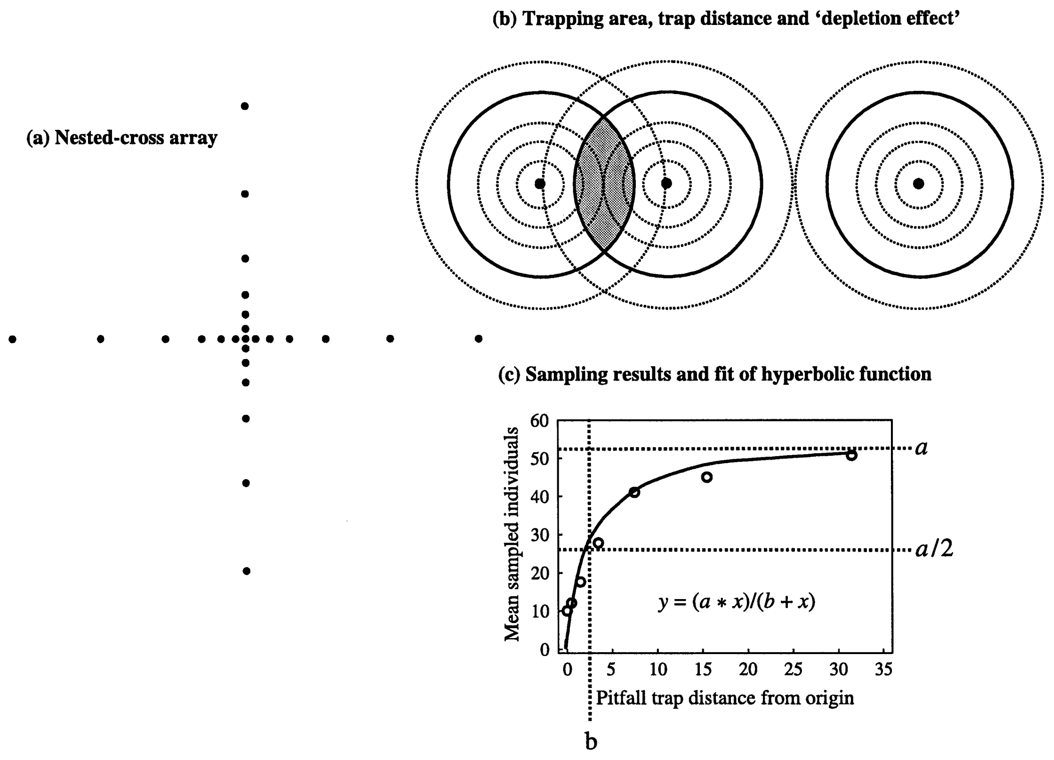

Fig. 1. Diagram to illustrate the coupling of nested-cross sampling outcome with the hyperbolic function parameters. (a) Nested-cross array with intertrap distances doubling from the centre to the periphery (drawn not true to scale). (b) Schematic presentation of specific trapping area (solid line) and the overlap between areas sampled by neighbouring traps (shaded region). Circles around the traps (dotted lines) indicate the different effective trapping areas that may exist for different species. (c) Plot of sample simulation results with the nested-cross array (empty circles; initial trap distance of 0·5 m used). All values mean numbers of individuals of the four traps equidistant from the centre except for values from the single central trap. The solid line illustrates the fitted hyperbolic function and the meaning of both function parameters *a* and *b*.

their accuracy is influenced strongly by the recapture rates of the individuals investigated and the procedures are very time-consuming (Samietz & Berger 1997).

To remedy these problems we developed a new sampling design to estimate population densities that is easy to use, and evaluated its reliability using simulations. We call this design the nested-cross array, as it is characterized by pitfall traps arranged in an equal armed cross in which the distances between traps double from the centre to the periphery (Fig. 1a). The efficiency of this design is based on the known increase in trapping efficiency with increasing intertrap distances ('depletion effect', e.g. Luff 1975; Adis 1979; Digweed *et al.* 1995; Kuschka 1998). We were also inspired by the nested plot sampling schemes introduced by plant ecologists to determine optimal plot size or detect vegetation pattern (e.g. Podani 1984; Barkman 1989).

To examine the efficiency of the nested-cross array we developed simulation models similar to those of Crist & Wiens (1995), who coupled mark–recapture field studies of darkling beetles with simulation modelling to determine how habitat-specific movements of individuals influenced pitfall trap capture rates and hence estimates of population size. We simulated a small and a large arthropod of carabid beetle type moving in a square arena containing the nested-cross array to show the effect on density estimation of the parameters (i) population density, (ii) turning-rate, (iii) trapping period, (iv) beetle distribution and (v) intertrap distance.

Materials and methods

DENSITY ESTIMATION PROCEDURE

Our approach to estimate the density of ground dwelling arthropods is based on the simple formula:

$$D = \frac{N}{A} \qquad \text{eqn 1}$$

where D is the animal density, N the number of captured animals (activity density) and A the area from which animals are trapped (within the effective trap radius). Provided the habitat is nearly homogeneous, the trapping area can be conceived of as a circle around the trap the radius of which differs between species depending on their body size, activity and turning rate (Fig. 1b). The nested-cross array design allows an estimate of effective trap radius because traps interfere with each other, in that each can trap animals that might have been caught in a neighbouring trap (shaded area in Fig. 1b). However, interference falls as intertrap distance increases (see trap areas of the right-hand trap in Fig. 1b). Therefore,

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capture rates should increase with increasing distance between traps, reaching an asymptote when traps are no longer close enough to interfere with each other (Fig. 1c). The number of animals caught (y) as a function of pitfall trap distance from the centre of the nested-cross (x) can be fitted by a single hyperbolic function, known as the saturation function, or Michealis–Menten-model (Fig. 1c):

$$y = \frac{(a \times x)}{(b + x)} \qquad \text{eqn 2}$$

This function provides the parameter a which represents the estimated asymptote of the y-axis and the parameter b which describe the value of the x-axis, where half of a is reached (Fig. 1c). Therefore, with b we have a parameter (the radius) to estimate A and with $a/2$ we have an estimate of N at b. Both should allow a density estimate ($\hat{D}$) of real density (D) with:

$$\hat{D} = \frac{(a/2)}{\pi \times b^2} = \frac{a}{2\pi \times b^2} \qquad \text{eqn 3}$$

SIMULATION MODEL AND NESTED-CROSS ARRAY

Our simulated carabid beetles were animated with correlated random walks (Kareiva & Shigesada 1983) with, as parameters, the mean distance moved per time step, the variances in distance per time step, turning rate (as defined below) and the number of time steps per day.

We generated the distances moved per time step using an erlang distribution, a subset of the gamma distribution, as for other observed and simulated movement data (e.g. McCulloch & Cain 1989; Crist *et al.* 1992). The erlang distribution provides high frequencies of short steps but also includes a proportion of long steps.

The beetles' turning rate was determined at each time step using a three-stage procedure (Kunert, Montag & Pohlmann 2001). First we divided the circle of possible movement into a varying number of equal segments, and secondly selected one of these following a binomial distribution symmetrical around 180° (straight ahead) of events between segments. Then, thirdly, we simulated a random direction within the selected segment. Thus, with two segments (0–180° and 180–360°), the number of events is equal between segments and so a right or left turn is equally likely. As the direction chosen within each of the two segments is random, the distribution of possible turns is equal around the entire circle and all directions are equally likely. However, as the number of segments is increased, the binomial distribution increasingly resembles a discrete Gaussian (normal) distribution with a central peak (Kunert, Montag & Pohlmann 2001) and therefore turns into segments near 180° are more likely than others. Random choices of direction within these narrow segments alter the distribution very little, so directions close to 180° are much more probable. Following this procedure with just two segments therefore approximates a random walk, but as the number of segments increases up to nine (0–40°, 40–80°, … , 320–360°) the walk becomes straighter. The number of segments thus determines movement pattern because it is correlated negatively with turning rate and we therefore use 'number of segments' as our measure of turning rate.

Table 1. Standard simulation parameters and the resulting net displacement per day used for both beetle types

Model parameters	*Pterostichus*-type	*Bembidion*-type
Used time intervals (s)	8	18
Mean distance moved per time step (m timestep^{-1})	0·08	0·02
Variance in distances per time step	0·64	0·04
Number of time steps per day	3000	3000
Displacement per day (m)	6·7	1·7

All beetles walked until they fell into a trap or until the chosen number of days was past. The number of time steps during each simulated day was selected to provide the finest spatial resolution of the simulated pathway and to match the activity patterns of real species. We therefore used short time intervals (Table 1) as this reproduces capture performance realistically (Crist *et al.* 1992; Crist & Wiens 1995), and estimated mean daily activity periods from those of published studies (Greenslade 1963).

Because catch rates are determined by organism characteristics we simulated two contrasting beetle types, one a large type based on the carabid species *Pterostichus melanarius* (Ill., 1798) (length ~15 mm) and the other a small type based on *Bembidion obtusum* Serv., 1821 (length ~3 mm), both very abundant in Thuringian farmlands (Perner & Malt 2002). Because *P. melanarius* is one of the most commonly studied carabids, a large amount of empirical data are available for it (e.g. Ericson 1978; Ericson 1979; Wallin & Ekbom 1988; Lys & Nentwig 1991; Lys & Nentwig 1992; Thomas, Parkinson & Marshall 1998). The mean daily net displacement, the straight distance between the position of a beetle on two consecutive days, ranges between 2 m (heterogeneous farmland) and 16 m (crop fields). No similar data are available for *B. obtusum*, so we parameterized our model with data for *B. lampros* (Hbst. 1784) that has an empirically determined daily net displacement of 1–3 m (Klazenga & de Vries 1994).

To identify reasonable parameters we conducted a preliminary simulation where we checked the combinations of parameters in which the mean distance per time step ranged from 2 to 10 cm, turning rate between 1 and 15 classes, number of time steps per day was increased from 2000 to 6000 and the variance of the mean distance per time step ranged from 4 to 100 cm while keeping the other parameters constant. Furthermore, we tested different field sizes to avoid edge effects between the nested-cross array and the border of the simulated field. The resulting daily net displacements of the simulations were compared with the data from the above-named field studies and we selected, as standard, parameters intermediate between those for heterogeneous and homogeneous habitats because these are likely to be appropriate for grassland habitats (Table 1). We simulated an area of 150 × 150m because it allows the simulation of densities comparable with real densities, and prevents interactions between the traps and the area edge. The nested-cross array (Fig. 1a) was established in the centre of this square and simulated beetles were released singly at random points in the area.

We assumed that an infinite field with the same density of beetles surrounded the simulated area. Therefore, the probability of leaving the area equals that of entering and animals leaving the area of the simulation are immediately compensated for by an equal number entering it. Thus, whenever a beetle left the area, another was released at a randomly chosen edge position randomly directed into the field. This procedure removes the need to simulate on a toroidal surface and more resembles what happens in the field.

SIMULATION PROTOCOL AND ERROR ESTIMATION

To verify how changes in population and model parameters affect simulated capture results and density estimates, we tested different parameter constellations for both beetle types (Table 2). We defined parameter constellation B (the most naturalistic constellation) as the standard set and varied each of the parameters in sequence to determine model sensitivity (Table 2). All parameter constellations were repeated 30 times except that because beetle densities of 0·1 m^{-2} produced highly variable simulated capture results, we increased the number of runs to 100 at this density to stabilize variances. However, high beetle densities of 10 m^{-2} produced low variances and we were therefore able to economize substantially on computer time by decreasing the number of runs to 10. We tested three different movement patterns of model beetles by varying the turning rate from a pure random walk to a straight walk, and we tested the effect of trapping period. We also examined the effect of beetle population structure by simulating aggregated, random and homogeneous distributions. Aggregated distributions were created by starting 15 beetles together on a randomly selected 5 m^2 square within the simulated field, and random distributions by starting each beetle at a randomly chosen pair of coordinates within the area. Homogeneous distributions were initialized by dividing the entire field into small squares sized so as to produce the required final density of beetles and releasing one beetle at a random position within each square. We also investigated the effect of intertrap distances by using distances between the central and the first traps of 0·2, 0·5 and 0·8 m (Table 2 and Table 3).

Before fitting single hyperbolic functions to the data observed we first took the average of the four traps at equal successive distances from the centre. This procedure was necessitated by the array design because there is only one central trap, but four at all other intertrap distances from the centre. Therefore, to equalize the weight with which intertrap distances are represented in function fitting, values for non-central traps were averaged within intertrap distances. Curve fitting was carried out in SigmaPlot (2001) but, to avoid solutions outside the range of the x-axis, we constrained parameter b (see eqn 2) to lie between the initial trap distance (e.g. 0·5 m) and the distance of the furthest trap from the origin (e.g. 31·5 m). We calculated the mean capture rate (in %) and the coefficient of variation (CV) of the calculated capture rate (see Table 4). Furthermore, we derived three measures of accuracy for each constellation of parameter values. The first of these was the proportion of runs for which functions could be fitted and the second was the variance (with percentiles) of the values given by successful fits. The third measure was the proportional deviation of $\hat{D}$ (density estimate) from D (real density in model) calculated as percentage accuracy (PA):

$$PA = \left(\frac{|D - \hat{D}|}{D}\right) \times 100 \qquad \text{eqn 4}$$

which enabled us to calculate a mean (median) percentage accuracy per simulation variant. Please note that low values indicate a high degree of accuracy.

Table 2. Simulation parameters used for both model beetles *Pterostichus*-type and *Bembidion*-type. Variant B was used as standard parameter set (bold type) and the simulation sets indicated as variants A and C are based on the parameter set of B except for changes in sequence in beetle density, turning rate, length of trapping period, beetle distribution or initial trap distance of the nested-cross array. Number of simulation runs given by superscript numbers: 1 = 100; 2 = 30; 3 = 10

Varied population and model parameters	Variant A	Variant B	Variant C
Beetle density (m^{-2})	0·1^1	**1·0^2**	10·0^3
Turning rate (no. of segments)	Pure random walk^2 (1)	**Intermediate walk^2** **(5)**	Straight walk- dominated^2 (9)
Length of trapping period	4 days^2	**7 days^2**	14 days^2
Beetle distribution	Aggregated^2	**Random^2**	Homogeneous^2
Initial trap distance in nested-cross array (m)	0·2^2	**0·5^2**	0·8^2

Table 3. Arrangements of nested-cross arrays with three different initial trap distances

	Initial trap distance (m)		
	0·2	0·5	0·8
No. of traps	Distance from origin		
1	0	0	0
4	0·2	0·5	0·8
4	0·6	1·5	2·4
4	1·4	3·5	5·6
4	3·0	7·5	12·0
4	6·2	15·5	24·8
4	12·6	31·5	50·4
4	25·4	–	–

Results

No function fit, and therefore no density estimation, occurred only in some runs with a density of 0·1 m^{-2} (*Bembidion*-type: 11 of 100 runs, *Pterostichus*-type: nine of 100 runs, Table 4). In all circumstances, estimated densities of both beetle types (*Bembidion*- and *Pterostichus*-type) (Fig. 2) tended to be underestimated in comparison to the real density (dotted lines in Fig. 2a–c). However, the variance of estimates decreased with increasing model density and was always substantially lower for the large (*Pterostichus*) than for the small (*Bembidion*) beetle type. The greatest proportional deviation from the model density occurred for the *Bembidion* type at 0·1 m^{-2} and the least for this type at 10·0 m^{-2}. For both beetle types the mean percentage accuracy lay between 96% and 17% (Table 4).

To evaluate the effects of various model and population parameters on the accuracy of the estimates, a density of 1·0 m^{-2} was used for the following simulations (Table 2, Fig. 3). A low turning rate overestimated density, an increase of spread and a considerable decrease of accuracy compared with the intermediate turning rates for both beetle types. The mean density estimates obtained from simulation with high turning rates overestimated densities of *Bembidion*-type, underestimated *Pterostichus*-type densities slightly more and were also less accurate compared with those estimated with intermediate turning rates (Fig. 3a, Table 4). For both turning rate variations, there was a comparable increase of runs for which no fits were possible (6–7 runs) for only the *Bembidion*-type (Table 4). A trapping period longer or shorter than 7 days reduced estimation accuracy and increased the number of runs for which no function fits

Table 4. Mean (median) percentage accuracy of density estimate (low values indicate a high degree of accuracy), percentage of runs for which fits were possible and mean capture rate (%) with the mean coefficient of variation (CV) for the different sets of simulation parameters (compare with Table 2)

Population and model parameters	*Bembidion*-type			*Pterostichus*-type		
	Variant A	Variant B	Variant C	Variant A	Variant B	Variant C
Beetle density	0·1	1·0	10·0	0·1	1·0	10·0
Mean accuracy (%)	96	44	17	69	30	24
Possible fits (%)	89	100	100	91	100	100
Mean capture rate (%)	0·58	0·60	0·60	3·47	3·50	3·50
with mean CV	29·2	6·0	2·5	10·8	3·2	1·1
Turning rate	Random	Intermediate	Straight	Random	Intermediate	Straight
Mean accuracy (%)	79	See	113	53	See	124
Possible fits (%)	77	above	80	100	above	100
Mean capture rate (%)	0·37	(var. B)	0·85	2·49	(var. B)	4·4
with mean CV	10·04		8·2	3·5		3·6
Length of trapping period (days)	4	7	14	4	7	14
Mean accuracy (%)23	62	See	59	29	See	23
Possible fits (%)	77	above	97	100	above	100
Mean capture rate (%)	0·38	(var. B)	1.07	2·25	(var. B)	6·12
with mean CV	10·3		9·1	4·1		2·5
Beetle distribution	Aggregated	Random	Homogeneous	Aggregated	Random	Homogeneous
Mean accuracy (%)	80	See	35	36	See	32
Possible fits (%)	90	above	100	100	above	100
Mean capture rate (%)	0·65	(var. B)	0·60	3·67	(var. B)	3·55
with mean CV	15·6		8·9	5·9		2·8
Initial trap distance (m)	0·2	0·5	0·8	0·2	0·5	0·8
Mean accuracy (%)	57	See	80	48	See	41
Possible fits (%)	100	above	70	100	above	100
Mean capture rate (%)	0·56	(var. B)	0·66	3·18	(var. B)	4·02
with mean CV	9·8		6·9	3·6		2·9

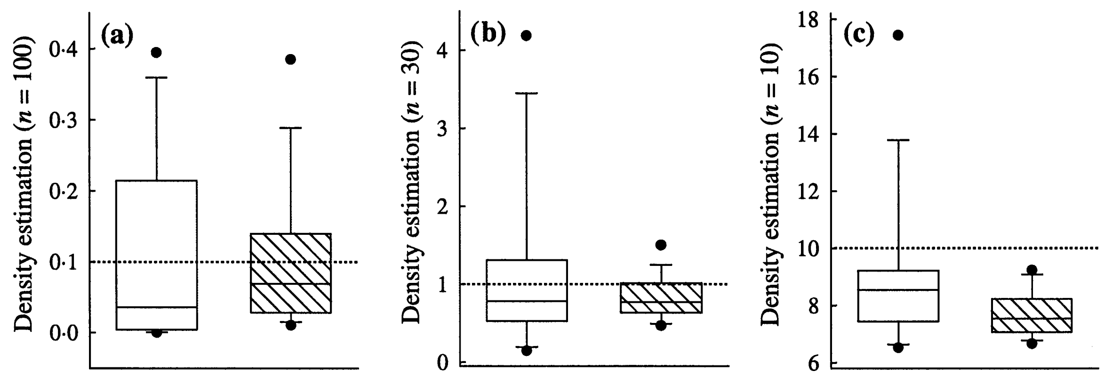

Fig. 2. Variance of density estimates for both beetle-types (empty boxes: *Bembidion*-type; hatched boxes: *Pterostichus*-type) based on three different population densities in the simulation (a) 0·1 m^{-2}, (b) 1·0 m^{-2}, (c) 10·0 m^{-2}. All other simulation parameters used corresponded to those in B (compare with Table 2). Box-plot indication: boxes, median with the 25 and 75 percentiles; whiskers, 10 and 90 percentle; points, 5 and 95 percentile.

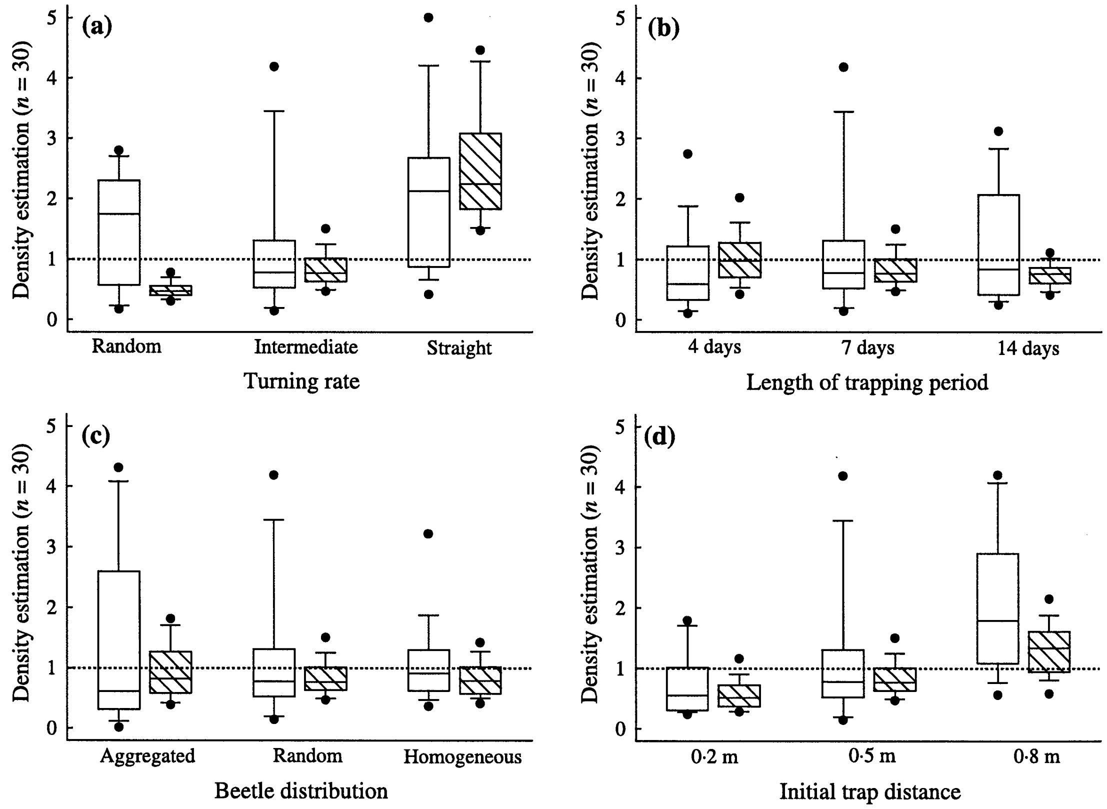

Fig. 3. Results of density estimation for both beetle-types (empty boxes: *Bembidion*-type; hatched boxes: *Pterostichus*-type) based on simulation parameter set B (compare with Table 2) where (a) the turning rate, (b) the length of trapping period, (c) the beetle distribution or (d) the initial trap distance of nested-cross array were varied. Box-plot indication: boxes, median with the 25 and 75 percentiles; whiskers, 10 and 90 percentle; points, 5 and 95 percentile.

were possible for the *Bembidion*-type. For the *Pterostichus*-type estimation accuracy is scarcely affected by the variation in trapping period, but the most precise density estimates were produced with a period of 4 days (Fig. 3b, Table 4). The initial distribution in simulations did not affect greatly the accuracy of density estimates except for aggregated *Bembidion*-type where the spread and error rate were nearly doubled (Fig. 3c, Table 4). A shorter initial trap distance reduced the estimate accuracy considerably for both beetle-types but lessened the spread in estimates for the *Bembidion*-type. However, a longer trap distance caused an overestimation of density for both beetle types and increased in particular the spread, the estimation error and the number of cases, for which no function fits were possible for the *Bembidion*-type.

Discussion

Our technique produces, in general, considerably more accurate density estimates for the large compared with the small beetle type. This pattern probably arises because the large *Pterostichus*-type has a larger displacement than the small *Bembidion*-type (Table 1), and the mean capture rate (probability) increases with beetle displacement (Table 4) that, in turn, increases the accuracy of estimation (Parmenter, MacMahon & Anderson 1989; Crist & Wiens 1995). With higher animal density, the accuracy of density estimates also increases for both beetle types (Table 4). Whereas the mean capture rate remains nearly unaffected by increasing beetle density for both types, the relevant mean coefficient of variation (CV) of the capture rate decreases considerably, which increases the accuracy of estimate. The simulated beetle densities of 0·1, 1·0 and 10 m^{-2} fall within the range of empirical estimates of beetle densities in different open habitats. This was underpinned by a large number of studies using a variety of techniques for the *Bembidion*-type (here *B. obtusum*; Desender 1986; Brenoe 1987; Hance 1992; Kennedy 1994) and in particular for the *Pterostichus*-type (here *P. melanarius*, e.g. Ericson 1977; Desender 1986; Purvis & Fadl 1996; Thomas, Parkinson & Marshall 1998).

The best density estimates were obtained by using an intermediate turning rate (Table 4, Fig. 3a). In nature, the movement behaviour of ground-dwelling arthropods, especially of carabids, may vary with season or with time of day (Greenslade 1963; Baars 1979; Rijnsdorp 1980; Johnson *et al.* 1992). During the main activity period the intermediate or nearly random walk pattern seems to be the dominant movement pattern (Kareiva & Shigesada 1983; McCulloch & Cain 1989). However, the straight walk-dominated pattern may occur at the beginning and end of the season (e.g. looking for over wintering places) or in the context of dispersal activities (Rijnsdorp 1980; Swingland & Greenwood 1984; Wallin & Ekbom 1988). Also, habitat-specific movement patterns seem to be possible and may influence the capture rates in the field (Crist & Wiens 1995; Melbourne 1999).

It is widely accepted that the spatial distribution pattern of ground-dwelling arthropods in farmlands is linked to the heterogeneity of a number of environmental factors. These include physical factors (e.g. soil type, pH and moisture, microclimate), vegetation structure and composition (e.g. cover, height) and prey distribution, as well as the type and quality of adjacent habitats (Thiele 1977; Dennis, Young & Gordon 1998; Holland, Perry & Winder 1999; Thomas *et al.* 2001; Maudsley, Seeley & Lewis 2002). Pitfall trapping success is affected considerably by arthropod distribution pattern (e.g. Thomas *et al.* 1998), but our method was stable to distribution changes. Divergence was greatest with the aggregated distribution. Our aggregation method used in simulation produced moderately clumped patterns, and undoubtedly stronger aggregation would reduce much more the accuracy of density estimation.

The effects of different initial trap distances with more accurate estimates for large beetles at large distances and for small beetles at small distances confirm the relationships known between animal movement, capture probability and trap array geometry (Parmenter, MacMahon & Anderson 1989; Crist & Wiens 1995; Parmenter *et al.* 2003). Therefore, we conclude that the initial trap distance used should be determined from the characteristics of the 'target' species. Studies focusing on species smaller (or with a lower displacement) than the *Bembidion*-type should use an initial trap distance lower than 0·5 m and studies on large arthropods should use greater than this value. This point is connected with another noteworthy fact. The probability of capturing any individual in a given trap increases with distance from the centre of the nested-cross due to trap interference; however, the probability that a given individual will be captured in any trap actually decreases from the centre to the periphery because of the decreasing trap density. To discuss this last point, which is the basis of the point estimators in distance sampling methods such as trapping webs, we presented the different capture rates calculated on the basis of stepwise enlargements of the circular area around the central trap of the nested-cross and the cumulative catches of the included traps (Fig. 4). We have called this parameter 'local capture rate' to distinguish this value from the capture rate calculated in Table 4 based on all beetles released in the simulated field. A strong decrease following an exponential decay function of the local capture rate could be observed for both beetle types. Whereas for the *Pterostichus*-type a capture rate below 100% was not reached until a radius of 23·5 m, for the

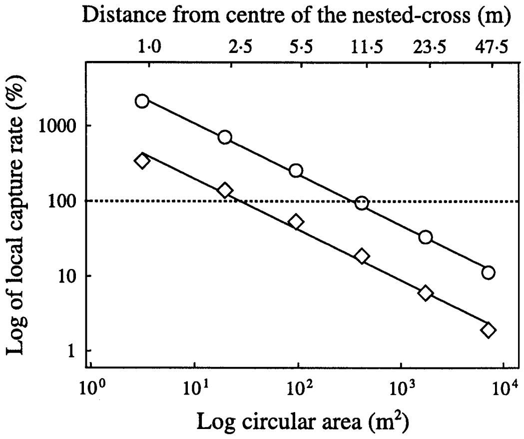

Fig. 4. Changes of local capture rate depending on increasing distance from the centre to the periphery of the nested-cross array. As an example, the parameter set B (see Table 4) is presented (circles: *Pterostichus*-type; diamonds: *Bembidion*-type). The calculations are based on stepwise enlargement of the central area of the nested-cross and the cumulative catches of the traps so included. The starting radius is 1 m (which includes the central trap and the four traps which are 0·5 m from the centre) with the increments thereafter equal to the distances from the centre to points halfway between the traps.

Bembidion-type this was already observed with a radius of 5·5 m, indicating the differences in the effective trapping area of the whole nested-cross between the both tested beetle types. Furthermore, this figure illustrates that in the direct surroundings of the nested-cross a mean decrease of population density of about 2% (for the small *Bembidion*-type) up to 11% (for the large *Pterostichus*-type) is to be expected if working with removal sampling or trapping preservatives.

Some trapping preservatives (e.g. formaldehyde solution) attract (or repel) arthropods (Waage 1985; Holopainen & Varis 1986; Topping & Luff 1995; Kuschka 1998). If such preservatives are used, we expect effects that may overlie the general shape of the sampling pattern (see Fig. 1c). In particular, the concentration of the traps in the centre of the nested-cross array would cause a proportionally greater attractive (or repellent) effect for ground-dwelling arthropods than the traps at the periphery and this will change the capture function considerably. Therefore, nearly neutral capture preservative (e.g. salt solution) should be used for field applications.

Our nested-cross array is a promising technique for density estimation of ground-dwelling arthropods, although it needs to be evaluated in the field. Compared with methods based on mark–recapture techniques the nested-cross array is a time-saving alternative (sampling periods of only 4–7 days are sufficient) that furthermore allows simultaneous density estimation for several target species and is also applicable for very small species, where labelling procedures are not practical. If a fit of the data sampled in the field is possible with the hyperbolic function, reliable estimates can be derived. The accuracy of density estimates and the probability that function fits match increase with body size, or rather net displacement, of ground-dwelling arthropods, increasing population density, a more random or intermediate movement pattern and more random or homogeneous spatial and temporal distribution patterns of target species.

On condition that the nested-cross arrays are used during a period where the target species are active and that the traps are filled with neutral preservative, the arrays are established in nearly homogeneous parts of the habitat under study and the arms of the nested-cross are distant enough from edge structures, we believe that this method has great potential for time-saving monitoring of ground-dwelling arthropods in agriculture or nature conservation.

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4. Manuskript III

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Assessment of changing agricultural land use: response of vegetation, ground-dwelling spiders and beetles to the conversion of arable land into grassland

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Abstract

An ecological indicator approach was used to examine the effects of changing agricultural land use on vegetation and ground-dwelling spider and beetle assemblages. An arable land site (control) and six differently managed grassland sites (with different time since conversion from arable land or time of current management) were comparatively investigated in a 3-year study. Whereas species richness increased with decreasing management impact for plants and spiders, the Camargo's evenness (E') index increased for all three examined assemblages. This suggests a very trustworthy community parameter for ecological indication studies. Differences did occur between the vegetation and the invertebrate groups in the assessment of the grassland sites. Ordination analysis indicated a much better separation of the different sites based on the invertebrate data than is possible on the basis of the vegetation data. These considerable differences were attributable to the short reaction time of these groups to changes in land use: ground-dwelling spiders and beetles mainly respond to changes in the microclimate and the soil-moisture. Efficient indication of restoration management is therefore possible after 3–5 years. Vegetation assemblages appeared as less powerful indicators of short-term restoration processes. We suggest that vegetation monitoring be used as a more powerful long-term approach but that it should be coupled with (short-term and sensitive) invertebrate monitoring (e.g. ground-dwelling spiders and beetles) especially at the beginning of the agricultural restoration processes.

Keywords: Araneae; Biodiversity; Bioindication; Coleoptera; Evenness; Agricultural land use changes; Restoration ecology; Species richness; Vegetation

1. Introduction

Changes in land use, habitat fragmentation, nutrient enrichment, and environmental stress often affect species diversity in ecosystems (Chapin et al., 1997; Vitousek et al., 1997). van der Putten et al. (2000) pointed out that, at both local and regional scales, land use changes are among the most immediate drivers of species diversity. Furthermore, they explained that one of the possible ways of counteracting the loss of biodiversity resulting from agricultural intensification during the last decades might be to reduce land use intensity. Duelli (1997) also mentioned that intensive agricultural management has led to an alarming level of 'ecological degradation' and that a less intensive land use could have two different effects. On the

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one hand, less intensive managed agricultural areas enrich regional species diversity while, at the same time those same areas could have a positive effect on beneficial arthropods by providing habitats after crop harvest or for hibernation. Goedmakers (1989) refers to the need to reduce overproduction and also to diminish agricultural pollution within the European Union from an economic perspective. Furthermore, Goedmakers points out that changing agricultural land into conservation areas increase substantially the ecological potential of the rural environment, as measured by species diversity or the presence of indicator species.

Bioindication has tended to be used somewhat "... loosely and has been adopted in a broad range of contexts, including the indication of habitat alteration, destruction, contamination and rehabilitation, vegetation succession, climate change and species diversity..." (McGeoch, 1998). More recently, the term and its many synonyms has been reclassified into three categories: (i) *environmental indicators* that reflect the biotic or abiotic state of an environment; (ii) *ecological indicators* that reveal evidence for, or the impacts of, environmental change; (iii) *biodiversity indicators* that specifically indicate the diversity of species, taxa, or entire communities within an area (McGeoch, 1998; Lawton and Gaston, 2001). Following this classification any attempt to identify the effects of changing agricultural land use on biotic systems should focus on *ecological indicators* defined as characteristic taxa or assemblages "... sensitive to identified environmental stress factors on biota, and whose response is representative of the response of at least a subset of other taxa present in the habitat..." (McGeoch, 1998).

Plants and plant communities are frequently used groups in ecological bioindication and monitoring (= repeated application of bioindicators; see McGeoch, 1998) studies, however inventories of animal taxa are often missing or at least reduced to vertebrate groups (e.g. birds), because of the high effort involved in investigation. There is, however, increasing evidence that invertebrates or invertebrate assemblages provide a good indication of changing environment (e.g. Majer and Nichols, 1998; Wheater et al., 2000; Andersen et al., 2001).

Using McGeoch's (1998) concept of ecological indicators we investigated agricultural land that had experienced a range of use and different times since conversion from arable land or time of current management. Studies were made from 1996 to 1999 in the Unstrut river floodplain region of Thuringia, Germany. To assess the effects of changing land use on different trophic levels as well as carrying out vegetation analysis we also investigated the spatial and temporal patterns of spiders (carnivorous) and beetles (carnivorous, detritivorous and herbivorous) in the community. Furthermore, the groundwater dynamics, nutrient balances, soil characteristics and microclimates of different sites were analysed. This paper aims to answer the following questions: (i) Do the two components of species diversity (richness and evenness) increase with decreasing management intensity within all three tested indicator groups? (ii) Are there differences in reaction time and sensitivity to changing agricultural land use between the investigated assemblages?

2. Material and methods

2.1. Study sites

The research area was located in the middle Unstrut floodplain, situated in the Thuringian basin (Germany) with annual average temperature of 9.6 °C and precipitation of <500 mm.

We investigated an arable land site (as control) and six different managed grassland sites (with different time since conversion from arable land or time of current management) in a 3-year study (see Table 1). All sites were similar in soil characteristics (Fluvisols, Clay-Vega or Vega-Clay). The groundwater level dynamics were more or less uncoupled from river table dynamics for the majority of the sites. Within the investigated sites there is a gradient in soil-moisture status ranging from 'wet' with surface near groundwater level (B1) through 'mesic humid' groundwater influenced sites with seasonal partial drought periods (A1, A2, A3, C) and sites with a groundwater level some depth from the soil surface and experiencing mild drought conditions especially in summer (B2, partly AD) to river-bank influenced sites (partly AD and C). For further details see Malt and Perner (2002) as well as Perner and Malt (2002).

Table 1
Description of sampling sites[a]

Site name	Abbreviation		Scores ordination axis 1	Location; coordinates[b]	Management/land use activities	Current management since	Flooding frequency	Groundwater level in dm min./max./mean
Arable land	A3	Decreasing management impact →	0	Near Altengottern; 51°08′N, 10°38′E	Conventionally managed, 1996/1997 winter wheat/1998 broad bean, 130 kg N/ha, pesticide application, harvest in August, ploughing in November	About 40 years	No inundation	7/17/14
Young sown grassland	A2		3.04	Near Altengottern; 51°08′N, 10°38′E	Mowing (one-cut in July) and low level cattle grazing (1.0 livestock unit/ha) September–April	1996, formerly arable land	No inundation	7/18/15
Permanent grassland	C		3.17	Near Sömmerda; 51°11′N, 11°05′E	Mowing, three-cuts per year (May, July, and September), liquid manure (about 50–80 kg N/ha)	1967, formerly arable land	Every 5–7 years	4/16/12
Sown grassland	A1		3.41	Near Altengottern; 51°08′N, 10°38′E	All year low level cattle grazing (1.0 livestock unit/ha) and mowing (one-cut in July)	1992, formerly arable land	No inundation	5/12/10
Re-wetted grassland (fallow)	B1		3.43	Near Thamsbrück; 51°07′N, 10°41′E	Yearly mulching in late summer/autumn	1994, formerly arable land	Since 1995 yearly inundation in spring	0/13/5
Embankment grassland	AD		4.14	Near Altengottern; 51°08′N, 10°38′E	Mowing (July) and/or sheep grazing (April and June)	About 30 years	Inundation about three times per century	14/22/19
Permanent grassland	B2		4.58	Near Thamsbrück; 51°07′N, 10°41′E	Mowing one-cut per year (July)	About 30 years, formerly arable land	Inundation about three times per century	15/21/19

[a] Sites arranged along decreasing dimension of management impact. The site-ranking is derived from the site scores of axis 1 using a Bray–Curtis ordination, which explained the predominant part (70%) of the variance included in the management matrix (see Section 2).

[b] Altitude of sites: 140–180 m about sea level.

2.2. Sampling methods

To compare the floristic species composition at each site, phytosociological plant samples according to Braun–Blanquet with species: area ratio after Wilmanns (1989) were carried out in ten 2 m × 2 m squares per site (except for site B2 where five 5 m × 5 m squares were taken). Plant samples were taken in spring and summer of both 1997 and 1998. Plant assemblages were classified according to the plant indicator values by Ellenberg et al. (1992).

Ground-dwelling arthropods were sampled with 10 plastic pitfall traps (⌀45 mm) per site, filled to one third height with 3% formaldehyde with some drops of detergent (in winter drops of glycerol were also added). The traps were positioned in two groups along a transect with five traps (trap–trap distance = 4 m, group distance = 20 m) per group. At site B1 there was a group distance of about 150 m dictated by a site-specific humidity gradient. Pitfall trapping was carried out from May 1996 to October 1998 with trap exchanges taking place every 14 days. Spiders and beetles were sorted and determined to species level in the laboratory as well as classified to ecotypes following Maurer and Hänggi (1990) and Platen et al. (1991) for spiders, and Koch (1989 ff.), Barndt et al. (1991), Korge (1991) and Winkelmann (1991) for beetles.

The surface microclimate around the trap-transects was surveyed using ONSET data loggers (temperature, light intensity, relative humidity). The physical and chemical properties of the soil were also investigated as were surface soil-moisture (Hydra Soil Moisture Probe from VITEL Inc.) and groundwater level. These were measured twice a month. These abiotic data sets were used for direct gradient analysis (RDA, see below) to identify key determinants of the species patterns.

2.3. Statistical analysis

Management activities were coded as follows: fertilisation (0: without, 1: <50 kg N/ha, 2: 50–100 kg N/ha, 3: 100–150 kg N/ha); pesticide application (0: without, 1: with); grazing (0: without, 1: temporary—low level, 2: whole year—low level); mowing (0: without, 1: one-cut per year, 2: two-cuts per year, 3: three-cuts per year); ploughing (0: without, 1: with); mulching (0: without, 1: with); age as time since conversion from arable land or time of current management (0: arable land, 1: 1–2 years, 2: 3–10 years, 3: 11–30years). This matrix were analysed with Bray–Curtis ordination techniques (Beals, 1984; McCune and Mefford, 1997) and site scores of the ordination axis 1 were used as an integrated measure of management impact (see Section 3 and Table 1).

To compare the species patterns of the three groups in different managed field sites, in addition to species richness Camargo's indices of evenness (E'; see Krebs, 1999) were also calculated. Camargo's index is unaffected by species richness and only slightly affected by the presence of rare species in a sample. Linear regression was used to determine the relation between site management intensity and the species richness and evenness of plants, spiders and beetles.

Similarity patterns in species composition and community structure between the sampling sites were explored using non-metric multidimensional scaling (NMDS) ordination for the plant, spider and beetle data separately (McCune and Mefford, 1997). NMDS is an iterative search for a ranking and placement of n entities (samples) on k dimensions (ordination axes) that minimises the stress of the k-dimensional configuration. The "stress" value is a measure of departure from monotonicity in the relationship between the dissimilarity (distance) in the original p-dimensional space and distance in the reduced k-dimensional ordination space (Clarke, 1993). As distance measure we used the Euclidean distance and for all three analysed data sets (plants, spiders, beetles) three ordination axes (dimensions) were sufficient to achieve low stress values. To evaluate how well the distances in the ordination space represent the distances in the original (unreduced) space the coefficient of determination (r^2) were calculated. This value is a measure of the quality of data reduction, along with an assessment of how the variance explained is distributed among the primary axes.

A code replacement of the Braun–Blanquet-scale (van der Maarel, 1979) was necessary for the plant data and the resulting ordinal scale (from 1 to 9) was square-root transformed. In preparation for the multivariate statistical analyses the spider and beetle data were ln-transformed and rare species (all species < 0.01% of catch in total) were omitted to reduce data noise.

To analyse the environmental factors having a potential influence on the studied arthropod assemblages we used the redundancy analysis (RDA) ordination technique (Jongman et al., 1995). The inclusive forward selection procedure was employed to sorting out the factors explaining the most variance in the species data and finally, Monte Carlo permutation procedures were carried out for significance testing of the selected environmental factors (Jongman et al., 1995; Ter Braak and Šmilauer, 1998). To remove weather effects between the different sampling years from the data we used a partial redundancy analysis (pRDA) by entering the total yearly precipitation from May to August into the RDA as covariable.

3. Results

Using a Bray–Curtis ordination the management impact of each of the sampling sites was estimated. As 70% of the variance included in the management matrix (see Section 2) was extracted along ordination axis 1 the site scores of this axis 1 were used to rank the investigated sampling sites (Table 1). A decreasing management impact could be detected from the arable land site (A3), through the young sown grassland (A2), the permanent grassland (C), the sown grassland (A1), the re-wetted grassland (B1), and the embankment grassland (AD) to the permanent grassland site (B2).

Overall 105 plant species, 120 species of adult spiders (56,067 individuals) and 502 species of beetles (77,684 individuals) were recorded from 1996 to 1998 (Table 2). The highest total number of plant species was observed in the re-wetted grassland (B1) while numbers of spider and beetle species were highest in the embankment grassland (AD).

Whereas plant and spider species richness increases with decreasing management impact (relation for spiders not significant, but $r^2 = 0.51$, $P = 0.07$), the species richness of the beetle assemblages is unrelated to the site's management impact (Fig. 1a–c). Detailed analysis of the different trophic guilds within the beetle assemblages show that while carnivore and detritivore species richness is unrelated herbivore beetle species richness does tend to increase with decreasing management impact ($r^2 = 0.34$, $P = 0.16$). Evenness increases with decreasing management impact in all three studied model groups, although for spiders this relationship is not significant ($r^2 = 0.50$, $P = 0.07$; Fig. 1d–f).

Fig. 2 shows the mean indicator values (after Ellenberg) of plants and the total number of hygrophilous species and individuals for spiders and beetles per site. A slight increase of plant moisture indicator value is detectable from the sown grassland (A2) to the re-wetted grassland (B1) and the embankment grassland (AD), whereas the other indicator values show no such tendencies (Fig. 2a). Spiders, and especially beetles, show a clear increase of hygrophilous species and a very strong increase of hygrophilous individuals from the sown (A1, A2) to the embankment (AD) and re-wetted (B1) grasslands (Fig. 2b and c).

To analyse and visualise the differences between the sampling sites in assemblage structure of plants, spiders and beetles we used NMDS ordinations (Fig. 3a–f). The ordination pattern for the plant data

Table 2
Number of species (and individuals) for plants, spiders and beetles caught at each site from 1996 to 1998 (for detailed species lists see Malt and Perner (2002) as well as Perner and Malt (2002))

	Plant species	Spiders		Beetles	
		Species	Individuals	Species	Individuals
Arable land (A3)	20	74	6850	205	18863
Young sown grassland (A2)	23	63	8845	249	21764
Permanent grassland/three-cuts (C)	27	72	14969	244	12972
Sown grassland (A1)	32	59	7119	196	4989
Re-wetted grassland (B1)	46	67	10156	188	4967
Embankment grassland (AD)	45	81	5642	312	11720
Permanent grassland/one-cut (B2)	30	69	2486	195	2409
Total	105	120	56067	502	77684

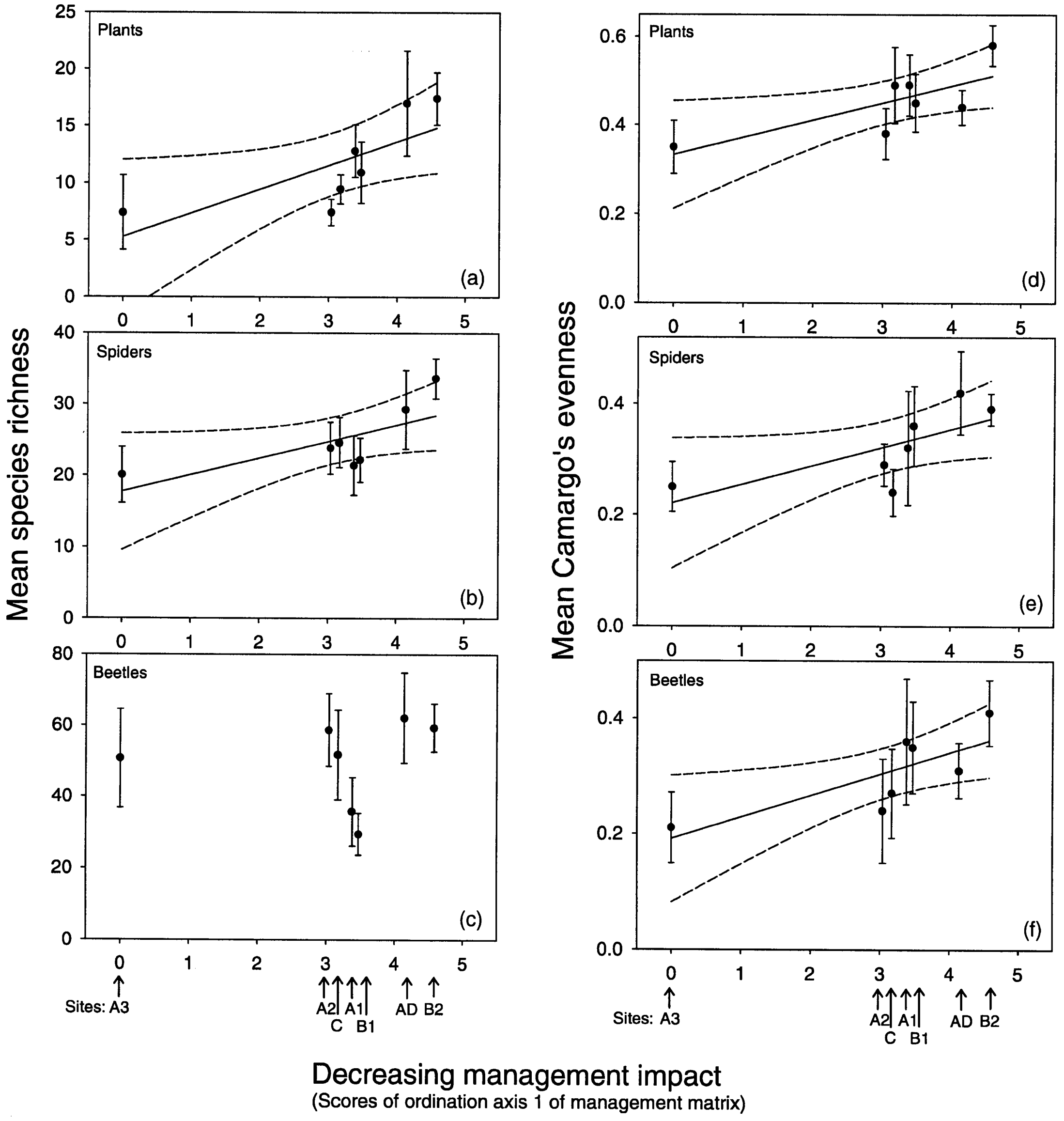

Fig. 1. Changes in mean species richness (a–c) and mean Camargo's evenness (d–f) of plants, spiders and beetles with decreasing management impact. Standard deviations (S.D.) and 95% confidence intervals of the linear models are displayed. Estimation of decreasing management impact derived from the site scores of axis 1 using a Bray–Curtis ordination, which explained 70% of the variance included in the management matrix (see Section 2). Decreasing management impact vs. mean species richness of (a) plants ($r^2 = 0.55$, $P < 0.05$), (b) spiders ($r^2 = 0.51$, $P = 0.07$), (c) beetles ($r^2 = 0.8$, $P < 0.01$) and vs. mean Camargo's evenness of (d) plants ($r^2 = 0.57$, $P < 0.05$), (e) spiders ($r^2 = 0.50$, $P = 0.07$) and (f) beetles ($r^2 = 0.60$, $P < 0.05$).

(cumulative r^2 for axis 1, 2 and 3 were 17.6, 62.2 and 77.3, respectively) shows that all sites with exception of both sites AD and B2 clumped together (Fig. 3a). Also the projection of axis 1 vs. axis 3 improves the separation of those sites only slightly (Fig. 3b). Ordination of spider (cumulative r^2 for axis 1, 2 and 3 were 36.8, 61.4 and 91.8, respectively) and beetle (cumulative r^2 for axis 1, 2 and 3 were 25.6, 62.1 and 89.0)

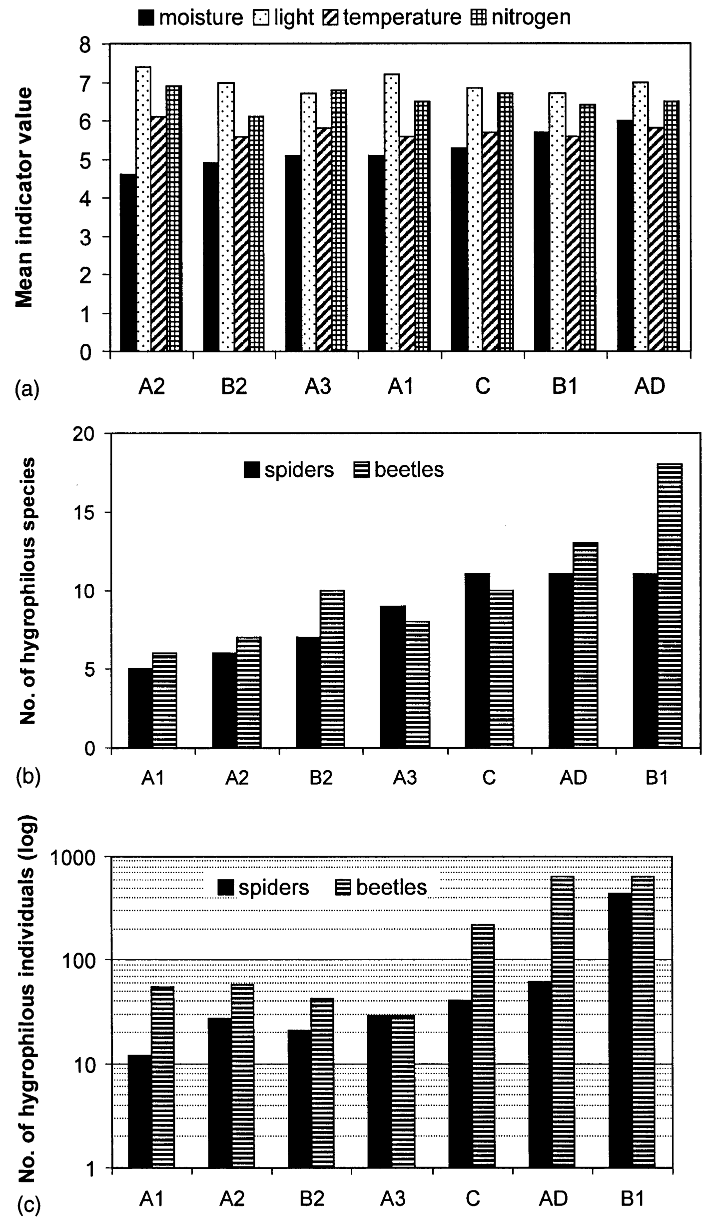

Fig. 2. Mean indicator values (after Ellenberg) of plants (a) for moisture, light, temperature and nitrogen, (b) numbers of hygrophilous species, and (c) individuals for spiders and beetles caught at each site. Sites arranged from lowest to highest moisture indicator values respectively amount of hygrophilous species.

assemblage provide an outstanding separation of data (Fig. 3c–f). Here, the examined set of agricultural land use types evokes distinct patterns of community structure. In both cases (spiders—Fig. 3c and d and beetles—Fig. 3e and f) arable (A3) and young sown grassland (A2) sites are close together. The good site separation based on spider and beetle data suggests that using procedures of direct gradient analysis to screen important (good describing) site parameters may be a promising avenue to follow. RDA (Fig. 4)

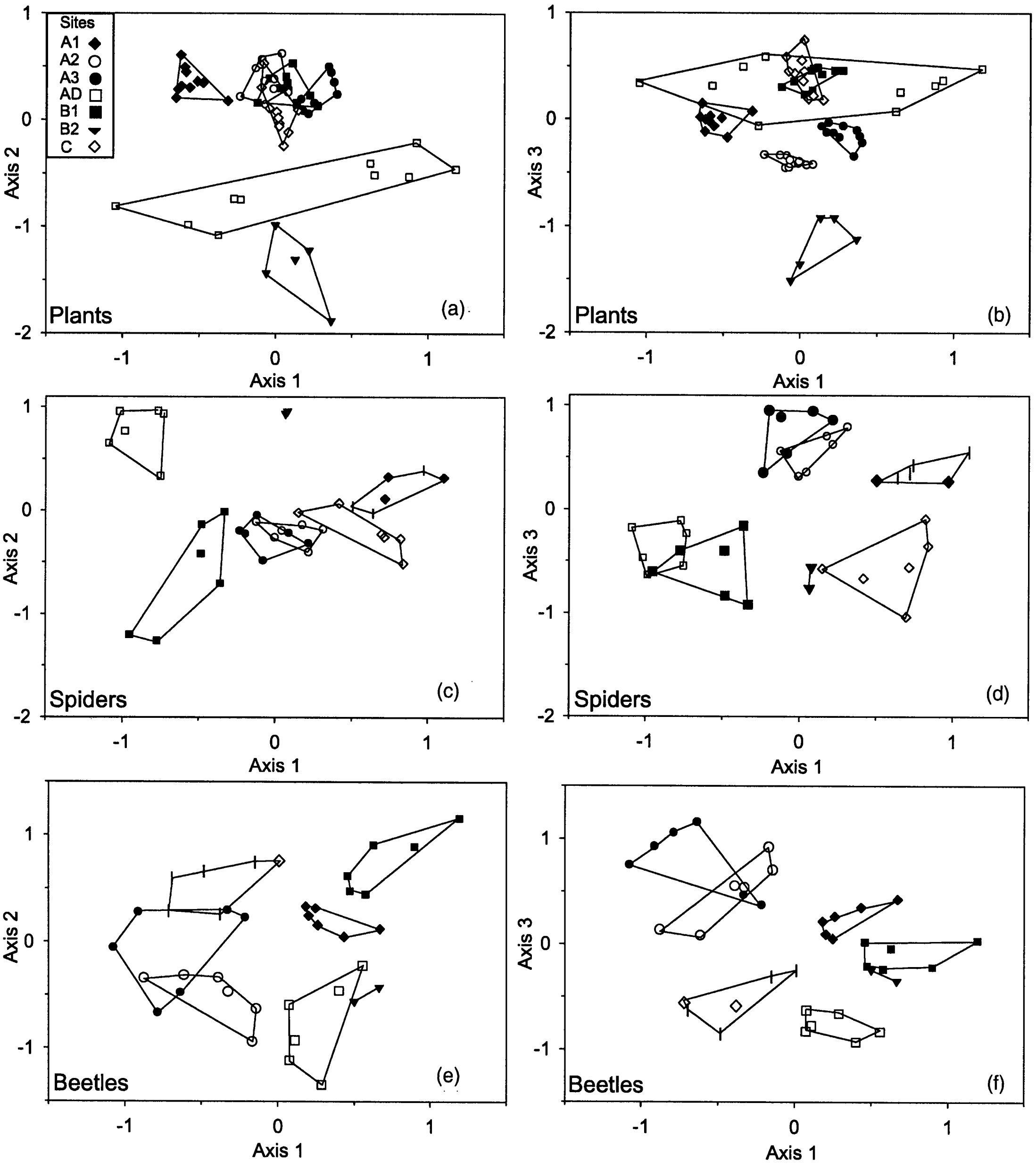

Fig. 3. NMDS ordinations of plants (a and b), spiders (c and d) and beetles (e and f) assemblages. For the plant data 10 samples per site (except site B2 only five samples) and the arthropod data six samples per site (two partial transects each with five pooled pitfall traps and 3 years, except site B2 only 1 year studied) have been plotted (see Section 2). See Table 1 for site abbreviations. Minimum stress values for (a and b) plants: axis 1 = 32.2, axis 2 = 20.6, axis 3 = 14.9, (c and d) spiders: axis 1 = 34.6, axis 2 = 16.0, axis 3 = 9.2 and (e and f) beetles: axis 1 = 36.4, axis 2 = 16.5, axis 3 = 10.0.

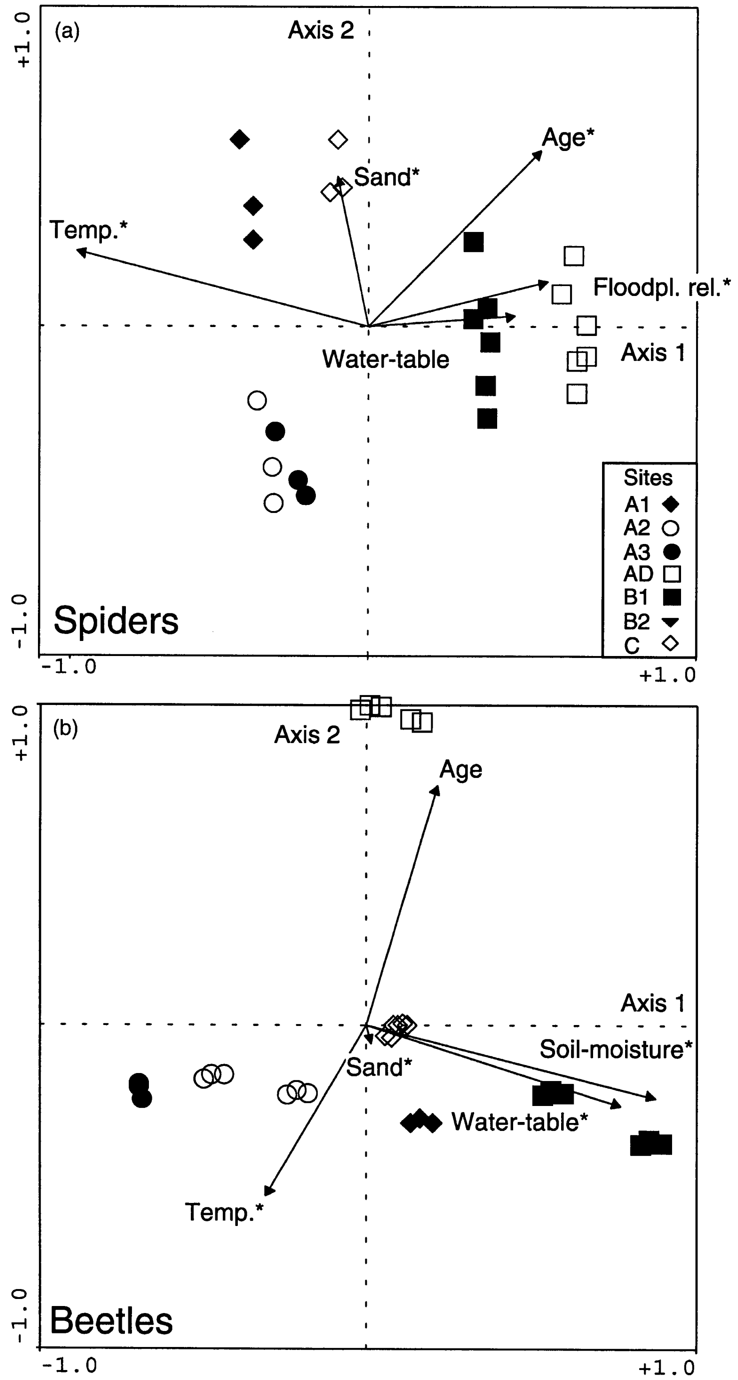

Fig. 4. pRDA of spider (a) and beetle (b) assemblages; database like Fig. 3c–f; used covariable: total of precipitation from May to August. See Table 1 for site abbreviations. Abbreviations of abiotic parameters: Age—time since conversion from arable land or time under current management, Floodpl. rel.—amount of floodplain relict habitats (e.g. backwaters, banks) within 100 m, Sand—mean amount of sand in the soil, Soil-moisture—mean amount of time per year with water saturation of the soil surface, Temp.—mean temperature differences on the soil surface during the vegetation period, Water-table—mean amount of time per year with ground-water level <100 cm; $^*P < 0.05$.

Table 3
Partial inter-set correlation coefficients of the selected environmental variables for the spider and beetles data sets[a]

Parameter	Lambda-*A*	Axis 1	Axis 2	Axis 3	Axis 4
SPIDERS—eigenvalues		0.2612	0.1411	0.1367	0.0623
Temp.*	0.227	−0.8545	0.2179	−0.2233	0.2302
Age*	0.125	0.5151	0.5398	−0.3348	−0.3941
Water-table	0.125	0.4347	0.0357	0.8422	0.1588
Sand*	0.096	−0.1082	0.4952	0.2299	−0.6868
Floodpl. rel.*	0.055	0.5279	0.1346	0.0935	−0.2183
% var. expl.	62.7				
BEETLES—eigenvalues		0.193	0.156	0.090	0.0580
Soil-moisture*	0.163	0.8312	−0.2218	0.1581	0.0066
Age	0.132	0.2064	0.7599	0.5534	−0.1282
Sand*	0.100	0.0093	−0.0598	0.7847	−0.5298
Temp.*	0.074	−0.2960	−0.5188	0.3385	0.6509
Water-table*	0.052	0.7306	−0.2432	−0.3164	−0.4457
% var. expl.	52.2				

[a] Weather effects were partialled out of the analysis by entering the total precipitation totals from May to August into the RDA as covariables. Environmental variables are given in the order of their inclusion in the model together with the additional variance each variable explains at the time it was included (lambda-*A*-value) and the total variance explained (% var. expl.) by the selected environmental variables.

illustrates that ground-water level (water-table), temperature on the soil surface during the vegetation period (Temp.), time since conversion from arable land (Age) and amount of sand in the soil (Sand) explain the majority of the variance in both spider and beetle data set. Floodplain relict habitat areas (Floodpl. rel.) and near-surface soil-moisture (Soil-moisture) identified as additional environmental factors for the spider (Fig. 4a) and beetle data set (Fig. 4b), respectively. With the exception of 'water-level' (spiders) and 'age' (beetles) all selected environmental parameters show significant relationships to patterns of species assemblages (see also Table 3).

4. Discussion

In this study we assessed the effects of changing agricultural land use on vegetation, spider and beetle assemblages. Overall, we found comparable relationships between the management impact and species richness (plants, spiders) and evenness (plants, spiders, beetles) for the different trophic levels (Fig. 1). When considered in detail specific differences were found to exist between the vegetation and the invertebrate groups (Figs. 1 and 3) in the different grassland sites (A1, A2, AD, B1, B2, C). Ecological effects at the vegetation level strongly depend on both the intensity of former arable management (e.g. nutrient balance, seed bank) and the initial conditions of grassland succession (e.g. seed mixture; van der Putten et al., 2000). Bakker and Berendse (1999) have shown that the development of species-rich vegetation on abandoned arable land is often constrained, even when natural abiotic conditions have been restored. Reasons for this constraint include a depleted seed bank, the poor seed dispersal of late-succession species as well as the fact that the first established competitive weedy species, which are already present in the seed bank of agricultural sites, prevent vegetation development for many years (Hansson and Fogelfors, 1998). Although the poor vegetation richness in our study shows considerable differences between the sites, the more quantitative measure of evenness, and especially the ordination patterns, demonstrate a weak separation of the most grassland sites (Fig. 3a and b). This is likely to have been caused by the dominance of competitive (persistent) weedy species (e.g. *Cirsium arvense*, *Elymus repens*, *Galium aparine*) and a general vegetation pattern existing among these sites at that time. While plant composition pattern show little differences between sites both invertebrate groups show clear separation between examined sites (Fig. 3c–f). It is well known that ground-dwelling spider and beetle (especially ground and rove beetles) assemblages are sensitive to habitat structure, microclimate and management (Luff and Rushton, 1989; McFerran et al., 1994; Ekschmitt et al., 1997; Topping and Lovei, 1997; Dennis et al., 1997; Wardle et al., 1999). In our study main source of variation within both invertebrate groups could be explained by environmental parameters such as 'temperature', 'age', 'water-level', 'sand', 'floodplain relict habitats' and 'soil-moisture' (Fig. 4a and b). Among these parameters temperature explained the largest proportion of variance in the spider data set and soil-moisture in the beetle data set (Table 3), which was many times mentioned as key factor for distribution patterns of ground beetle assemblages (e.g. Rykken et al., 1997). It is also well-documented that vegetation structure (height and density) is important for spiders (Greenstone, 1984; White and Hassall, 1994), and our results are not inconsistent with these findings. Vegetative structure especially frequency and time of disturbances (e.g. harvesting or mowing), would have resulted in significant microclimatic and particularly also soil surface temperature differences between the sites.

Often, if not in most cases, it is difficult (and in this context not absolutely necessary) to disentangle the causal mechanisms of response. These extracted 'factors' should therefore be seen as (statistically significant) model descriptors for system patterns. In the context of GIS-technology such descriptors should enable us to make spatial extrapolations of and provide us with predictions for success of restoration processes.

The hygrophilous habitat specialists within the spider and beetle assemblages are an useful "quick assessment tool" for monitoring the efficiency of restoration projects in agricultural floodplain landscapes (Fig. 2b and c). The high colonisation potential of spider (air ballooning) and many beetle (flight, air plankton) groups suggests that the increased number of species, and especially individuals of hygrophilous habitat specialists, may indicate the success of the changing agricultural land use. On the other hand, it is also a measure for the proportion of floodplain relict habitats in the agricultural landscape (e.g. backwaters and banks, and also embankment habitats) and their connectivity of the landscape elements, because a high amount of relict habitats should reduce the time of conversion considerably (Collinge and Forman, 1998).

Despite the recognised problems of using Ellenberg's indicator values (Ter Braak and Gremmen, 1987) the moisture value of plants produce approximately the same ranking of sites as both invertebrate groups using the numbers of hygrophilous species or individuals (Fig. 2). But in general, it seems that assessment based on vegetation tends to over-emphasise the similarities between the sites. We therefore suggest vegetation monitoring should be seen as a more powerful long-term approach complemented by a time-interrupted (e.g. 3 year intervals) short-term sensitive invertebrate monitoring (e.g. ground-dwelling spiders and beetles). This is especially true at the beginning of the restoration process, when information needed about the success of selected habitat management. Wheater et al. (2000) came to the same conclusions in the context of monitoring reclaimed limestone quarry landforms and Mattoni et al. (2000) argued that because of their high turnover and growth rates arthropods serve as probes that quickly respond to environmental change and are therefore most likely to provide the most convincing monitoring for estimating the success or failure of any given habitat restoration project.

The link between species richness and ecosystem function has been intensively discussed over the past 10 years (Johnson et al., 1996; Peterson et al., 1998). Despite a growing body of literature supporting this linkage and its use in defence of the conservation of biodiversity its importance is still debated (Chapin et al., 1997; Schwartz et al., 2000). At the heart of this debate is the notion that loss of plant and/or animal species: (1) will bring an ecosystem closer to collapse (Schwartz et al., 2000); (2) increase ecosystem vulnerability to invasions by alien species (Knops et al., 1999). In our study the species richness of plants and spiders increases with the degree of low intensity management (Fig. 1a and b). This suggests a higher level of resilience at low intensity managed sites against environmental variability. However, locally detected species richness is not only determined by site-specific attributes, but also by surrounding habitat variability (Duelli, 1997). This is of particular importance for very mobile assemblages (e.g. beetles) and can reduce the value of species richness as a trustworthy community parameter for ecological indication.

When Wagner et al. (2000) studied habitat variability and heterogeneity based on the partitioning of landscape species diversity into additive components and then linked them to patch-specific diversity measurements, they concluded, on the one hand, that landscape composition is apparently a key factor for explaining landscape species richness while, on the other hand landscape composition hardly affects evenness. As second aspect of species diversity (Smith and Wilson, 1996) the evenness provides an useful measure of the degree of resource balancing and partitioning within the assemblages. Wagner et al.'s (2000) findings support the assumption that evenness appears less 'biased' by habitat environment and may therefore be a useful and trustworthy parameter to assess the effects of site-specific changes on assemblages. In our study the Camargo's evenness (E') measure increased with decreasing management impact in all examined groups and highlighted the usefulness of this complex community parameter for ecological indication of land use change in agricultural ecosystems.

5. Conclusions

Overall, plants, spiders and beetles are all suitable as ecological indicators of restoration effects in agricultural landscapes. However, the assemblages show considerable differences in reaction times to changes in land use. Ground-dwelling spiders and beetles mainly respond to changes in the microclimate and the soil-moisture and therefore allow an efficient indication of restoration management after 3–5 years. Vegetation monitoring, on the other hand, appears as a more powerful long-term assessment. The most productive monitoring system would complement the frequently used vegetation monitoring with a sensitive short-term invertebrate monitoring especially at the beginning of agricultural restoration projects.

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5. Manuskript IV

Perner, J., Wytrykush, C., Kahmen, A., Buchmann, N., Egerer, I.,
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Ecography, in press

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Effects of plant diversity, plant productivity and habitat parameters on arthropod abundance in montane European grasslands

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Abstract

Arthropod abundance has been hypothesized to be correlated with plant species richness but the results of previous studies have been equivocal. Other factors, in particular plant productivity, vegetation structure, abiotic site conditions, and the physical disturbance of habitats have been shown to influence arthropod abundance. Therefore, we studied the combined effect of plant species diversity, productivity and site characteristics on arthropod abundance in 71 managed grasslands in central Germany using multivariate statistics. For each site we determined plant cover, plant community biomass (productivity), macro- and micronutrients in the soil, and characterized the location of sites with respect to orographic parameters as well as the current and historic management regimes. Arthropods were sampled using a suction sampler and classified *a priori* into functional groups (FGs). We found that arthropod abundance was not correlated with plant species richness, effective diversity or Camargo's evenness, even when influences of environmental variables were taken into account. In contrast, plant community composition was highly correlated with arthropod abundances. Also, plant community productivity influenced arthropod abundance although explaining only a small proportion of the variance. Abundances of the different arthropod FGs were influenced differentially by agricultural management, soil characteristics, vegetation structure and by interactions between different FGs of arthropods. Herbivores, carnivores and detritivores reacted differently to variation in environmental variables in a manner consistent with their feeding mode. Our results show that in natural grassland systems arthropod abundance is not a simple function of plant species richness, and emphasize the important role of plant community composition for the abundance patterns of the arthropod assemblages.

Introduction

In the current debate about the relationship between biodiversity and ecosystem functioning most studies have focussed on the ecosystem-level consequences (e.g. productivity) of changes in plant diversity (e.g. Tilman et al. 1996, Hector et al. 1999, Loreau et al. 2001, Schmid et al. 2001, Loreau et al. 2002, Schmid 2002). In contrast, diversity effects of higher trophic levels for ecosystem functioning are only beginning to be explored (e.g. Wallace and Webster 1996, McGrady-Steed et al. 1997, Naeem and Li 1997, Cardinale et al. 2002, Wardle 2002). Since producers are ultimately determining the amount of carbon that enters the food web in an ecosystem, any change in plant diversity and biomass will also have consequences for the diversity and abundance of organisms of higher trophic levels, which in turn will feed back to ecosystem functions (Tilman et al. 1996, Loreau et al. 2002, Wardle 2002). Although the effect of plant diversity and productivity on diversity or abundance of herbivores, carnivores and detritivores has been described by a variety of models and hypotheses (Hairston et al. 1960, Pimentel 1961, Root 1973, Rosenzweig 1995), empirical results supporting this relationship are limited.

Arthropods are a dominant component of the herbivore, carnivore and detritivore trophic structure in most terrestrial ecosystems and several hypotheses predict that arthropod abundance should be influenced by plant diversity and productivity. Root (1973) proposed two different hypotheses to account for an observed decrease in arthropod herbivore abundance with increasing plant diversity. Herbivore densities should be lower in more diverse plant communities either because of a lower concentration of the host plants in these communities ('resource concentration hypothesis') or because of a higher diversity and density of predators and parasitoids in more diverse plant communities ('natural enemies hypothesis'). Most of the tests come, however, from agro-ecosystems or silvicultures. In theses systems the range of plant species diversity was usually limited to only a few species and the generality of these hypotheses for natural systems remains unclear (Root 1973, Risch et al. 1983, Andow 1990, Koricheva et al. 2000).

Besides plant diversity, arthropod abundance in an ecosystem has been shown to depend on several other biotic and abiotic parameters. For example, Abrams (1995) has shown that arthropod abundance does not only depend on plant species richness, but also on productivity. Furthermore, a number of studies have shown that fertilisation, which increases productivity, also increases the density of consumers although sometimes no relationship was found (Sedlacek et al. 1988, Kyto et al. 1996, Siemann 1998, Haddad et al. 2000). Additionally, patterns of arthropod abundance have been shown to be greatly affected by physical habitat conditions. For example, plant structural complexity or the height of the vegetation had an affect on arthropod numbers in different agroecosysems (Borges and Brown 2001, Kruess and Tscharntke 2002, Brose 2003). Disturbances, both natural and anthropogenic may decrease arthropod population densities, especially immediately following the disturbance (Völkl et al. 1993, Cagnolo et al. 2002). Generally, characteristics of the physical environment and management practices are important drivers of arthropod abundances and may complicate any effect of plant productivity and diversity on arthropod abundance (Perner et al. 2003).

In this paper we investigated arthropod abundance pattern in 71 grasslands and asked the following questions: (1) How is arthropod abundance related to management and physical conditions of a habitat? (2) Is there a relationship between arthropod abundance and plant diversity or productivity when differences in habitat characteristics and management are accounted for? (3) Do patterns of abundance differ among arthropod functional groups (FGs) of different trophic levels?

Material and methods

Study sites

The study was conducted in the Thüringer Schiefergebirge/Frankenwald, a plateau-like mountain range at the Thuringian/Bavarian border in central Germany which reaches a maximum height of 870 m. The bedrock material in the investigated area produces a carbonate poor, nutrient poor soil. Average annual precipitation is above 1000 mm with a slight summer maximum. Annual average temperature is 5°C. Before human settlement montane spruce-fir-beech forests were the natural vegetation in the area. Since human settlement in the medieval period much of the forest was converted into an agricultural landscape with a high proportion of different types of montane hay meadow grasslands (*Geranio - Trisetetum*, Knapp ex Oberd. 1957) (Hundt, 1964). The 71 grasslands investigated in this study were at least one hectare in size, and only sites with comparable elevation, edaphic and climatic factors were selected. Grasslands had to be uncut by the time of the survey, excluding very intensively managed sites with more than three cuts per year. A more detailed description of the studied plant communities can be found in Kahmen et al. (subm.).

Sampling of environmental, productivity and vegetation data

All samples were collected between May, 28th and June, 9th 2001, coinciding with the typical first seasonal cut of grasslands in this area. All abiotic and vegetation structure parameters were sampled within a 2 m x 2 m quadrat. The following parameters were determined and grouped into four parameter-groups for statistical analyses (see Kahmen et al. subm. for a full description of how these variables were obtained):

Parameter-group I: soil properties, site characteristics and management parameters

The following edaphic parameters were determined: soil moisture (%vol.; mean: 27.9±7.30%), top soil pH (pH; mean: 5.5±0.55), total concentrations of soil nitrogen (N_{total}; mean: 4.1±0.65

mg/g), soil carbon (C_{total}; mean: 49.5±10.84 mg/g), the carbon-nitrogen ratio (C:N; mean: 14.0±1.84), extractable phosphorus (P_{total}; mean: 0.04±0.07 mg/g), and extractable ion concentrations of potassium (K^+; mean: 0.05±0.05 mg/g), calcium (Ca^{2+}; mean: 1.2±0.69 mg/g), magnesium (Mg^{2+}; mean: 0.23±0.14 mg/g), and sulfate (SO_4^{2-}; mean: 0.03±0.01 mg/g), as well as the amount of mineral nitrogen (N_{min}; mean: 3.0±2.93 g/mg).

To characterize the sites, geographic position (GPS coordinates), altitude (range: 499-841 m above sea level), exposition (range: pure North to pure South) and inclination (range: 0-20°C) were determined. Based on exposition and inclination, we calculated mean potential direct solar insolation (PDSI; range: 2.7-3.2 kJ $cm^{-2}d^{-1}$; Homann, Schumacher and Perner, unpublished software program, algorithm based on Volz 1959). Furthermore, we determined the distance to the nearest woodland habitat (wood-distance; range: 15-188 m) to account for potential woodland edge effects.

To determine site management regimes in 2001 (current management) and the past 10 years (historic management) each farmer was interviewed using a standardized questionnaire. These survey data were coded to obtain numerical data. The recent as well as the historical cutting regime were coded using a combination of the date and the frequency of cutting. The code replacement of the recent as well as historical grazing regime is based on the number of livestock per hectare and the frequency and timing of grazing events. To numerically describe the fertilization status the average amount of artificial fertilizers and/or manure applied as well as the grazing intensity were considered (for details of the coding procedure see Kahmen et al. subm.).

Parameter-group II: vegetation structure

To assess vegetation structure, the following variables were measured: total plant cover (mean: 96.5±4.46%), plant height (mean: 0.9±0.19 m), leaf area index (LAI; mean: 5.2±1.63), percent cover and height separately for tall-grasses (mean: 40.3±29.57% / 0.78±0.45 m), short-grasses (mean: 40.4±35.66% / 0.36±0.30 m), forbs (mean: 70.0±20.37% / 0.81±0.23 m) and mosses (mean: 46.4±30.64% / 0.03±0.02 m).

Parameter-group III: plant productivity, diversity and composition

All plant species within the quadrat were identified and percent cover of each species was estimated. To determine aboveground plant community productivity, four sub-samples of 20 cm x 50 cm were taken. Plant material was cut 2 cm above the ground dried at 60°C and weighed.

Arthropod sampling

The arthropods were collected in an area immediately adjacent to the 2 m x 2 m plots. A round mesh cage (basal area: 0.5 m^2) was placed over the vegetation and arthropods were collected using a Uni-Vac suction sampler. A pilot study in similar grasslands had shown that the number of invertebrates caught saturated after about 15 minutes (Wytrykush, unpublished data). Therefore two separate 20 minute samples were taken at each site.

Arthropods were assigned to different functional groups (FGs) based on equivalent functional roles in communities (Blondel 2003). Because for the vast majority of arthropod species there is not sufficient functional information available for a numerically supported classification scheme, we followed an *a priori* classification approach used by Voigt et al. (2003) and Perner et al. (2003) in our study. Thus, the FGs are mainly based on feeding traits (functional feeding groups), and not exclusively on taxonomic membership (Table 1). Consequently, for some groups (e.g. Heteroptera, Diptera, Coleoptera) different species of the same taxon that are members of different trophic levels are allocated to different FGs. Although defining FGs in such a way is not a perfect approach we think it is an efficient and useful step forward to relate diversity and ecosystem function (Bengtsson 1998, Tilman 2001).

Assignment to a FG was mainly based on the order- or suborder-level. Where necessary, specimens were identified to family- or species-level to determine their FG affiliation (e.g. adult Coleoptera, Diptera, Hymenoptera). For taxa where shifts between trophic levels occur during development, classification is based on the feeding strategy of the immature stages; these are the most important life stages when considering abundance and biomass. Only taxa with more than 50 sampled individuals (in total) were included in the analyses (Table 1).

Statistical analysis

Data analysis proceeded in five steps. In the first three steps, the dependent and independent data were transformed as necessary, diversity indices were calculated and data were condensed for further analysis using a number of techniques . The relationship between environmental parameters and arthropod abundances of the different functional groups was then calculated using multivariate (step 4) and univariate (step 5) models.

Plant and insect data were transformed in a first step for consecutive statistical analyses. While, plant species cover data were square-root transformed for analysis, arthropod data (average of sample 1 and sample 2) were standardized (z_i = [y_i - mean of y] / s_y; see Legendre and Legendre 1998) for multivariate analyses and log-transformed for univariate regression analyses. Variables describing edaphic parameters, site characteristics, vegetation structure as well as plant productivity, species richness and species composition were entered as numeric variables into the analyses described below.

In a second step, the variables of parameter-groups I and II were standardized and condensed using principal component analysis (PCA; CANOCO, ter Braak and Smilauer 2002) so that the scores of the resulting PCA axes could be used as new independent variables in consecutive multivariate analyses. PCA reduces the total number of variables and ensures orthogonality of variables (e.g. Legendre and Legendre 1998). Four separate PCAs were performed for the soil-, management- and site parameters (parameter-group I) and vegetation structure (parameter-group II). From each PCA, the first four axes (explaining most of the variance) were extracted resulting in the new PCA-derived variables, in the following used as independent parameters. Very little information was lost by this procedure since the extracted axes explained most of total variance contained in the original parameter-groups.

In a third step, we computed various diversity measures from the plant cover data (parameter-group III). In particular, we calculated plant species richness (PSR), effective diversity (N_1; also called heterogeneity or exponential Shannon-Wiener), and Camargo's evenness (E') for each site (calculation algorithms see Krebs 1999). To analyse the compositional differences among plant communities of the 71 studied grassland sites we performed non-metric multidimensional scaling (NMDS) ordination techniques (Clarke 1993) with the square-root-transformed quantitative plant data using PC-ORD (McCune and Mefford 1997). NMDS is an iterative search for a ranking and placement of n entities (samples) in k dimensions (ordination axes) that minimizes the stress of the k-dimensional configuration. The 'stress'-value is a measure of departure from monotonicity in the relationship between the dissimilarity (distance) in the original p-dimensional space and distance in the reduced k-dimensional ordination space (Clarke 1993). As a distance measure we used the Bray-Curtis coefficient (also known as Sørensen or Czekanowski coefficient), which is one of the most robust measures for this purpose (Faith et al. 1987). In our analysis of the plant data set two ordination axes (dimensions; NMDS1, NMDS2) were sufficient to achieve low stress values so that the scores of these two axes were used in consecutive analysis as numerical values for community composition.

In a fourth step, we tested if the abundance of arthropods within a FG depends on the variables of the three parameter-groups listed above (parameter-groups I-III) using multivariate statistics. The standardized abundances of FGs were analysed separately for each trophic level to account for different responses to the independent variables (parameter-groups) between herbivores, carnivores and detritivores. Because preliminary examinations showed that linear models are more appropriate for the data than unimodal models (for details see Jongman et al. 1995, ter Braak and Smilauer 2002) redundancy analyses (RDAs) were used. In these analyses, we also included the abundances within those FGs as independent variables which we *a priori* expected to influence the abundances of the target trophic layer (in the following referred to parameter-group IV). Thus, for the analysis of herbivore and detritivore abundances, we included carnivore abundances, and for the analysis of carnivore abundances we used herbivore and detritivore abundances as independent variables. RDA is a canonical extension of PCA that uses, instead of the original values, the fitted values of a multiple linear regression of species data (here abundance data within FGs) on the explanatory variables (here variables of parameter-groups I-IV). Only statistically significant explanatory variables (tested with Monte-Carlo permutation procedures) were included into the model. The results of the individual RDAs give the percentages of variance of the abundances within a FG of a particular trophic level that are explained by the variables of a particular parameter-group. To decompose the variance of the response matrix (abundances within FGs) explained by the different parameter-groups, we used a method proposed by Borcard et al. (1992, see also Legendre and Legendre 1998). Partial RDAs (pRDA) were carried out in which variables of one parameter-group significant in standard RDA were included as explanatory variables in a new pRDA model that also included the significant variables of the remaining parameter-groups as co-variables. This procedure of variance partitioning allows disentanglement of the variance explained exclusively by the variables of the tested parameter-group ('pure' fraction of variance) from the variance which is explained by the variables of the remaining parameter-groups (shared fraction of variance or ‘variance overlap’). In a final analysis, all significant variables (parameter-group I-IV) were included in a single RDA to determine the total variance explained by these variables.

In a fifth step, we used simple and multiple linear regressions to directly test for correlations between the explanatory variables plant diversity, plant species composition, and plant productivity and abundances within FGs. While this method partly replicates some of the results of the multivariate analyses, it allows one to directly test the dependence of arthropod abundances on plant diversity and productivity.

Results

Data base

Altogether 26,929 arthropods of 15 functional groups (FGs) were sampled in the 71 studied grasslands (Table 1). The number of individuals collected for each FG in the first sample at each site closely matched the number of individuals in the second sample (Table 2). The detritus grazers (DGR, Collembola) as well as the vascular suckers (HVS, Auchenorrhyncha) and colonial suckers (HCS, Aphidina) were by far the most abundant FGs (Table 1), followed by the detritus biting suckers (DBS, Diptera) and the parasitoid wasps (CPW, Hymenoptera).

For parameter-group I we performed three separate principal component analyses (PCA) for the soil, site characteristics and management variables, to extract uncorrelated variables which were used for further analysis. In the first PCA of parameter-group I based on the edaphic parameters the first four axes (soil1 - soil4) explained 76% of the whole variance in data. In a second PCA on the variables describing site characteristics the first four axes (site1 – site4) explained 100% of the variance. In a third PCA on management variables the first four axes (manage1 - manage4) were extracted for further analysis and explained in total 98% of the variance (for detailed results see Appendix 1). For parameter-group II, a single PCA on the vegetation structure parameters resulted in an explained variance along the first four axes (vegstru1 - vegstru4) of 79% (Appendix 1). Thus, very little of the information contained in parameter-groups I and II was lost by the PCA based data reduction because the extracted PCA-axes explained nearly all of the total variance.

In parameter-group III, we calculated five variables describing plant diversity and community composition for further analyses. In the 71 sites, mean plant richness was 20 species (range: 8 - 33), effective diversity (N_1) averaged at 11.4 ± 3.6 (range: 4.3 – 19.4), and mean Camargo's evenness (E') of 0.43 ± 0.1 (range: 0.28 – 0.54) was found. Mean above-ground plant dry-biomass (productivity) was 358 g m^{-2} ± 109 (range: 125 g m^{-2} - 610 g m^{-2}). Plant species richness was not correlated with productivity ($r = 0.11$, $p = 0.34$, $N=71$). Similarly, N_1 ($r = 0.15$, $p = 0.20$, $N = 71$), and E' ($r = 0.07$, $p = 0.55$, $N = 71$) were not correlated with productivity. The non-metric multidimensional scaling (NMDS) analysis of the plant cover data showed that a two dimensional solution was sufficient to achieve low stress values (1st axis/dimension = 23.3, 2nd axis/dimension = 16.1, $r^2 = 0.73$). For further analyses we therefore used the scores of the first two axes as plant community parameters (following called NMDS1 and NMDS2) which contain condensed information about the plant community composition based on plant cover.

Multivariate analysis of arthropod abundance patterns

The results of the RDAs analysing the arthropods' FG-abundances separately for the herbivore, carnivore and detritivore trophic level are shown in Table 3. The columns 'pure variance explained' and 'variance overlap' in Table 3 give the results of the separate pRDAs where the significant variables of one parameter-group were included as explanatory variables and the significant variables of the remaining parameter-groups were included as co-variables.

Herbivores: One soil variable ('soil1'), three vegetation structure parameters ('vegstru1', 'vegstru3', 'vegstru4') and one variable describing plant community composition ('NMDS2') were significantly correlated with the abundances of herbivores (Table 3). Furthermore the log-abundances of four carnivore FGs were correlated with the FG-abundances of herbivores. In total 27.6% of the variance were explained by all these variables and the variance overlap was only 3.2% (Table 3). However, Fig. 1a illustrates that the relationship between the abundances within the herbivore FGs and the selected predictor variables was variable. While the colonial suckers (HCS, Aphidina) and the mining flies (HMI, Diptera) were correlated more closely with vegetation structure (positive with vegstru3 and vegstru4; negative with vegstru1) and the (log) abundances within two carnivore FGs (CPW, parasitoid Hymenoptera; CWS, Araneae) the plant chewers (HCW, Coleoptera) and vascular suckers (HVS, Auchenorrhyncha) were more closely correlated to the variables NMDS2 and soil1 (HCW: positive; HVS: negative) and to the (log) abundances of two other carnivore FGs (CSH, Heteroptera; CCH, Coleoptera).

Carnivores: All together, 22.2% of the variance in the abundances of the carnivore FGs was explained by the selected predictor variables (Table 3). In addition to the parameters 'soil1', 'vegstru1' and 'NMDS2' which were also significantly correlated with herbivore abundances, some additional variables were significantly related to FG-abundances of carnivores, in particular a soil parameter ('soil2'), a vegetation structure parameter ('vegstru2') and the (log) abundances of one detritivore FG (DBS, Diptera) and two herbivore FGs (HMI, Diptera; HTS, Heteroptera). As in the case of the herbivores a low variance overlap of 5.0% was detected, highlighting the low correlation level of the selected parameters and the multifactorial caused variance pattern of the arthropod FGs. This pattern is presented in Fig. 1b showing the detailed correlation structures between the carnivore groups and the significant explanatory variables. The abundances of biting suckers (CBS, Diptera), parasitoid wasps (CPW, Hymenoptera), webspinners (CWS, Araneae) and parasitoid flies (CPA, Diptera) were all highly correlated to the soil parameter 'soil2' and to the (log) abundances of the abundances of the herbivore FGs HMI (Diptera) and HTS (Heteroptera). Three carnivore FGs (CCH, Coleoptera; CSH, Heteroptera; CHG, Formicidae) were highly correlated with 'soil1' (CCH: positive correlation, CSH, CHG negative correlation), the vegetation structure parameter 'vegstru2' (CCH: negative correlation) and the plant community composition 'NMDS2' (CCH: positive correlation, CSH, CHG: negative correlation).

Detritivores: The variance patterns of the three analysed detritivore FGs were significantly correlated with two soil variables ('soil1', 'soil2'), two management variables ('manage1', 'manage2') and one vegetation structure parameter ('vegstru2'), as well as with plant community composition ('NMDS2'), plant evenness (E'), and with the abundance of chewing hunters (CCH, Coleoptera). In total 38.7% of the variance was explained by these selected explanatory variables. In contrast to the results of the herbivores and carnivores, a high variance overlap of 14.6% was detected which is caused by the high correlation of the plant evenness (E') and the management (manage1 and 2) parameters. This pattern is also deducible from Fig. 1c. Furthermore this figure illustrates the strong relation of all three detritivorous FGs to the variables 'NMDS2' and 'soil1'.

Univariate correlation and regression analysis of arthropod abundances

Arthropod abundance and plant community productivity: Total arthropod abundance (summed over all FGs) was weakly (but significantly) correlated with plant productivity ($r^2 = 0.06$, $p = 0.04$, $N = 71$; Fig. 2a). If correlations are performed for each FG separately, only the abundances of mining flies (HMI, Diptera), parasitoid wasps (CPW, Hymenotera) and detritus biting suckers (DBS, Diptera) were positively correlated with productivity (Fig. 3a-c; Table 4). The abundances of all other FGs were not correlated with productivity.

Arthropod abundance and plant diversity: Total arthropod abundance was not correlated with plant species richness (PSR) ($r^2 < 0.01$, $p = 0.998$, $N = 71$; Fig. 2b). When FGs were analysed separately, none of the FGs were significantly correlated with PSR (Table 4). The effective diversity was significantly positively correlated with the abundances of parasitoid wasps (CPW, Hymenoptera) and detritus grazers (DGR, Collembola) and Camargo's evenness were positively correlated with the abundances of five FGs (Fig. 3d-f; Table 4). However, after Bonferroni corrections the only remaining significant correlations were between detritus biting suckers (DBS, Diptera) and effective diversity, and between the abundance of detritus grazers (DGR, Collembola) and Camargo's evenness. Thus, in our study, the commonly used measures of plant diversity were generally not correlated with arthropod abundances.

Arthropod abundance and plant community composition: NMDS2 was significantly correlated both with total arthropod abundance ($r^2 = 0.12$, $p = 0.03$, $N = 71$; Fig. 2c) as well as with the abundances of 10 of the 15 FGs analysed (Fig. 4a-f). After Bonferroni corrections, five of these correlations remained significant (Table 4). Although NMDS2 and productivity are significantly correlated ($r^2 = 0.30$, $p < 0.001$, $N = 71$), NMDS2 was a better predictor for FG-abundances than productivity, and in all but one case explained a higher percentage of the variance in arthropod abundances (Table 4). Thus, plant community composition but not species richness or diversity was significantly correlated with the abundances of major arthropod FGs.

Correlations when plant community productivity and community composition are controlled for: To analyse the relationship between plant diversity and arthropod abundances independent of plant community composition (NMDS2) and productivity, both variables were controlled for in separate partial linear regressions. When NMDS2 was controlled for, arthropod abundance within FGs was not significantly related to any of the plant diversity measures (PSR, N_1, E'), with the exception of a significant relationship between detritus grazers (DGR, Collembola) and Camargo's evenness (E'; $r^2 = 0.12$, $p = 0.003$). Also, the relationships between arthropod abundance within FGs and productivity were no longer significant, when NMDS was controlled for. If productivity was used as a control-variable (Table 4), detritus grazers (DGR, Collembola: $r^2 = 0.06$, $p < 0.05$) was significantly correlated with effective diversity (N_1) and plant chewers (HCW, Coleoptera: $r^2 = 0.07$, $p < 0.03$), chewing hunters (CCH, Coleoptera: $r^2 = 0.06$, $p < 0.04$), detritus biting suckers (DBS, Diptera: $r^2 = 0.21$, $p < 0.001$) and detritus grazers (DGR, Collembola: $r^2 = 0.27$, $p < 0.001$) were significantly related to Camargo's evenness (E'). However, the only significant correlations after Bonferroni corrections were between DBS as well as DGR and E'. In contrast, when productivity was controlled for, the abundances of eight FGs were still significantly related to NMDS2 and three of these remained significantly after Bonferoni adjustment (Table 4). Finally, when both plant community composition (NMDS2) and productivity are controlled for in partial multiple regressions, no significant relations existed between arthropod abundances and plant diversity measures, for any of the FGs analysed.

Discussion

It is well-known that plant species identity strongly influences which insects occur in a particular site, and that the abundance of a particular plant species will affect the abundances of the insects depending on it (Price 1997). However, if plant diversity has, as proposed, an overriding effect on arthropod, and in particular insect abundance (Pimentel 1961, Root 1973), it should be possible to detect the signature of these plant diversity effects also in a field study, especially if confounding variables are controlled for. This we did not find. In fact, there was no evidence that plant diversity, expressed in any of the commonly used indices of diversity, influenced arthropod abundances. However, we did find a measurable influence of plant productivity and in particular plant community composition on arthropod abundances within different functional groups (FGs). Thus, it is tempting to conclude that simple measures of diversity are insufficient descriptions of those vegetation characteristics that are relevant for arthropod abundances. This finding corresponds to the conclusions of some other recent studies in artificially assembled plant communities (e.g. Siemann et al. 1998, Koricheva et al. 2000). In this respect it is interesting to note that the vast majority of studies that found significant effects of plant species richness on arthropod abundances, were strongly influenced by diversity gradients that always included monocultures and mixtures of only two or very few species, conditions rarely found in natural systems (Pimentel 1961, Lee and Wood 1971, Root 1973, Risch et al. 1983, Andow 1990, but see Siemann 1998).

To describe plant community composition we used information on plant species occurrence and abundance (cover) which was condensed using non-metric multidimensional scaling (NMDS) analysis. The scores of ordination axis 2 (NMDS2) were significant predictors of the abundance patterns within most arthropod FGs at all trophic levels (herbivores, carnivores, detritivores). The scores of NMDS2 correspond to gradual changes in plant community composition from less productive but species richer grasslands (*Geranio-Trisetetum nardetosum*) to more productive, generally species-poorer grasslands (*Geranio-Trisetetum alopecurosum*) (see Kahmen et al. 2004). The fact that plant community composition significantly correlates with arthropod abundances while plant species diversity does not implies that in the montane grasslands the presence of particular plant species and combinations of species is more important for the occurrences and population sizes of arthropods then the mere number of different resources available. While this result may not be entirely surprising given that many invertebrate species are resource specialists, the strong correlation between arthropod abundances and plant community composition is striking. To more fully understand the mechanisms underlying this relationship requires a detailed analysis of the different species traits, which was beyond the scope of the current paper. Among the detritivores, all FGs increased in abundance with increasing

NMDS2 scores (Fig. 4c, f). In contrast, the herbivore and carnivore FGs showed a mixed response. While the abundances of mining flies (HMI, Diptera), plant chewers and chewing hunters (HCW, CCH, Coleoptera), and parasitoid wasps (CPW, Hymenoptera) were positively related to the NMDS2 parameter, the abundances of vascular suckers (HVS, Auchenorrhyncha), social hunter-gatherers (CHG, Formicidae) and sucking hunters (CSH, Heteroptera) were negatively related to NMDS2 (Fig. 4a, b, d, e; Table 4). Such differing response patterns within the same trophic level have already been observed in other empirical studies (Cagnolo et al. 2002, Perner et al. 2003). For example, the vascular suckers (HVS, Auchenorrhyncha) are a strongly grass-associated group (Tscharntke and Greiler 1995) which is reflected in part in the detected NMDS2 - gradient.

A second main result of our study was that in the semi-natural grasslands above-ground plant productivity was only weakly related to arthropod abundances. Significant influences of productivity on arthropod abundances have been observed in earlier studies (e.g. Sedlacek et al. 1988, Siemann 1998, Haddad et al. 2000, Koricheva et al. 2000). However, these studies differed in the ways in which productivity was manipulated, with important consequences for the interpretation of the results. If plant productivity is manipulated by the application of fertilisers, than the short-term response is an increase of productivity with a concomitant change in plant nutritional value and vegetation structure, but no change in plant species composition (e.g. Kytö et al. 1996, Siemann 1988, Sedlacek et al. 1988). In contrast, the longer-term response to fertilisation is a change in plant species composition with a concomitant change in plant productivity (e.g. Siemann 1988, Haddad et al. 2000). Finally, in experiments where plant species richness is manipulated, increased productivity is often the result of increasing species richness, without changes in the fertilisation status of the sites (e.g. Koricheva et al. 2000, Joshi et al. 2004). Thus, to understand why arthropod abundance depends on plant productivity, it is necessary to consider the covariation of other factors with productivity. In our study we measured in all sites, in addition to plant productivity, a number of parameters such as plant available soil nutrients the physical structure of the vegetation and the management regime. These parameters, along with the interactions between the different trophic levels, explained between 22% and 39% of the variance in the abundances of the different arthropod FGs when tested in a RDA (Fig. 1). The edaphic parameter ‘soil1’, which was significantly related to the abundances of FGs in all trophic levels investigated (Table 3), was mainly correlated with pH, the concentrations of SO_4^{2-}, Ca^{2+}, Mg^{2+}, N_{min} and soil-moisture and is hence related to the fertility status of the soil (Appendix 1). However, in our analysis only the detritivore FGs responded uniformly to the fertility status of sites and increased with increasing values of ‘soil1’ (Fig. 1c), the responses among the herbivore and carnivore FGs, however, were inconsistent (Figs 1a, b). Because ‘soil1’ is correlated with plant community composition and with plant productivity, but not with nutrient content in the plants (Kahmen et al. 2004), the likely scenario is that the main effect of 'soil1' is to affect arthropod abundances through its effect on plant community composition which itself influences productivity. In fact, in our study, the influence of productivity on arthropod abundances disappeared when plant community composition was controlled for in multiple regressions.

In addition to soil fertility status, productivity and plant community composition, a number of other variables did significantly influence the abundances of the different arthropod FGs, in particular grassland management, vegetation structure, and the abundances of other FGs (Table 3). For grasslands, it has been repeatedly shown that the management regime affects the assemblage structures of arthropods (e.g. Cagnolo et al. 2002, Kruess and Tscharntke 2002, Perner and Malt 2003). In the extreme case, frequent mowing may not allow insects to complete their life-cycle and results in very low species numbers and abundances. However, in our grassland study only the detritivore FGs were significantly correlated with the management regime of sites (Table 3). A likely reason is that in the montane grasslands investigated, management was never extremely intensive with more than three cuts per year or permanent high stocking densities of cattle. In addition, management was correlated with plant community composition (Kahmen et al. 2004), and with soil fertility status (e.g. the correlation between 'soil1' and the management parameters in Fig. 1c), resulting for example in a rejection of management variables in the statistical analysis when, the soil fertility status was already selected as a significant variable (RDA, Table 3). Furthermore, vegetation structure explained between 7% (carnivores) and 10% (herbivores, detritivores) of the variances in FG-abundances (variable 'vegstru', Table 3). Such vegetation structure effects on arthropod abundances have been identified for herbivores, detritivores and carnivores in a number of studies (Lagerlof and Wallin 1993, Dennis et al. 1998, Borges and Brown 2001, Kruess and Tscharntke 2002, Brose 2003). Proximate mechanisms include changes in microclimate and microhabitat coupled with changes in the 3-dimensional arrangement of the plants (Andow and Prokrym 1990, Fahrig and Jonsen 1998). Finally, differing response pattern among the herbivore and carnivore FGs result in low explanatory power when these groups were analysed together with multivariate statistics (RDA; Table 3). For example, sucking herbivores such as the mainly grass-feeding Auchenorrhyncha (HVS) are generally more sensitive to cutting and grazing than chewing herbivores (e.g. HCW; Tscharntke and Greiler 1995).

The fact that a relatively large proportion of the variance in arthropod abundances was explained by interactions with other arthropod FGs (parameter-group IV, Table 3, Fig. 1), is interesting. In our analyses, we included as independent variables only the abundances of those FGs which we *a priori* expected to influence the abundances of a target trophic layer (i.e. predator-prey interactions). Such effects on other trophic layers are expected by theory (e.g. Hassell 2000) yet it is striking to see that these correlations are so strong in our analyses. Herbivore abundances were significantly affected by all carnivore groups except by biting suckers (CBS, Diptera), social hunter-gatherers (CHG, Formicidae) and parasitoid flies (CPA, Brachycera). A possible reason for the non-significance of these FGs may again be the fact that in redundancy analysis (RDA) multicollinearities are prevented and only those variables of a cluster of closely correlated variables are selected which explain most of the variance. The strong correlations between biting suckers (CBS, Diptera) and parasitoid wasps (CPW, Hymenoptera) on the one hand and on the other hand parasitoid flies (CPA, Diptera) and web-spinners and hunters (CWS, Araneae) may illustrate this point (see Fig. 1b). For detritivore abundances, the only FG with significant relationships were chewing hunters (CCH, Coleoptera; Table 3), consistent with the expectation that top-down effects should be stronger for herbivores than for detritivores. Finally, for carnivores, both one detritivore FGs and two herbivore FGs were significantly correlated with their abundances. Taken together, the inclusion of interactions between trophic levels into the analysis greatly improved the fit of the abundance models.

Our arthropod abundance data were obtained during a very short period in the year and each field site was investigated only once. They therefore represent a 'snapshot' of what is happening in the communities and are not comprehensive descriptions of these grasslands. It is well known that longer sampling periods and a higher number of replications within each site increase the precision of sampled arthropod data (e.g. Duelli 1997, Perner 2003). Nevertheless, because all grassland sites were visited during the same period of the season and were sampled using the same standardized method, the data are comparable among sites and yield a fair description of the relative abundances of the different FGs at this time of the season in the study area. The close correspondence between the abundances in the first and second sample (Table 2) also suggests sampling was representative for all sites at that time.

In our study we aimed to gain a deeper insight into the importance of plant diversity for arthropod abundance in natural systems by (1) sampling arthropods from a large number of grassland sites, (2) separating arthropods into different functional groups (FGs) and (3) by simultaneously measuring plant diversity and productivity as well as a number of environmental variables that may also affect arthropod abundance. Our results show that arthropod abundances are influenced by a variety of factors including the interactions between different trophic levels, which are consistent with a number of earlier works. In contrast, we found no support for the ‘resource concentration’ or the ‘natural enemy hypothesis’, i.e. there were no simple correlations between plant species diversity and arthropod abundances. It therefore appears that instead of searching for conditions under which there are correlations between arthropod abundance and simple measures of plant diversity, it may be more fruitful to identify descriptions of plant communities and their environment that allow for predictions of arthropod abundances under field conditions.

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Table 1. Description of used functional groups (FGs) and numbers of individuals sampled in the 71 grassland sites. Only taxa with > 50 individuals were considered.

[1] includes also the tissue sucking species of the Typhlocybinae; [2] in addition to hunting species also carrion-feeding, honey dew and plant seed eating species included; [3] this group contains species which colonize and feed either on pure detritus or on organisms fixed to detritus (bacteria, algae or fungi)

Abbrev. of FG	Describtion/ functional feeding traits	Taxonomic group	No. of individuals
Herbivores			
HCS	colonial suckers	Aphidina	3252
HCW	plant chewers	Coleoptera	268
HMI	mining flies	Diptera (Brachycera+Nematocera)	478
HTS	cell-tissue suckers	Heteroptera	356
HVS	(mainly) vascular suckers[1]	Auchenorrhyncha	3706
Carnivores			
CBS	biting suckers	Diptera (Brachycera)	397
CCH	chewing hunters	Coleoptera	224
CHG	social hunter-gatherers[2]	Formicidae	325
CPA	parasitoids (flies)	Diptera (Brachycera)	98
CPW	parasitoids (wasps)	Hymenoptera	1395
CSH	sucking hunters	Heteroptera	59
CWS	web-spinners and hunters	Araneae	1028
Detritivores			
DBS	detritus biting suckers	Diptera (Brachycera+Nematocera)	1769
DGR	detritus grazers[3]	Collembola	13504
DCW	detritus chewers	Coleoptera	70

Table 2. Means and standard errors of the number of individuals in each arthropod functional group (FG), collected with the suction sampler in the 71 field sites. The second sample was taken immediately after the first sample. See text for explanations. * indicate significant differences between both samples (t-test; $p < 0.05$).

FG	Sample 1	Sample 2
HCS	25.75 ± 5.62	23.41 ± 3.55
HCW	2.04 ± 0.20	1.79 ± 0.32
HMI	3.45 ± 0.40	3.38 ± 0.45
HTS	2.63 ± 0.41	2.45 ± 0.44
HVS	29.71 ± 5.14	23.23 ± 4.43
CBS	3.10 ± 0.65	2.57 ± 0.41
CCH	1.67 ± 0.28	1.53 ± 0.26
CHG	3.41 ± 1.30	1.20 ± 0.46
CPA	0.68 ± 0.12	0.72 ± 0.11
CPW	10.61 ± 1.07	9.30 ± 0.91
CSH	0.37 ± 0.09	0.46 ± 0.12
CWS *	8.30 ± 0.82	6.39 ± 0.64
DBS	12.54 ± 1.56	12.74 ± 1.50
DGR	105.20 ± 12.93	87.71 ± 10.27
DCW	0.53 ± 0.09	0.47 ± 0.12

Table 3. Results of variance partitioning for the different trophic levels between the four examined parameter-groups using redundancy (RDA) and partial redundancy analyses (pRDA). For explanations of the used significant parameters see Material and methods section as well as Appendix 1.

Parameter-group (PG)	Significant variables	Variance explained (%)	Pure variance explained (%)	Variance overlap (%)
	Herbivores			
PG I	soil1	3.6	2.1	1.5
PG II	vegstru1, vegstru3, vegstru4	10.2	6.1	4.1
PG III	NMDS2	7.0	5.7	1.3
PG IV	logCPW, logCSH, logCCH, logCWS	17.0	10.5	6.5
all significant parameters together		**27.6**	**24.4**	**3.2**
	Carnivores			
PG I	soil1, soil2	8.9	2.8	6.1
PG II	vegstru2, vegstru1	7.0	3.8	3.2
PG III	NMDS2	5.4	1.0	4.4
PG IV	logDBS, logHMI, logHTS	14.1	9.6	4.5
all significant parameters together		**22.2**	**17.2**	**5.0**
	Detritivores			
PG I	soil1, manage2, manage1, soil2	29.3	10.5	18.8
PG II	vegstru2	10.1	0.7	9.4
PG III	NMDS2, evenness (E')	27.9	8.9	19.0
PG IV	logCCH	10.3	4.0	6.3
all significant parameters together		**38.7**	**24.1**	**14.6**

Table 4. Correlations of log-transformed abundances of functional groups (FGs) with plant productivity, plant species richness and various measures of diversity as well as plant community composition (NMDS2). Significant correlations ($p < 0.05$) are shown in bold. After Bonferroni corrections, only correlations with $p < 0.05/15 = 0.0033$ are significant (marked with *).

[1] Correlations of FG abundances and the plant community composition (NMDS2) after controlling the effects of plant productivity.

	Plant productivity		**Plant species richness (PSR)**		**Effective diversity (N_1)**		**Camargo's evenness (E')**		**NMDS2**		**NMDS2 [1]**	
FG	r^2	p	r^2	p	r^2	p	r^2	p	r^2	p	r^2	p
HCS	<0.01	n.s.	0.01	n.s.	0.03	n.s.	0.03	n.s.	<0.01	n.s.	<0.01	n.s.
HCW	0.02	n.s.	0.04	0.08	<0.01	n.s.	0.08	**0.02**	0.1	**0.007**	0.06	**0.04**
HMI	0.11	**0.005**	0.02	n.s.	0.04	0.09	0.04	n.s.	0.11	**0.005**	0.11	**0.005**
HTS	<0.01	n.s.	0.02	n.s.	0.01	n.s.	<0.01	n.s.	0.01	n.s.	0.01	n.s.
HVS	0.02	n.s.	<0.01	n.s.	<0.01	n.s.	<0.01	n.s.	(-) 0.13	***0.002**	0.13	***0.002**
CBS	<0.01	n.s.	<0.01	n.s.	<0.01	n.s.	<0.01	n.s.	<0.01	n.s.	<0.01	n.s.
CCH	0.03	n.s.	<0.01	n.s.	<0.01	n.s.	0.06	**0.03**	0.12	***0.003**	0.06	**0.03**
CHG	<0.01	n.s.	0.01	n.s.	0.02	n.s.	0.03	n.s.	(-) 0.09	**0.01**	0.09	**0.01**
CPA	0.01	n.s.	<0.01	n.s.	<0.01	n.s.	0.05	**0.05**	<0.01	n.s.	<0.01	n.s.
CPW	0.11	**0.004**	0.02	n.s.	0.06	**0.05**	0.04	0.08	0.08	**0.02**	<0.01	n.s.
CSH	0.04	n.s.	<0.01	n.s.	<0.01	n.s.	0.02	n.s.	(-) 0.09	**0.01**	0.04	0.1
CWS	0.01	n.s.	<0.01	n.s.	<0.01	n.s.	0.02	n.s.	<0.01	n.s.	0.01	n.s.
DBS	0.23	***<0.001**	<0.01	n.s.	0.05	0.06	0.19	***0.002**	0.46	***<0.001**	0.22	***<0.001**
DCW	0.05	0.07	<0.01	n.s.	<0.01	n.s.	0.04	0.09	0.14	***0.001**	0.07	**0.03**
DGR	0.05	n.s.	<0.01	n.s.	0.07	**0.03**	0.27	***<0.001**	0.23	***<0.001**	0.13	***0.002**

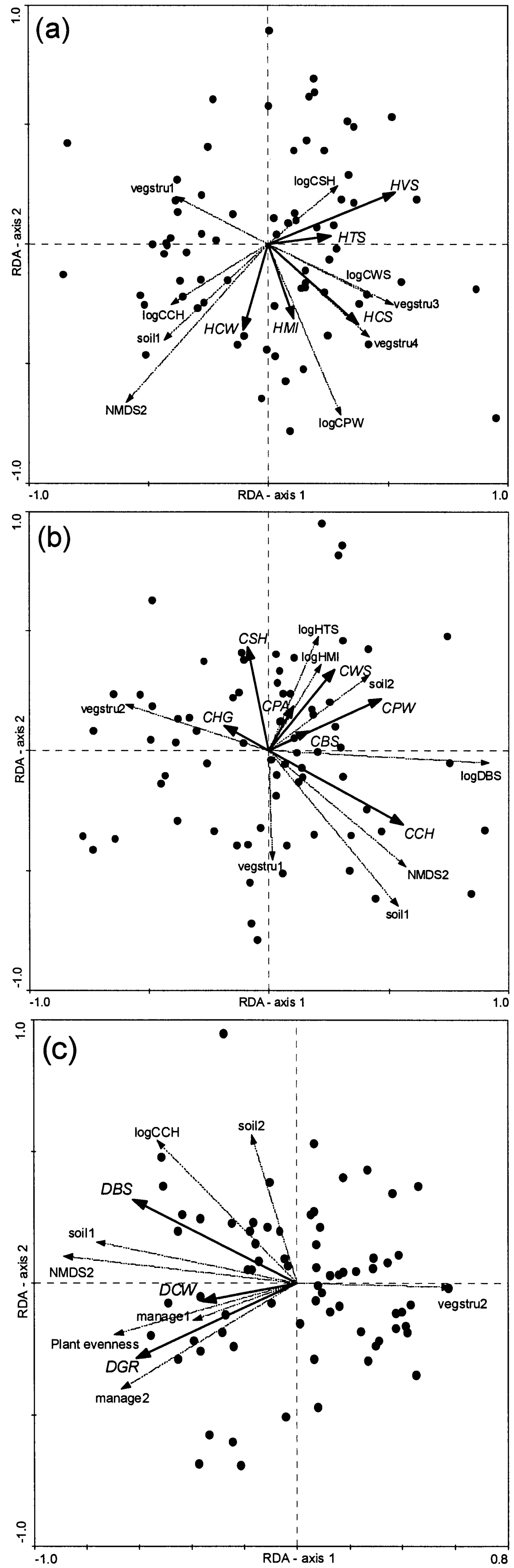

Fig. 1. Ordination diagram of redundancy analyses (RDA) with sites (points), abundances of functional groups (FGs; arrows) and significantly related site parameters (compare with Table 3; dotted arrows) for the different trophic levels: herbivores (a), carnivores (b) and detritivores (c). For the used abbreviations see Table 1, Appendix 1 and the Material and methods section.

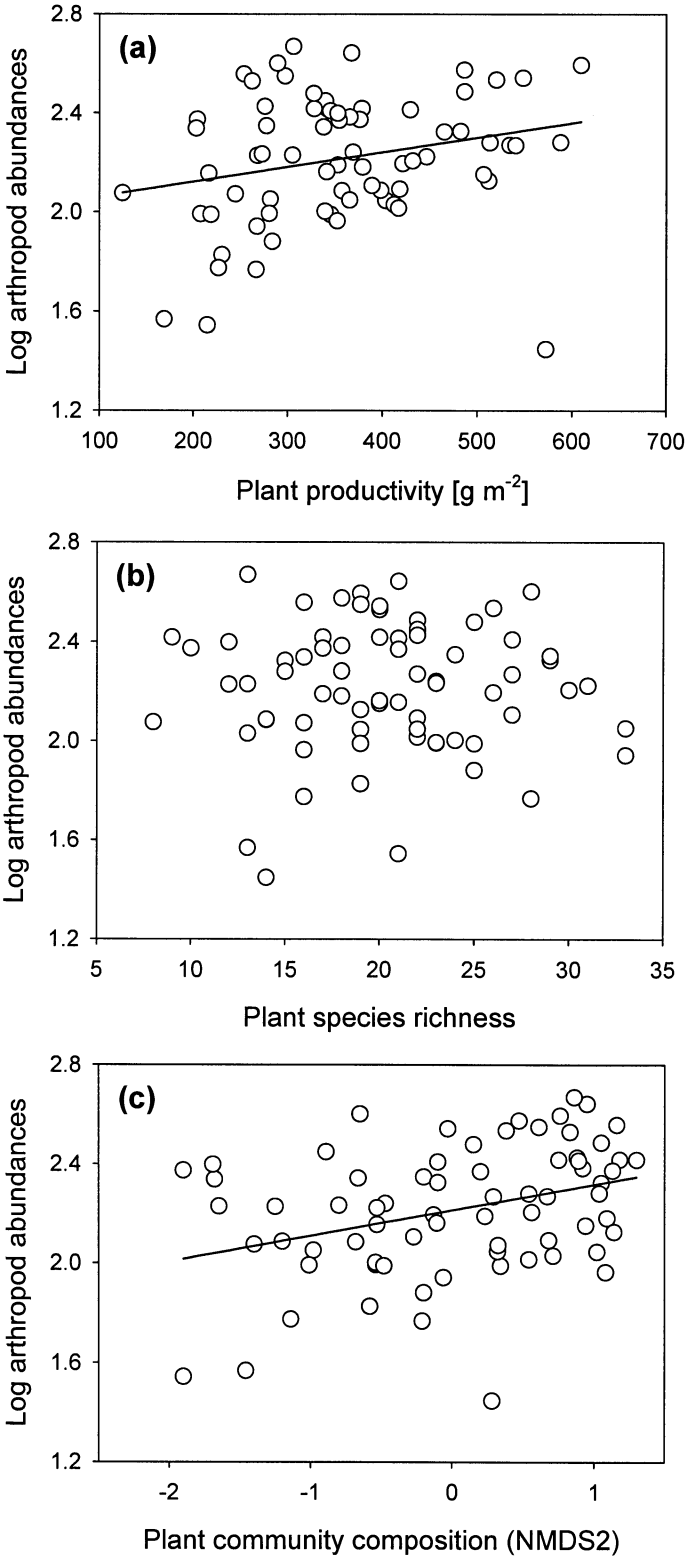

Fig. 2. Dependence of arthropod abundance in the 71 grassland sites on (a) productivity, (b) plant species richness and (c) plant community composition. See text for explanation.

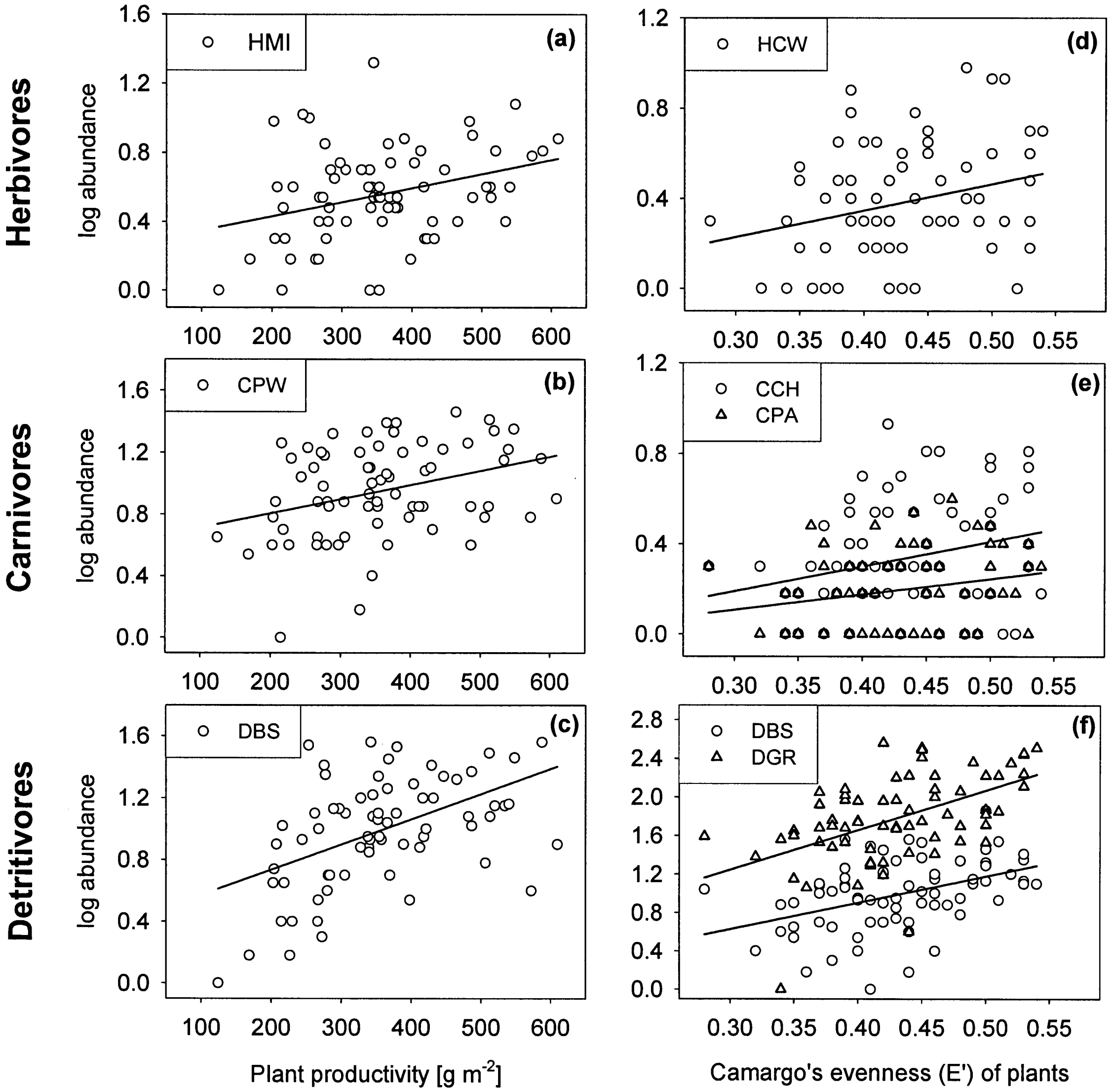

Fig. 3. Significantly related functional group (FG) abundances of herbivores (a, d), carnivores (b, e) and detritivores (c, f) to plant productivity (a, b, c) and plant Camargo's evenness (E') of plant communities (d, e, f). For abbreviations of FGs see Table 1, for r^2- and p- values see Table 4.

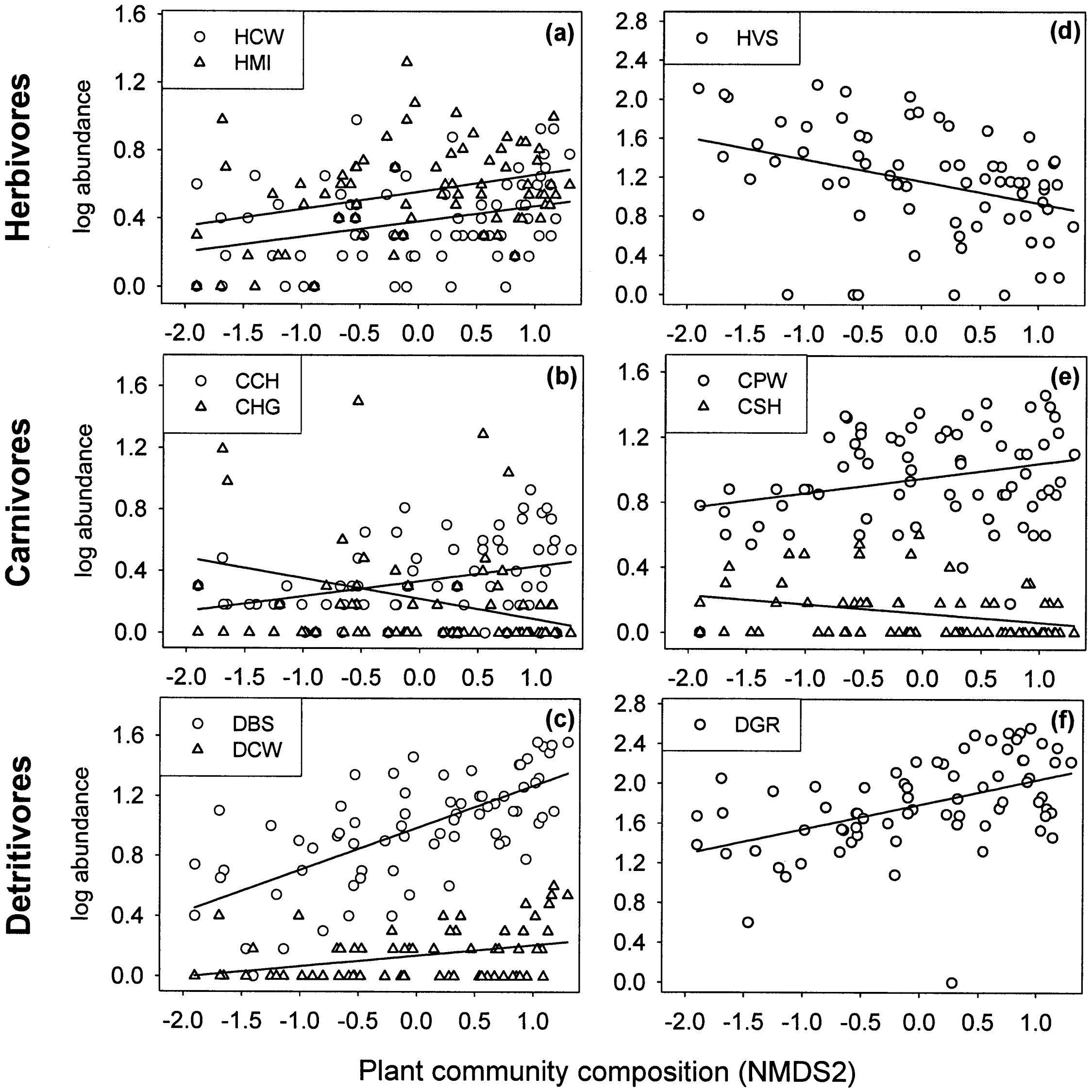

Fig. 4. Significantly related functional group (FG) abundances of herbivores (a, d), carnivores (b, e) and detritivores (c, f) to plant community composition (NMDS2). For abbreviations of FGs see Table 1, for r^2- and p- values see Table 4.

Appendix 1. The eigenvalues and the eigenvector coefficients (loadings) of a standardized principal component analysis (PCA) of the variables contained within parameter-groups I and II. Loadings > 0.5 are shown in boldface type to highlight the meanings of the representative axes (for explanations of used abbreviations see methods section).

((next page))

	PCA	**axis 1**	**axis 2**	**axis 3**	**axis 4**
		Edaphic factors			
PG		**soil1**	**soil2**	**soil3**	**soil4**
	Eigenvalues	*0.3524*	*0.2179*	*0.0986*	*0.0928*
I	C_{total}	-0.4003	**0.8924**	0.0045	0.0130
I	N_{total}	-0.1806	**0.7403**	-0.2764	-0.0778
I	C-N ratio	-0.4619	**0.6062**	0.3597	0.1360
I	K^+	0.1943	-0.0665	**0.7679**	0.4171
I	Mg^{2+}	**0.6696**	0.3260	0.1939	-0.0012
I	P_{total}	0.3944	0.2433	-0.2734	**0.5986**
I	SO_4^{2-}	**-0.7869**	0.0415	-0.1508	0.4807
I	Ca^{2+}	**0.7776**	0.3830	-0.0033	-0.2289
I	N_{min}	**0.6662**	0.2479	-0.3210	0.2919
I	pH	**0.8520**	0.3662	0.1687	-0.1068
I	soil-moisture	**-0.6591**	0.4138	0.1504	-0.2888
		Site characteristics			
		site1	**site2**	**site3**	**site4**
	Eigenvalues	*0.3904*	*0.2515*	*0.2186*	*0.1394*
I	Altitude	-0.4268	**-0.7337**	-0.4837	0.2135
I	Inclination	**0.8156**	-0.1347	0.1499	0.5424
I	PDSI	**-0.6776**	**0.5669**	-0.0951	0.4586
I	Wood-distance	-0.5042	-0.3595	**0.7807**	0.0836
		Management			
		manage1	**manage2**	**manage3**	**manage4**
	Eigenvalues	*0.5088*	*0.3633*	*0.0652*	*0.0421*
I	Cutting_2001	-0.4163	**0.8580**	-0.2116	0.0261
I	Grazing_2001	**0.9354**	-0.1041	-0.2361	-0.2143
I	Fertilization_2001	0.7224	0.5441	0.3329	-0.2563
I	Cutting_historical	-0.3565	**0.8872**	-0.1738	-0.1085
I	Grazing_historical	**0.9263**	-0.0413	-0.3332	0.1326
I	Fertilization_historical	0.7054	0.5899	0.1970	0.3331
		Vegetation structure			
		vegstru1	**vegstru2**	**vegstru3**	**vegstru4**
	Eigenvalues	*0.3103*	*0.2716*	*0.1380*	*0.0696*
II	Total plant cover	**-0.7689**	-0.3290	0.0855	0.0336
II	Tall-grasses cover	**0.6245**	**-0.5231**	0.1534	0.2448
II	Short-grasses cover	**-0.8523**	0.2764	-0.1220	0.0739
II	Forbs cover	**-0.6865**	-0.2466	0.0272	0.1491
II	Mosses cover	-0.2923	0.3714	**0.6995**	-0.2821
II	Total plant height	-0.1301	**-0.9165**	0.0256	-0.2098
II	Tall-grasses height	0.0896	**-0.6523**	0.4313	0.4962
II	Short-grasses height	**-0.8724**	0.2028	-0.0957	0.0997
II	Forbs height	-0.0440	**-0.8084**	-0.0073	**-0.5355**
II	Mosses height	-0.0722	0.1974	**0.8851**	-0.0405
II	LAI	**-0.5962**	**-0.5758**	-0.0567	0.0930

6. Manuskript V

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Responses of arthropods to plant diversity: changes after pollution cessation

Jörg Perner, Winfried Voigt, Rudolf Bährmann, Wolfgang Heinrich, Rolf Marstaller, Bärbel Fabian, Karsten Gregor, Dorit Lichter, Friedrich W. Sander and T. Hefin Jones

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Data collected from three different polluted sites in the vicinity of a phosphate fertilizer factory that was closed in 1990 are used to test with Mantel tests and smoothing techniques whether the rapid increase of plant species richness following cessation of pollution enhanced associated arthropod assemblage diversity. 132 plant species (between 1990 and 1999) and 66 413 individuals of 680 arthropod species (using sweep net sampling between 1990 and 1996) were recorded. Using top soil pH as a representative pollution parameter we detected an increase of plant species richness, effective diversity and evenness of plant community with decreasing pH both in space and time. While the richness of all studied functional groups of herbivores increased with plant species richness, only the richness of one carnivore functional group showed a similar pattern. Plant species richness was significantly correlated to the abundance patterns of two herbivore and two carnivore groups. But contrary to theoretical predictions consumer abundance tended to decrease with increasing plant diversity only between a plant species richness range of 10 to ca 35. Our results support the findings of previous studies that highlight how increased plant species and functional group richness may result in higher herbivore species richness, and that carnivore richness may be influenced by herbivore and detritivore richness. The functional group approach used in this study has enabled us to detected the very individual interaction patterns that occur between different groups within the same trophic level.

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Continuing loss of species diversity arising as a consequence of human activity has prompted increased concern that the "service" capabilities of ecosystems may be compromised (Baskin 1997). The exact role of species diversity in determining ecosystem structure and function remains the focus of debate (see Loreau et al. (2002) for recent review). Recently, the importance of plant diversity in determining the diversity of higher trophic levels has also received attention (e.g. Wardle et al. 2000, Haddad et al. 2001, Hartley and Jones 2003). The majority of theoretical, experimental and observational studies suggest that important links exist between plant and herbivore species diversity (e.g. Rosenzweig 1995) and that, through an upwardly-cascading mechanism (consumer resource models), changes in herbivore diversity may be transmitted to and affect the carnivore level (Hunter and Price 1992, Knops et al. 1999). Plant diversity may also indirectly affect herbivore diversity by influencing and even modifying the interactions that occur between herbivores and carnivores. For example,

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Siemann et al. (1998) showed that although an increased number of plant species and functional groups increased the number of arthropod species, herbivore diversity was more strongly correlated with parasitic and predator diversity than with plant diversity. Both direct and indirect mechanisms play a role in determining the effects of changing plant diversity on insect abundances (Koricheva et al. 2000, Haddad et al. 2001).

In an attempt to investigate these "diversity cascades" within the context of a specific anthropogenic activity Haddad et al. (2000) explored the effects of long-term nitrogen loading on grassland insect communities. They found that plant and insect species richness were strongly positively correlated and that along a gradient of increasing nitrogen loading both plant and insect species richness decreased. Insect abundance, however, increased.

Industrial pollution also results in major changes in plant assemblages, with an associated decrease in species diversity (Salemaa et al. 2001). Frequently, at least in the case of pollutants, the shift from diverse to species-poor plant assemblages results in the dominance of few, well-adapted plant species (Heinrich 1984, Schmeisky and Podlacha 2000). Such changes are likely to affect the diversity of both herbivore and higher consumer levels (Schäller et al. 1987).

In an attempt to consider the generality of Haddad et al. (2000)'s findings, we use data collected from three different polluted sites in the vicinity of a phosphate fertilizer factory that was closed in 1990 to test the hypothesis that decreasing pollution residuals, and the tightly-linked rapid increase of plant species richness, have an enhancing influence on the diversity of higher trophic levels. Past studies on the effect of changes in both total plant and plant functional group diversity have tended to concentrate either on overall consumer trophic levels (e.g. herbivore, carnivore (predator and parasitoid) and detritivore (Siemann 1998, Siemann et al. 1998, 1999, Haddad et al. 2000)) or on individual insect orders or other higher taxa (Koricheva et al. 2000, Symstad et al. 2000). In this study we consider the impact of changes in plant diversity on different functional groups (FGs) within the same trophic level. We speculate that because of variation in the foraging, reproduction and hibernation behaviour of FGs within a particular trophic level, the likelihood of there being a general single trophic level response is relatively low.

Table 1. Mean (±SE) concentrations (ppm except pH) of selected pollution parameters from top soil (0-10 cm) of Sites U, M and O sampled after closure of the fertilizer factory in 1990 (after Metzner et al. 1997).

	Sites		
Parameters	U	M	O
pH-value	9.0 ± 0.4	8.3 ± 0.3	7.7 ± 0.1
Cd	9.2 ± 6.9	3.1 ± 1.0	1.8 ± 0.5
F [$\times 10^3$]	10.2 ± 4.1	3.0 ± 1.1	1.2 ± 0.3
K [$\times 10^3$]	7.3 ± 3.8	15.1 ± 1.6	15.1 ± 2.1
Mg [$\times 10^3$]	4.5 ± 0.9	5.1 ± 0.9	4.9 ± 0.9
Na [$\times 10^3$]	13.8 ± 6.0	9.6 ± 2.6	7.4 ± 1.1
P [$\times 10^3$]	64.6 ± 34.8	15.0 ± 4.4	5.7 ± 2.1

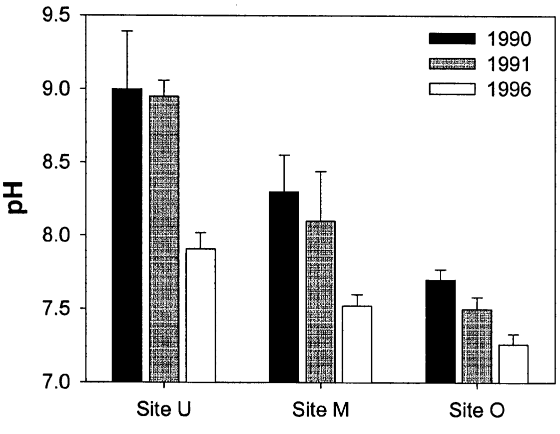


Fig. 1. Soil pH (mean + SE) 1990–1996 at Sites U, M and O (after Metzner et al. 1997).

Material and methods

Study area and sampling sites

Our study area is a sloping grassland adjacent to a former phosphate fertilizer factory 18 km to the north of Jena (Germany, Thuringia, 51°00'N, 11°46'E). After an active production life of 30 yr the factory was closed in 1990. The prevailing wind, orographical situation and distance from the pollution source have given rise to a decreasing pollution gradient from the lower to the upper region of the slope (Metzner et al. 1997). The composition of the factory's dust emissions reflected the raw material used, namely apatite ($Ca_5(Cl, F)(PO_4)_3$), soda (Na_2CO_3) and quartz sand. Missing filter systems in the production process resulted in depositions of Na, P, F and Cd, as well as high pH, particularly at Sites U and M (see below), attributable to the alkaline character of the dusts. Chemical analyses (including pH measurements) of the top soil were carried out immediately after closure in 1990, in 1991 and again in 1996 (Metzner et al. 1997; Table 1, Fig. 1).

Three sampling sites were selected along the pollution gradient, each with its own chemical characteristics (Table 1); Site U, a heavily degraded area in the lower region of the slope (mean distance to the pollution source = 100 m; mean inclination 33°; exposition SE); Site M, considered a degraded area and situated towards the middle region of the slope (mean distance to the pollution source = 200 m; mean inclination 10°; exposition ESE); and Site O, a moderately degraded

Table 2. Summary of the numbers of species and individuals collected within each trophic level. Data are pooled over the three sites (arthropods in total – 680 species, 66 413 individuals; for Diptera and Coleoptera only imagines were used).

Trophic level	Abreviation	Guild	Taxon	Species	Individuals
Primary producers				132	
	PAF	Annual forbs	Spermatophyta	38	
	PGR	Grasses	Spermatophyta	17	
	PMO	Mosses	Bryophyta	18	
	PPF	Perennial forbs	Spermatophyta	44	
	PWP	Woody plants	Spermatophyta	15	
Herbivores				348	44 642
	HCW	Chewers	Coleoptera	144	2977
	HMI	Miners	Diptera (Brachycera)	67	9751
	HTS	Cell-tissue suckers	Heteroptera	60	5287
	HVS	Vascular suckers	Auchenorrhyncha	77	26 627
Carnivores				245	17 992
	CBS	Biting suckers	Diptera (Brachycera)	56	2957
	CCH	Chewing hunters	Coleoptera	74	1160
	CPA	Parasitoids	Diptera (Brachycera)	17	145
	CSH	Sucking hunters	Heteroptera	11	936
	CWS	Web-spinners	Araneae	87	12 794
Detritivores				87	3779
	DBS	Biting suckers	Diptera (Brachycera)	61	3394
	DCW	Chewers	Coleoptera	26	385

area in the upper region of the slope (mean distance to the pollution source = 250 m; mean inclination 5°; exposition ESE). The abbreviations attributed to the three sites are based on the German site names "Unten" = lower region, "Mitte" = middle region and "Oben" = upper region (for more details see Heinrich et al. 2001). In 1990, immediately after factory closure, the lower slope (Site U) was characterized as a monospecific *Puccinellia distans* grassland, the middle slope (Site M) was a species-poor *Elytrigia repens* dominated grassland while the upper slope (Site O) was classified as a ruderal *Arrhenatherum elatius* grassland (Heinrich and Schäller 1987, Heinrich et al. 2001).

Data collection

A systematic stratified sampling design was used to analyse vegetation pattern. A grid of 24 permanent plots (5 x 5 m; 4 rows parallel to the slope and each row consisting of 6 plots bordering on one another) were established in the centre of each site. From 1990 the vegetation was assessed annually using the combined abundance cover estimation method of Braun-Blanquet (Glavac 1996). In this study we use the data collected between 1990 and 1999 (Heinrich et al. 2001). Plants were grouped as mosses (PMO), grasses (PGR), annual forbs (PAF), perennial forbs (PPF) or woody plants (PWP). Additionally, the total number of plant species (P_{total}) and the changes in the number of plant functional groups (P_{FG}) were calculated for each site and year. (Table 2; Appendix 1).

The arthropod data (1990–1996) were collected using standardized sweep-netting (linen net of 30 cm diameter) techniques (10 randomly distributed sub-samples within or in the immediate vicinity of the vegetation grid; each sub-sample consisting of 10 double swings covering ca 8 m^2 (see Witsack 1975, Köhler 1987)). Arthropods were sampled at midday every 2 weeks from the end of April to mid-October in all three sites (U, M and O). For reasons of logistics some arthropod groups were not considered each year, data available are presented in Appendix 2. Arthropods were identified to species level and characterised according to functional group (FG). These groups had been defined a priori (Table 2) based on information available on feeding characteristics (functional feeding groups) and irrespective of taxonomic membership. Consequently for some groups (e.g. Heteroptera, Diptera, Coleoptera) different species of the same taxon found in different trophic levels appear in different FGs. For those groups where shifts between trophic levels occur during development classification is based on the feeding strategy of the immatures, this being the most important life stage when considering abundance and biomass. Herbivores were classified as chewers (HCW; Coleoptera), miners (HMI; Diptera/Brachycera), cell-tissue (HTS; Heteroptera) and vascular (HVS; Auchenorrhyncha) suckers; carnivorous consumers as biting-suckers (CBS; Diptera/Brachycera), chewing (CCH; Coleoptera) and sucking (CSH; Heteroptera) hunters, parasitoids (CPA; Diptera/Brachycera) and web-spinners (CWS; Araneae); and detritivores as biting-suckers (DBS; Diptera/ Brachycera) and chewers (DCW; Coleoptera) (Table 2).

Data analysis

Plant and arthropod data were pooled to provide a single value for each functional group (FG) per site and year. For each sample the species richness, abundance, effective diversity (see Ricklefs and Miller 2000) or heterogeneity ($N_1 = e^{H'}$, exponential Shannon-Wiener), and evenness (E' = Camargo's Evenness) were calculated. Other diversity (Brillouin, reciprocal Simpson's) and evenness (Smith-Wilson evenness, modified Nee) measures were also calculated but as the results were not at variance with those listed above they have not been included (calculation algorithms see Krebs 1999). For the period between 1991 and 1996 when no samples were taken pollution data were interpolated. This was possible because of the strong and clear data trends both in time (1990–1997) and space (U, M and O).

To analyse the compositional changes in the plant communities of Sites U, M and O between 1990 and 1999 non-metric multidimensional scaling (NMDS) ordination techniques (see Clarke 1993) were applied using the program PC-ORD (McCune and Mefford 1997). As a distance measure we used the Bray-Curtis coefficient (also known as Sørensen or Czekanowski coefficient), which is one of the most robust measures for this purpose (Faith et al. 1987), and compared the similarity pattern based on both presence-absence and square-root-transformed quantitative plant data. Because no significant improvement of the minimum stress values was found when moving from two to more-than-two dimension solutions, only two dimensions were considered in both analyses. Since no substantial differences were detected between the ordination plots of both analyses, only that based on the quantitative data is presented.

The correlation between the pollution parameters of top soil, plant and consumer species diversities and $\log_2$-transformed abundance data were explored using simple Mantel test procedures (Mantel 1967, Legendre and Fortin 1989). Because our data samples are not independent (with no "real" replication) and the variables (both biotic and abiotic) are both temporally and spatially autocorrelated no confirmatory parametric statistics (e.g. linear regressions) could be used. Mantel tests account for such autocorrelation patterns by being based on resemblance matrices whose cells correspond exactly and relate to the same spatial or temporal samples. Unlike simple correlation of two data matrices the Mantel test approach measures the extent to which the variations in the distances of one matrix correspond to the variations in the second distance matrix (Legendre 1993). The calculated standardized Mantel statistic (r_M) for the correlation between any two matrices should be interpreted in the same way as Pearson's product-moment correlation coefficient. Statistical significance is tested by a permutation test procedure (for more details see Legendre and Legendre 1998).

To investigate correlations between overall plant community diversity and different consumer levels (herbivores, carnivore, detritivores) the species richness and number of individuals for each FG were analysed together after standardization using adjustment by maximum ($y_i = x_i/x_{max}$).

Potential relationships between consumer FGs across different trophic levels were analysed (in the case of significant correlations between the tested consumer groups and the plant species richness) using partial Mantel tests where the effects of plant species richness on consumer group richness were statistically controlled (see Sokal and Rohlf 1995, Legendre and Legendre 1998). Such an analysis helped us to avoid spurious correlations.

Smoothing techniques were applied in cases of significant Mantel test correlations presented as scatter plots. These procedures are useful tools to describe empirically the relationship between two variables and to show trends without being restricted to a specific model structure. Such smoothing functions are sometimes referred to as "non-parametric regressions" (Legendre and Legendre 1998, Quinn and Keough 2002). In our analyses we used LOESS smoothing (also called LOWESS smoothing: LOcally WEighted Scatterplot Smoothing, Cleveland 1979) – considered to be one of the most popular and robust smoothers (Trexler and Travis 1993). To chose the smoothing parameter (f) that determined the size of the window for the applied local regressions (for details see Cleveland 1979, Goodall 1990), we followed the recommendation of Trexler and Travis (1993). Starting with a (low) initial value f was increased in steps of 0.1 until a value is reached where a non-random pattern appears in the residuals along the x-parameter. A slightly smaller (by 0.1) f was then finally used for the analysis. The software of Bonnet and Van de Peer (2002) was used for the Mantel test analysis and for LOESS smoothing we used the routines available in the SigmaPlot package (Anon. 2001).

Results

Throughout the study a total of 132 plant species and 66413 individuals of 680 arthropod species were recorded (Table 2).

Between 1990 and 1999 plant species richness increased in both Sites U and M. There was negligible change in the least degraded site (Site O) during the same period (Fig. 2a). All five functional groups (FGs) of plants (annual forbs – PAF, grasses – PGR, mosses – PMO, perennial forbs – PPF, woody plants – PWP) present at Site O in 1990 had already re-established in Site M by 1992 whereas this was not true at Site U until 1997 (Fig. 2b). The temporal changes in species richness

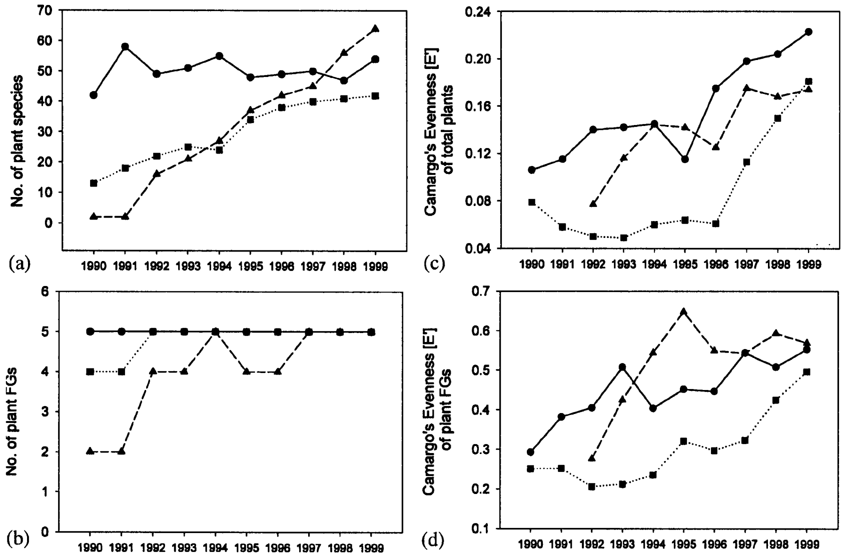


Fig. 2. (a) Total number of plant species (P_{total}), (b) number of plant functional groups (FGs) and (c, d) Camargo's Evenness (E′) of plants at both species and functional group (FGs) levels at Sites U, M and O, 1990–1999 (triangles: Site U, squares: Site M, circles: Site O).

within the various plant FGs (1990–1999) were most marked in Site M: for PAF from 4 to 11 and for PPF from 2 to 14 species; and Site U: for PGR from 1 to 8, for PAF: from 1 to 19 and for PPF from 0 to 24 species. Both plant community effective diversity (N_1) (Appendix 1) and evenness (E′) (Fig. 2c) increased from 1990 to 1999. Similar patterns were observed when plant FGs were analysed (Appendix 1, Fig. 2d). To describe the compositional changes in the plant assemblages of Sites U, M and O from 1990 to 1999 non-metric multidimensional scaling (NMDS) ordinations were applied. Figure 3 reveals the dynamics of the temporal pattern for the three sampling sites based on the quantitative (square-root transformed) plant data. Whereas only marginal changes were observed in Site O, a strong convergence of plant community composition to that of Site O is detectable in both Sites M and U over the period 1990–1999. A very similar pattern occurred on the basis of the pure qualitative (presence-absence transformed) plant data (not presented), although a higher degree of similarity between Site U and Sites O and M was observed. This difference arises mainly from the considerable differences existing in the rank-abundances pattern of plant species between the sites considered in the quantitative plant data (Fig. 3).

Because of the high inter-correlation (multi-co-linearity) between the sampled pollution parameters (Table 1) several significant correlations (as determined with simple Mantel tests) were found between these parameters and plant species richness (P_{total}): P_{total} vs Cd: $r_M = 0.23$, $p < 0.01$; P_{total} vs Mg: $r_M = 0.15$, $p < 0.05$; P_{total} vs Na: $r_M = 0.30$, $p < 0.01$; P_{total} vs P: $r_M = 0.24$, $p < 0.05$; P_{total} vs F: $r_M = 0.50$, $p < 0.001$). pH attained the highest correlation to $P_{total} - r_M = 0.71$, $p < 0.001$ – we limit further consideration to this parameter.

Plant species richness increased with decreasing top soil pH (Fig. 4a). Species richness within all plant FGs show similar significant correlations (simple Mantel tests: PAF – $r_M = 0.25$, $p < 0.05$; PGR – $r_M = 0.73$, $p < 0.001$; PMO – $r_M = 0.22$, $p < 0.05$; PPF – $r_M = 0.70$, $p < 0.001$; PWP – $r_M = 0.58$, $p < 0.001$) and trends (Fig. 4b). Interestingly, species richness of PAF seems to be unrelated to pH values between 7.2 and 8.2. While the effective diversities of both total plant species ($P_{total}N_1$: $r_M = 0.27$, $p < 0.01$) and plant FGs ($P_{FGs}N_1$: $r_M = 0.23$, $p < 0.01$) are also significantly correlated with pH, a similar significant pattern with Camargo's Evenness was only observed with species ($P_{total}E'$: $r_M = 0.54$, $p < 0.01$).

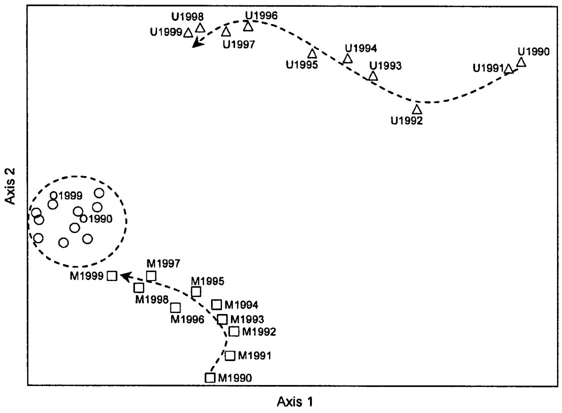


Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of the plant communities for Sites U, M and O (triangles: Site U, squares: Site M, circles: Site O – only years 1990 and 1999 are labelled). Data square-root transformed data; minimum stress values: 1st dimension (axis) = 16.35, 2nd dimension (axis) = 7.34.

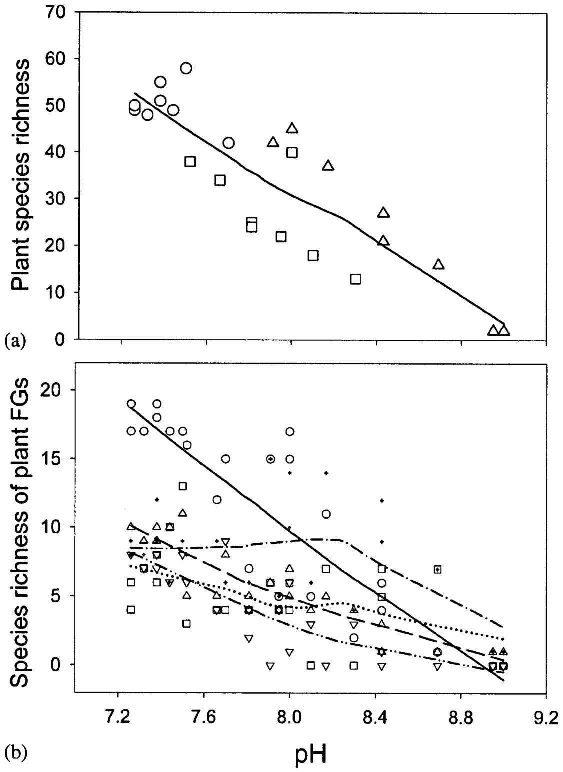


Fig. 4. Changes in (a) total plant species richness and (b) species richness of plant functional groups (FGs) with top soil pH. LOESS smoother used with smoothing parameter f = 0.8 (PAF – crosses, dash-dot line; PGR – triangles pointing up, long-dash line; PMO – squares, dotted line; PPF – circles, solid line; PWP – triangles pointing down, dash-dot-dot line).

Temporal patterns for the consumer (herbivore, carnivore and detritivore) groups were not so clearly defined (Fig. 5). Although there is an obvious higher species richness in Site O compared to Site U there are no recognisable general temporal patterns of FG response within each trophic level in each site. In Site U, both effective diversity (N_1) as well as evenness (E′) tend to increase for most consumer groups between 1990 and 1996 (Appendix 2), whereas in Site M while N_1 appears relatively constant for all FGs E′ shows a decreasing trend, at least for some groups (DCW, CSH, HCW). The response of N_1 and E′ over time in Site O shows a very high degree of variability with a tendency to increase from 1990 to 1996 for the majority of consumer groups (Appendix 2).

Only the richness of two herbivore (HCW: $r_M = 0.56$, $p < 0.001$; HVS: $r_M = 0.37$, $p < 0.01$) and one carnivore (CSH: $r_M = 0.50$, $p < 0.05$) group produce significant correlations with top soil pH; in all cases richness tend to increase with decreasing top soil pH.

The species richness of all herbivore groups, both individually (HCW: $r_M = 0.35$, $p < 0.05$; HMI: $r_M = 0.53$, $p < 0.05$; HTS: $r_M = 0.73$, $p < 0.01$; HVS: $r_M = 0.26$, $p < 0.05$) and as a total (using standardized species richness, see Methods, $r_M = 0.43$, $p < 0.01$), is significantly correlated and tends to increase with plant species richness (Fig. 6a). Among the carnivores (Fig. 6b) and detritivores (Fig. 6c) only the sucking hunters produced a significant correlation with plant species richness (CSH: $r_M = 0.52$, $p < 0.05$). Only four significant correlations were found between the abundance of consumer groups and plant species richness (HCW: $r_M = 0.30$, $p < 0.05$; HVS: $r_M = -0.18$, $p < 0.05$; CBS: $r_M = -0.33$, $p < 0.05$; CCH: $r_M = 0.34$, $p < 0.01$). It is noteworthy that no monotonic increasing or decreasing trends were observed along the whole range of plant species richness (Fig. 7a–d).

To filter out potential interactions between the richness of carnivore groups and that of herbivore or detritivore groups, all possible group constellations were analysed with Mantel test procedures. Significant

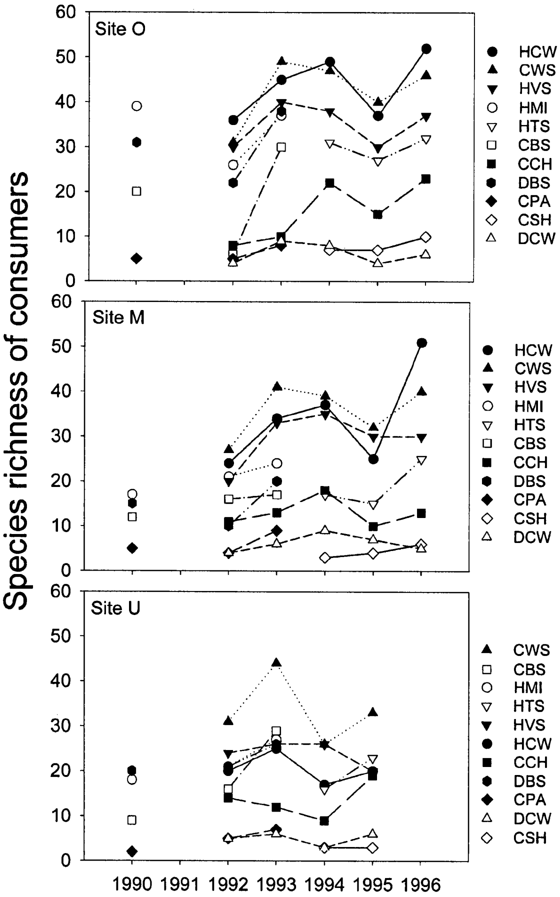


Fig. 5. Temporal variation in arthropod species richness between 1990, 1992–1996 for Sites U, M and O (HCW – filled circles; HMI – empty circles; HVS – filled triangles pointing down; HTS – empty triangles pointing down; CCH – filled squares; CBS-empty squares; CPA-filled diamond; CSH – empty diamond; CWS – filled triangles pointing up; DCW – empty triangles pointing up; DBS – filled circles).

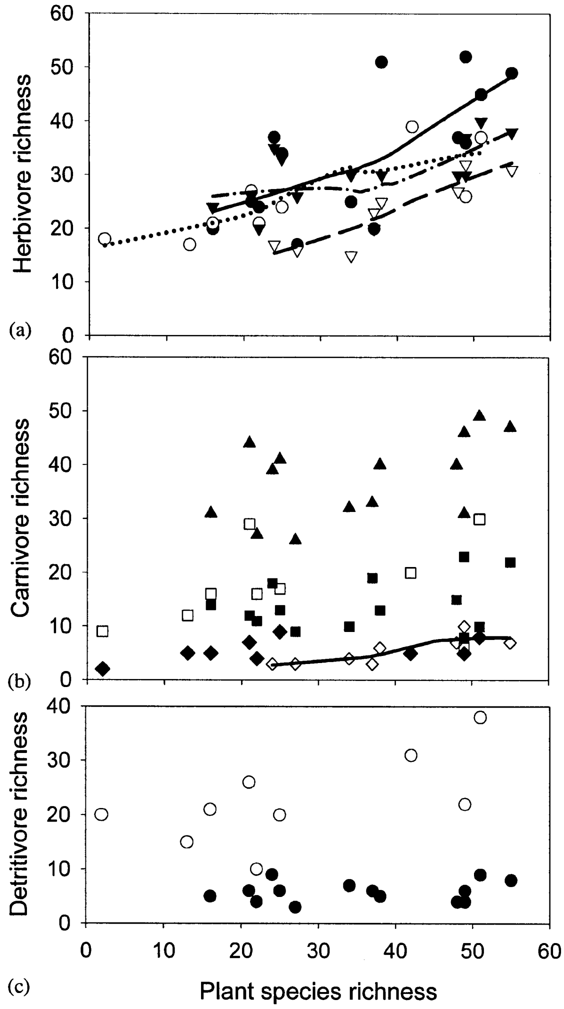


Fig. 6. Changes in consumer functional group species richness with plant species richness (LOEES smoothing lines presented only for significant Mantel test correlations, smoothing parameter f = 0.8). All data collected 1990, 1992–1996 were used. (a) Herbivores (HCW – filled circles, solid line; HMI – empty circles, dotted line; HVS – filled triangles pointing down, dash-dot line; HTS – empty triangles pointing down, long-dash line), (b) Carnivores (CCH – filled squares; CBS – empty squares; CPA – filled diamond; CSH – empty diamond, solid line; CWS – filled triangles pointing up), and (c) Detritivores (DCW – empty triangles pointing up; DBS – filled circles).

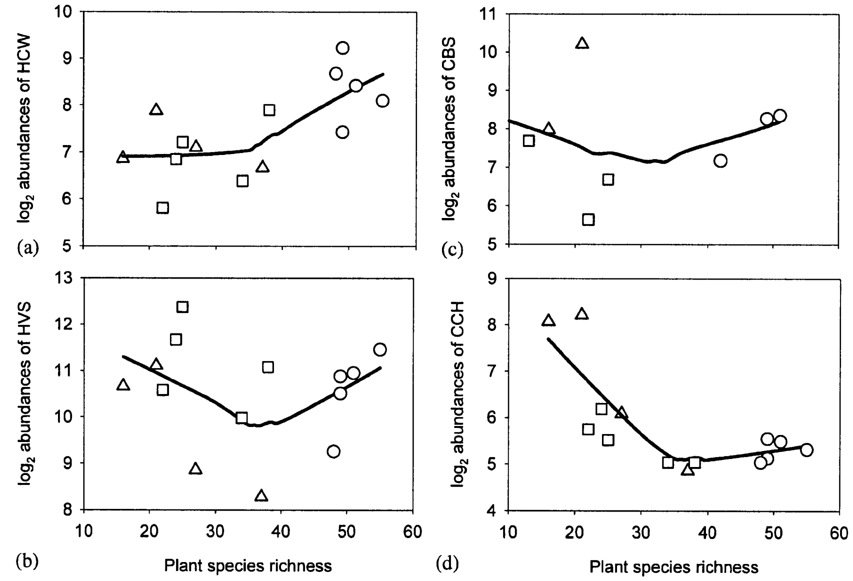
correlations between carnivores and herbivores could be detected for chewing hunters and cell-tissue suckers (CCH vs HTS: $r_M = 0.46$, $p < 0.03$), web spinners and all four herbivore groups (CWS vs HCW: $r_M = 0.46$, $p < 0.01$; CWS vs HMI: $r_M = 0.51$, $p < 0.05$; CWS vs HTS: $r_M = 0.55$, $p < 0.05$; CWS vs HVS: $r_M = 0.49$, $p < 0.01$) and for sucking hunters and both herbivore chewers (CSH vs HCW: $r_M = 0.44$, $p < 0.05$) and cell-tissue suckers (CSH vs HTS: $r_M = 0.65$, $p < 0.01$). Because CSH and both herbivore groups (HCW and HTS) are also significantly correlated with plant species richness (see above) we tested for spurious correlations (arising from co-linearity effects) with partial Mantel tests. Even after controlling the effects of plant species richness (as a third matrix) relationships remain significant (CSH vs HCW: $r_M = 0.45$, $p < 0.05$; CSH vs HTS: $r_M = 0.46$, $p < 0.05$). Significant correlations were also found between sucking hunters and detritivore chewers (CSH vs DCH: $r_M = -0.30$, $p < 0.05$) and between web spinners and both biting suckers (CWS vs DBS: $r_M = 0.57$, $p < 0.01$) and the detritivore chewers (CWS vs DCH: $r_M = 0.30$, $p < 0.05$).

Discussion

The spatial and temporal autocorrelation of our data encouraged us to use only nonparametric explorative methods (Mantel tests, smoothing techniques) to estimate the potential interaction patterns and trends between plant and consumer FGs, and the consumer groups themselves. Although our empirical data do not allow us to draw causal conclusions, the correlation patterns do help us to understand possible pathways of food web responses after vegetation recovery. The decreasing influence of pollution residuals over the time period 1990–1999 resulted in a rapid increase in total plant species richness in the two most polluted sites (U and M). There was also a significant correlation between the effective diversity (N_1) of the plant communities and the pH of top soil, highlighting the key role of this parameter in determining vegetation pattern. In a related study, Heinrich et al. (2001) proposed that allogenic (abiotic) parameters were the driving force affecting vegetation dynamics in the more devastated locations of Sites U and M, while in Site O (but also for Sites U and M from 1996/97), autogenic parameters (e.g. competition) had an increasing impact on vegetation dynamics.

A comparable rapid increase of species richness, effective diversity (N_1) or evenness (E′) was not detected in the FGs of consumers (Fig. 5; Appendix 2). Although most consumer groups exhibited lower species richness no clear increasing trends were recognisable between 1990 and 1996 in the most polluted sites (Sites U and M). This could be due to either the rapidly changing plant species richness resulting in a "time lagged" consumer-response (Lawton 1995) or a consequence of the sampling sites being situated tightly next to each other and the data being biased by the case with which the more mobile insect groups could potentially move in or out between sites. Furthermore, the higher concentration of pollution residuals (e.g. F or Na, see Table 1) in top soil may suppress the successful establishment of new species especially in the most polluted sites (U and M). This is particularly relevant

Fig. 7. Responses of consumer group abundances ($\log_2$ transformed) to changing plant species richness (triangles: Site U, squares: Site M, circles: Site O). Only cases with significant correlations in Mantel test analyses are presented. Trends calculated with LOESS smoothing (f = 0.8).



to those arthropod species where the frequently sensitive larval and hibernation stages are in contact with the top soil for a longer period (Madden and Fox 1997). Consumers are more affected by annual weather conditions and variability than plants (Harrington and Stork 1995, Voigt et al. 2003). This differential sensitivity to climate may be founded on the different degrees in which density dependence, metabolic rates and resource availability are associated with various climate conditions. This would result in more noisy consumer group data making it more difficult to recognise trends in such a relatively short time series.

To identify general patterns we analysed the three sites and the years between 1990 and 1996 together. All herbivore and one carnivore (CSH) group showed significant correlations to increasing plant species richness. Although some FGs (HCW, HVS, CSH) also exhibited a significant correlation with pH (because of the collinearity between pH and plant species richness); effects mediated through the changes in vegetation pattern, at least for herbivore FGs, seem more plausible (Madden and Fox 1997, Borges and Brown 2001). Furthermore, the carnivore FGs, CCH, CSH and CWS, are significantly correlated to the richness of herbivores. That such inter-trophic dependencies occur support results from both theoretical (Leibold 1996) and experimental (Siemann 1998, Siemann et al. 1998) studies that highlight a strong positive relation between herbivore and carnivore diversities. This positive relationship may arise from local herbivore richness being maintained by a diversity of carnivores thus preventing competitive exclusion and allowing a high diversity of herbivores to coexist on the same resource (Levin et al. 1977, Tilman 1986). Some carnivore FGs (CSH, CWS) are correlated both to herbivore and detritivore richness suggesting that they may be able to decouple themselves, at least partially, from the plant richness-herbivore richness-upwardly cascading chain. There may also be a further possible explanation, mediated through the herbivores, for the weak correlations between carnivores and vegetation diversity. In particular, web-spinners (CWS) richness explained a strong correlation pattern to the analysed FGs of herbivores and detritivores. In detail, significant correlations were found with all herbivore, as well as both detritivore, groups. This is attributable to the polyphagous feeding strategy of web-spinners and underline their role as a central carnivorous group of the forb layer (Malt et al. 1990, Sunderland 1999, Borges and Brown 2001).

Although the two detritivore FGs are the dominant groups in the forb layer, the majority of detritivores tend to be active either below- or at ground level. These detritivore groups would not have been sampled by sweep netting and although no biomass data were collected in the present study detritivore species richness and abundance are know to be strongly dependent on plant biomass (Siemann 1998, Wardle et al. 1999, Haddad et al. 2000).

Studies exploring the dependence of arthropod, or insect, species richness on plant diversity vary in their conclusions. In some studies a marked positive relationship is found between arthropod consumers and both plant species and functional group richness (Crisp et al. 1998, Siemann et al. 1998, 1999, Haddad et al. 2000). In others, no relationships have been recorded (Symstad et al. 2000). This variation is not entirely surprising as more detailed examination of the data illustrates how different trophic levels can respond in frequently opposing ways. Virtually in all the studies listed above herbivore richness is positively related to increasing plant species richness, but the results for carnivores (predators, parasitoids) and detritivores vary considerably. The richness patterns of herbivores may frequently be modified by interactions with parasites and predators (e.g. Siemann et al. 1998), and the final relationship between trophic levels and plant diversity may appear negligible or at very most weak and undeterminable. How each trophic level responds is often determined by the dominant arthropod groups present within that level (Symstad et al. 2000) and this is likely to differ between regions and between ecosystems. In addition, when considering trophic levels as entities, without any differentiation of the different feeding groups that are found within each level, sampling protocol can markedly bias the observed pattern of interaction. For example, the composition (percentage of caught taxa) of the herbivore "community" when sampled by sweep-netting will be very different from its composition if sampled by pitfall trapping (Perner 1997). Less varying results may be obtained by assessing the most abundant species within each trophic level but this approach makes general extrapolation very difficult (Siemann et al. 1999, Haddad et al. 2000). In this study we have used an approach in which FGs of consumers have been classified on the basis of their feeding characteristics. In this way we have been able to explore potential relationships not only between trophic levels but also individual relationships between FGs and trophic level. For example, although in simple Mantel tests all FGs of herbivores were significantly correlated to plant species richness, there were also considerable differences in the strength of their correlation (see r_M values and Fig. 6a). Similarly, although most carnivores did not appear to be related to plant species richness, for one feeding group (CSH) there were significant correlations (see r_M values and Fig. 6b).

Root (1973) proposed two hypotheses ("Resource concentration" and "Enemies") both of which predict that increasing plant species richness should decrease herbivore abundance. Both hypotheses were supported by studies from agricultural ecosystems where monocultures had higher insect abundances than polycultures (Risch et al. 1983). Koricheva et al. (2000) tested these hypotheses and found that among the herbivores only leafhopper, and among the predators only carabid beetle and spider, abundance decreased with increasing plant species richness. In a long-term nitrogen loading grassland study, Haddad et al. (2000) found that plant biomass and the abundance of herbivores and detritivores were positively related to decreasing plant species richness (induced by long-term nitrogen loading). In our study the decreasing top soil pH, with its coupled increase of plant species richness, results in a significant correlation to the abundance pattern for two herbivore (HCW, HVS) and two carnivore (CBS, CCH) groups. The estimation of trends with LOESS smoothing illustrate that along the whole range of plant species richness no monotonic abundance trends occur (Fig. 7a–d). Between plant species richness of 10 to ca 35 the abundances decrease (for HVS, CBS, CCH; approximately constant for HCW) with increasing plant diversity. This supports Root's (1973) hypothesis and the empirical findings listed above. Detailed exploration suggests that these decreasing abundance trends were induced particularly by the plant richness changes in the most polluted sites (U and M; Fig. 7a–d). However, above 35 consumer group abundances tend to increase. Haddad et al. (2001) discussed three hypotheses that might explain this opposite trend. Firstly, they argued that individual species abundances may not related to plant species richness, but that due to larger numbers of insect species in more diverse sites total community insect abundances may be positively related to plant species richness. This scenario does correspond to our present situation. Secondly, higher plant diversity may increase the availability of alternate resources. And thirdly, more diverse sites (with higher plant diversity) may have been more structurally complex, providing suitable habitat or greater space for more insects, independent of the amount of food available.

The FG approach adopted in this study has enabled us to detect the very individual interaction patterns of the different FGs within the same trophic level. The complex and diverse nature of such interaction webs at this trophic level explains why the characterisation of simple cascading-up mechanisms may rarely be detectable. We propose that using a FG approach of consumers provides an encouraging step forward as we attempt to disentangle further the web of interactions between plant and consumer diversity, and ecosystem functioning.

Although our analyses are limited by the exploration of only one case study the results may have some general implications, particularly in the field of restoration ecology. Bradshaw (2000) pointed out that in the interest of economy and the maintenance of our natural resources recovery processes such as those after pollution effects should be studied in detail. With the caveat that each situation is site-specific and that the dynamics of food web recovery depends on a set of various parameters (e.g. strength of pollution, soil structure, seed bank diversity, neighbouring habitat diversity) our study highlights the huge regeneration potential of natural systems. Indeed, from this one case study it would appear that in situations of relatively localised pollution considerable food-web diversity recovery may happen within 10 yr of the cessation of pollution.

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Appendix 1. Species richness, effective diversity [N_1] and Camargo's Evenness [E′] for plants. Data are given for totals (P_{total}) as well as for all functional groups (P_{FGs}) separately.

Sites	U										M										O									
Years	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
No. of plant species (P_{total})	2	2	16	21	27	37	42	45	56	64	13	18	22	25	24	34	38	40	41	42	42	58	49	51	55	48	49	50	47	54
No. of plant FGs (P_{FGs})	2	2	4	4	5	4	4	5	5	5	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
Species richness																														
PMO	0	0	7	7	5	7	6	6	10	9	0	0	4	4	4	4	3	4	6	4	4	13	10	8	6	7	6	4	7	5
PGR	1	1	1	1	3	5	6	7	8	8	4	4	4	4	5	5	5	5	6	7	8	11	10	9	10	9	10	10	10	10
PAF	1	1	7	9	12	14	15	14	16	19	4	6	5	6	6	9	8	10	7	11	6	9	6	9	12	8	8	9	5	10
PPF	0	0	1	4	6	11	15	17	20	24	2	5	5	7	7	12	16	15	16	14	15	17	17	18	19	17	17	19	16	19
PWP	0	0	0	0	1	0	0	1	2	4	3	3	4	4	2	4	6	6	6	6	9	8	6	7	8	7	8	8	9	10
Effective diversity [N_1]																														
P_{total}	1.00	1.00	1.27	2.85	5.18	6.87	6.69	10.30	12.60	14.94	1.03	1.05	1.08	1.16	1.46	2.54	2.57	4.78	7.56	10.19	4.77	7.71	8.82	9.37	10.38	6.18	11.38	13.12	12.83	16.22
P_{FGs}	1.00	1.00	1.21	2.12	3.07	3.25	2.64	3.07	3.22	3.26	1.01	1.03	1.06	1.11	1.34	1.98	1.84	1.98	2.62	2.97	1.61	2.32	2.51	3.11	2.45	2.88	2.72	3.36	3.17	3.40
PMO	0.00	0.00	4.09	3.43	3.02	3.53	2.80	2.89	2.68	2.99	0.00	0.00	3.45	3.73	3.69	3.65	2.44	2.26	1.97	1.36	3.29	4.09	2.47	2.06	2.43	2.24	2.53	2.31	1.46	1.88
PGR	1.00	1.00	0.00	0.00	1.00	1.01	2.93	4.92	4.09	4.37	1.02	1.01	1.01	1.03	1.05	1.14	1.31	2.12	2.62	3.44	2.85	3.32	3.99	5.11	4.81	4.70	5.43	4.56	5.63	6.14
PAF	0.00	0.00	2.62	2.11	1.86	1.70	2.40	3.72	5.96	5.92	3.34	4.34	4.96	2.71	1.38	1.74	1.63	3.40	2.96	2.90	3.05	2.06	1.84	1.65	2.13	1.24	1.36	3.02	1.58	3.07
PPF	0.00	0.00	0.00	2.98	2.32	1.72	1.96	3.71	3.54	4.76	1.45	3.26	3.42	3.81	4.23	2.88	4.09	5.81	4.03	4.42	7.25	8.08	7.62	5.83	3.65	3.47	3.23	4.27	2.62	3.78
PWP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.34	2.39	2.18	2.18	1.56	2.00	1.17	1.28	1.44	1.81	3.63	3.52	4.02	4.15	4.13	3.70	3.67	3.60	3.68	4.78	3.53	4.02
Camargo's Evenness [E′]																														
P_{total}	–	–	0.08	0.12	0.14	0.14	0.13	0.18	0.17	0.17	0.08	0.06	0.05	0.05	0.06	0.06	0.06	0.11	0.15	0.18	0.11	0.12	0.14	0.14	0.15	0.12	0.18	0.20	0.20	0.22
P_{FGs}	–	–	0.28	0.43	0.54	0.65	0.55	0.54	0.59	0.57	0.25	0.25	0.21	0.21	0.24	0.32	0.30	0.32	0.43	0.50	0.29	0.38	0.41	0.51	0.40	0.45	0.45	0.54	0.51	0.55
PMO	–	–	0.45	0.39	0.48	0.40	0.38	0.37	0.22	0.28	–	–	0.72	0.79	0.80	0.77	0.66	0.45	0.28	0.30	0.68	0.25	0.20	0.21	0.33	0.26	0.36	0.45	0.19	0.32
PGR	–	–	–	–	0.33	0.20	0.39	0.58	0.41	0.43	0.25	0.25	0.25	0.25	0.21	0.22	0.24	0.35	0.35	0.40	0.28	0.23	0.31	0.44	0.37	0.40	0.43	0.36	0.44	0.48
PAF	–	–	0.29	0.19	0.13	0.11	0.16	0.23	0.28	0.23	0.69	0.59	0.93	0.39	0.21	0.16	0.17	0.26	0.37	0.21	0.42	0.19	0.25	0.15	0.15	0.14	0.16	0.27	0.26	0.23
PPF	–	–	–	0.59	0.30	0.13	0.11	0.17	0.15	0.15	0.62	0.54	0.54	0.43	0.46	0.22	0.21	0.30	0.20	0.24	0.37	0.36	0.34	0.26	0.17	0.19	0.17	0.19	0.14	0.16
PWP	–	–	–	–	–	–	–	–	0.59	0.47	0.61	0.61	0.35	0.40	0.54	0.29	0.22	0.27	0.50	0.48	0.34	0.39	0.54	0.41	0.35	0.40	0.36	0.47	0.30	0.31

Appendix 2. Species richness, number of individuals caught, effective diversity (N_1) and Evenness (E′) for the functional groups of the three consumer levels (herbivores, carnivores and detritivores) between 1990–1996 at Sites U, M and O.

Sites	U					M						O					
Years	1990	1992	1993	1994	1995	1990	1992	1993	1994	1995	1996	1990	1992	1993	1994	1995	1996
Abbrev.	No. of species																
HCW		20	25	17	20		24	34	37	25	51		36	45	49	37	52
HMI	18	21	27			17	21	24				39	26	37			
HTS				16	23				17	15	25				31	27	32
HVS		24	26	26	20		20	33	35	30	30		30	40	38	30	37
CBS	9	16	29			12	16	17				20	6	30			
CCH		14	12	9	19		11	13	18	10	13		8	10	22	15	23
CPA	2	5	7			5	4	9				5	5	8			
CSH				3	3				3	4	6				7	7	10
CWS		31	44	26	33		27	41	39	32	40		31	49	47	40	46
DBS	20	21	26			15	10	20				31	22	38			
DCW		5	6	3	6		4	6	9	7	5		4	9	8	4	6
	No. of individuals																
HCW		116	223	111	87		56	147	115	84	237		172	342	274	411	602
HMI	169	1942	2582			130	391	2015				1201	465	856			
HTS				854	335				785	306	604				794	383	1226
HVS		1616	2213	464	311		1528	5288	3266	1013	2161		1463	1980	2825	611	1888
CBS	387	253	1178			206	50	103				145	308	327			
CCH		269	310	94	44		54	47	73	33	35		35	45	41	33	47
CPA	3	17	48			10	17	21				7	12	10			
CSH				21	29				208	84	138				133	136	187
CWS		606	1491	339	489		437	892	819	660	863		997	1426	1178	1184	1413
DBS	51	737	1285			73	128	224				186	108	602			
DCW		15	58	39	17		4	9	38	31	40		9	29	27	12	57
	Effective diversity [N_1]																
HCW		4.0	4.4	5.2	9.8		18.5	18.4	20.6	12.3	20.6		18.7	8.9	16.4	5.1	12.7
HMI	8.8	2.9	3.9			8.3	5.5	3.3				11.7	8.4	11.2			
HTS				4.1	8.7				2.4	2.4	4.7				4.2	7.7	6.5
HVS		4.9	5.4	10.4	6.3		5.0	6.2	6.9	7.1	7.9		8.3	9.1	10.8	14.3	12.3
CBS	3.9	6.6	7.1			3.6	8.4	10.6				4.6	1.7	3.7			
CCH		5.5	2.9	3.8	11.9		6.4	6.9	10.1	7.2	8.2		3.8	5.4	16.0	11.2	16.8
CPA	1.9	3.4	3.7			4.1	3.1	7.7				4.4	4.6	7.6			
CSH				1.7	2.4				1.4	1.4	1.4				3.0	2.2	2.4
CWS		11.5	9.6	9.7	14.0		9.4	9.3	9.5	9.4	8.1		10.5	10.7	12.5	9.7	15.0
DBS	12.5	3.0	3.7			7.6	1.9	7.7				13.7	12.5	16.2			
DCW		2.6	1.6	1.4	2.9		4.0	4.9	3.6	3.6	2.3		3.4	6.9	3.5	3.7	2.6
	Camargo's Evenness [E′]																
HCW		0.26	0.23	0.28	0.41		0.61	0.42	0.46	0.44	0.36		0.41	0.23	0.31	0.18	0.23
HMI	0.37	0.12	0.12			0.38	0.22	0.12				0.23	0.27	0.24			
HTS				0.21	0.30				0.12	0.17	0.20				0.15	0.25	0.18
HVS		0.17	0.17	0.31	0.27		0.20	0.15	0.16	0.20	0.20		0.21	0.18	0.22	0.36	0.25
CBS	0.33	0.32	0.19			0.25	0.45	0.47				0.23	0.23	0.17			
CCH		0.30	0.22	0.33	0.53		0.45	0.45	0.45	0.56	0.52		0.39	0.43	0.62	0.62	0.61
CPA	0.83	0.55	0.42			0.68	0.63	0.69				0.77	0.77	0.85			
CSH				0.46	0.63				0.40	0.31	0.22				0.33	0.26	0.22
CWS		0.29	0.17	0.32	0.34		0.26	0.19	0.20	0.23	0.19		0.26	0.18	0.22	0.21	0.26
DBS	0.52	0.12	0.13			0.41	0.19	0.31				0.36	0.44	0.32			
DCW		0.47	0.26	0.40	0.46		1.00	0.72	0.36	0.42	0.38		0.69	0.60	0.41	0.79	0.34

7. Manuskript VI

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Shifting average body size during regeneration after pollution –
a case study using ground beetle assemblages.
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Shifting average body size during regeneration after pollution – a case study using ground beetle assemblages

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Abstract. 1. Pitfall data, collected periodically between 1980 and 1996, were used to analyse the spatial and temporal body size pattern of ground beetle assemblages (Carabidae) in a former polluted grassland.

2. Two hypotheses were tested: (i) Siemann *et al.*'s *efficiency–specialisation hypothesis* that predicts that during succession (or regeneration) processes the mean body sizes of consumer assemblages decrease and (ii) Blake *et al.*'s hypothesis that predicts that smaller body sizes are found with increasing level of disturbance.

3. Biovolume was considered as a determinant of ground beetle body size. This was analysed by using a digital–optical volume measurement. The mean error associated with the idealisation of the ground beetle body shape as an ellipsoid was determined as 10.24 ± 2.5%.

4. A significant decrease in average ground beetle body size was recorded in moving from the pollution (1980) to the post-pollution (1996) period. The mechanisms linked with ecological succession after factory closure (1990) were discussed as the main causal factor sustaining Siemann *et al.*'s hypothesis.

5. The analyses of the mean body size during the transition period from the pollution to the post-pollution period demonstrate that Blake *et al.*'s hypothesis was also partly supported, and may overlay the effects driven by succession.

6. It is therefore concluded that both hypotheses may be used to explain not only the change in body size from a highly polluted to a less polluted area, but also the relationship between habitat structure and predatory ground beetles.

Key words. Biovolume, body size, Carabidae, efficiency–specialisation hypothesis, grassland regeneration, pollution.

Introduction

Potential ecological relationships between body size and the structure of animal communities have been the focus of much attention in ecological studies. Body size is correlated with many aspects of life history, for example metabolic efficiency, generation time, metabolism, reproduction rate, and dispersal (Peters, 1983; Morse *et al.*, 1988; Brown, 1995; West *et al.*, 1997). Body size may also determine whether, within any particular assemblage, an organism is a potential predator or prey (Peters, 1983). While many studies have explored the relationship between body size and the abundance of individual species (Morse *et al.*, 1988; Currie, 1993; Stork & Blackburn, 1993; Tokeshi, 1993), others have examined the relationship between resource availability and body size variation of selected species (Richards, 1948; Palmer, 1985; Brown & Maurer, 1987; Maurer *et al.*, 1992). The past decade has seen the application of a combination of both approaches in an attempt to find a trans-specific explanation for average body size distribution within or between different habitats (Basset *et al.*, 1994;

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Blake *et al.*, 1994; Ribera *et al.*, 2001). Some studies have been designed to explore relationships between different disturbance intensity and body size (Sustek, 1987; Blake *et al.*, 1994; Niemalä & Kotze, 2000) by comparing various disturbed habitats. In general, these studies have found a decrease in body size in the more acutely disturbed areas. Siemann *et al.* (1999) pursued another approach where average body size in arthropod assemblages was examined along different seral stages. They found that average body size tended to decrease with increasing seral stage, but that only with herbivores was this correlation significant. Various attempts have been made to apply the *efficiency–specialisation hypothesis* to this latter pattern. Based on the specialisation hypothesis (Margalef, 1968; Odum, 1969; Brown & Southwood, 1983; Brown & Hyman, 1986), the efficiency–specialisation hypothesis argues that as herbivore generalists tend to have a high metabolic efficiency and specialists do not, generalists should be able to use the lower C:N plant tissue found in earlier seral stages more efficiently than specialists (Tilman, 1990). Specialists, however, should be at an advantage in late seral stages as they will be more capable to cope with the higher vegetative heterogeneity characteristic of those communities (Morse *et al.*, 1985; May, 1986; Shorrocks *et al.*, 1991). The potential trade-offs and their consequences for higher trophic levels, however, are disregarded in this theoretical consideration. A direct trade-off may exist between the average body size of herbivores and that of predators, via a predator–prey size relationship (Belaoussoff *et al.*, 2003). An indirect relationship based on changes in metabolic efficiency of predators is also conceivable. Thus, an increasing diversity and level of specialisation of herbivores in late seral stages could favour more diverse and smaller, increasingly more specialised, predators.

In this study, pitfall data, collected periodically between 1980 and 1996, were used to analyse the spatial and temporal body size pattern of ground beetle assemblages (Carabidae) in a formerly polluted grassland. This predaceous taxon was selected for a number of reasons. Not only are the ecological characteristics of ground beetles well-known (e.g. Barndt *et al.*, 1991; Turin, 2000) but carabids are also excellent ecological indicators of habitat quality and environmental modification (e.g. McGeoch, 1998). Furthermore, changes in insect fauna generally provide excellent indicators of the environmental modifications caused by anthropogenic influences (Paje & Mossakowski, 1984; Rushton *et al.*, 1990; Eyre, 1994). This study is based on information collected in the environs of a fertiliser factory that, during the period 1960–1990, was a major pollutant source (Heinrich, 1984; Schäller *et al.*, 1987; Heinrich *et al.*, 2001; Perner *et al.*, 2003). Areas formerly seriously disturbed by such chemical deposition provide suitable environments in which to explore potential functional correlations between average body size of arthropod assemblages and their environment. The combination of regeneration processes and the presence of different succession stages over the time period provide a unique opportunity to investigate changes in both the composition and energetics of animal communities (Odum, 1969; Brown & Southwood, 1983).

Using ground beetle assemblages two hypotheses were tested: (1) the *efficiency–specialisation hypothesis* of Siemann *et al.* (1999), which states that during succession (or regeneration) processes the mean body sizes of consumer assemblages decrease, and (2) the hypothesis of Blake *et al.* (1994), which states that smaller body sizes are found with increasing level of disturbance.

Methods

Study area and pollution details

The study area is located in the valley of the river Saale, north of Jena near the village of Steudnitz (Germany, Thuringia, 51°00′N, 11°46′E). The site is located on an east–south-east exposed slope near a former fertiliser factory that produced phosphate fertilisers from 1960 to 1990. During the latter part of this period potassium–magnesium–phosphate fertiliser was also manufactured (Heinrich, 1984; Heinrich *et al.*, 2001). The lack of environmental control between 1960 and 1990 resulted in the deposition of a dust layer of phosphorus (P), sodium (Na), and cadmium (Cd) on most of the surrounding vegetation. This led to marked structural modifications in the stock of vegetation throughout the adjoining area. For the purpose of study the area was divided into three main sites: U, M, and O. The abbreviations are based on the German terms *Unten* = lower region, *Mitte* = middle region and *Oben* = upper region (for more details see Heinrich *et al.*, 2001). The lower site (U) was next to the emitter and experienced the strongest anthropogenic impacts. This led to a very rapid demise of all vascular plants that resulted in areas close to the factory remaining virtually free of vegetation, except for the occasional sward of *Puccinellia distans* (Jacq.). In contrast to the prevailing rendzina strata present in site U, the thick loess stratum that occurs in site M is several metres deep. Macroscopical changes provided evidence of the consequences of the pollutant emission on vegetation in this area; there was clear foliar necrosis on wood plants and an obvious dust layer on all plants. The dominant vegetation was mainly couch grass (*Elytrigia repens* (L.)) swards with occasional shrubs (*Rosa canina* L. and *Crataegus* sp.). The thickness of the loess stratum decreases markedly in moving from site M to site O with the appearance of subjacent rock (coquina). Changes in vegetation structure as a consequence of pollution were visible in this area too, but to a far smaller extent than in either site U or site M. Species-rich swards with both *Festuca rubra* L. and *Bromus erectus* Huds. established in this area.

Since the 1960s the level of pollutant emission in the study area was characterised not only by the increasing level of emission from the fertiliser factory but also by the increase in soil pH value. Most notably in site U, the Na concentration increased to a level that was toxic to plants (Heinrich, 1984), and its high concentration to depths of more than 50 cm led to deterioration of the ground structure. The consequences of this increased Na concentration included modification of the calcium (Ca), magnesium (Mg), potassium (K), and phosphate (PO_4) mineral balance as well as effects on the copper (Cu), iron (Fe), manganese (Mn), and molybdenum (Mo) content. On closing the factory in 1990 most pollutant elements showed a rapid and clear decline (Metzner *et al.*, 1997).

Sampling design

Ground beetle capture was accomplished by pitfall trapping during 1980, 1981, 1991, and 1996 on all three sites: U, M, and O. The sampling design in 1980 and 1981 (Peter, 1984; Sander, 1984) differed from that in 1991 and 1996 (J. Perner, unpubl. data). In the earlier years the study area was subdivided into five sections and within each section five pitfall traps were positioned in a transect set horizontally to the slope (number of pitfalls = 10, 5, and 10 in sites U, M, and O, respectively). In 1991 and 1996 a transect of 40 pitfall traps was arranged across the three sites and vertical to the slope (number of pitfalls = 17, 10, and 13 in sites U, M, and O, respectively). By using transects with trap–trap distances of about 4 m in all cases the trapping area for each pitfall was approximately equal across all sites and years. To placate any concerns regarding the different approaches used for comparisons based only on abundances all data were recalculated as numbers of individuals per trap and site (see also Appendix). Furthermore, the data were also restricted to the period between April and November when data were sampled at all sites and in all years. For the comparisons focusing on mean biovolume the effect of variation in the number of pitfalls was negligible (see below).

Determination of the ground beetle biovolume

As dry weight estimation was not possible across the years, biovolume was used as a determinant of ground beetle body size. This was carried out using a digital–optical volume measurement that idealised the ground beetle body as an ellipsoid. Ellipsoid biovolume (EV) was determined from $EV = (\pi/6) \times \text{length} \times \text{height} \times \text{width}$ (Kuschka, 1994). Using a digital camera, body measurement could be made with an accuracy of 0.01 mm. Body length was defined as the distance between labrum and elytron, cross-body distance as maximum elytra width, and the height as the maximum thickness of the left side of the beetle body. An assessment of the accuracy of the computed ellipsoid volume was made by comparing estimates to real volume determined by immersion. Calibration of immersion measurement was carried out against defined volume of three different sized bullets; the mean error was $2 \pm 1.5\%$. Alcohol preserved material of three reference species, each with 20 individuals, was measured by both immersion in alcohol (70%) and by the digital–optical method described above.

For all ground beetle species sampled in the study area five individuals were measured using the above technique. Values were averaged and this mean biovolume of species (quoted in mm^3) was then used as basis for the calculation of the mean ground beetle biovolume per site and year.

Data analyses

Following Preston (1948), body size classification and distribution followed a $\log_2$ scaling. To test for any temporal changes in mean biovolume on each of the three sites a one-way ANOVA (GLM) was used and differences between treatments identified using *post hoc* tests (LSD). Instead of using only unweighted mean biovolume values of assemblages, the biovolume was weighted by the abundance of each species. To homogenise the variance in biovolume data, $\log_{10}$ of values was calculated before analysing.

Plant species data were obtained from other studies: 1980 data from Heinrich (1984), and data for 1991 and 1996, from Heinrich *et al.* (2001). Effective diversity indices (identical to *equal common species* (Krebs, 1999)) were calculated on the basis of the Shannon–Wiener index. The ecological characteristics of ground beetle species immigrating into and emigrating from ecological areas can help to explain the relationship between the structure of habitat and the ground beetle assemblage during particular time windows. Data from 1981, 1991, and 1996 were analysed and 1981 data were compared with those from 1991, and subsequently 1991–1996. All species were characterised by biovolume (see above), wing morphology and hibernation type (Barndt *et al.*, 1991; Turin, 2000). *Total species number* gave the number of species in each class.

Results

Over the whole study period 5028 individuals from a total of 63 species were recorded. At all sites both the numbers of individuals and species increased as time from factory closure become longer (Fig. 1). Significantly more individuals were recorded at site U than at either site M (paired *t*-test: $t_3 = 3.27$, $P = 0.047$) or site O (paired *t*-test: $t_3 = 3.95$, $P = 0.03$). Although there were in general fewer individuals in site M than O there was no significant difference between them (paired *t*-test: $t_3 = -0.054$, $P = 0.96$). The number of species remained relatively similar at all sites (paired *t*-tests: U–M, $t_3 = 1.65$, $P = 0.2$; U–O, $t_3 = 0.93$, $P = 0.42$; M–O, $t_3 = -0.47$, $P = 0.67$).

The mean error associated with the idealisation of the ground beetle body shape as an ellipsoid was determined as $10.24 \pm 2.5\%$ (Table 1). When the distribution of species number was considered on the basis of body size in the three sites over the years between 1980 and 1996 there was an obvious increase in most volume classes (Fig. 2). There were, however, negligible differences across all sites between 1980 and 1981. During this period, and although the distribution of biovolume was very irregular, most species were

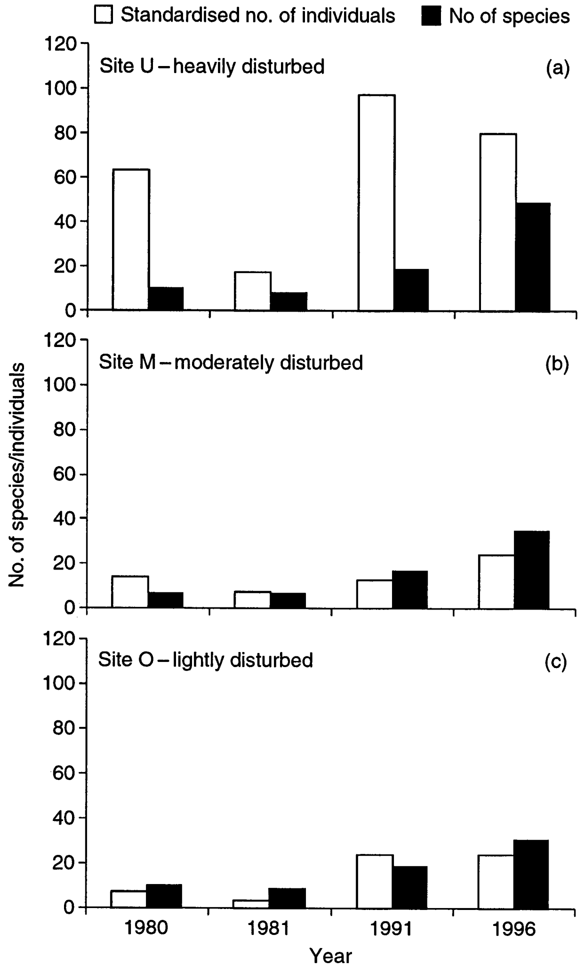

Fig. 1. Trends in number of species and individuals in 1980, 1981, 1991, and 1996 at (a) site U, (b) site M, and (c) site O. The numbers of individuals are standardised as individuals per site avoiding confusion as a consequence of the variable number of pitfall traps. In total, 63 species with 5028 individuals of ground beetles were recorded.

found in volume class 128. There was also a peak of species in volume class 128 in 1991 but only in site U was there a clear preference for this class. In the other two sites there was a shift of this peak to biovolume classes 64 (site M) and 32 (site O). With data from 1980 being representative of the period up to 1990 (when pollution was still active), 1991 may be characterised as a transition between the pollution period and 1996. In 1996 there is a clear unimodal pattern of biovolume distribution with most species occurring in volume class 32. That is, there was a noticeable change of the distribution peak from volume class 128 (1980/1981) to volume class 32 (1996) in the time period covering the change from pollution to the closing of the factory.

At all three sites significant differences were recognisable between the four years (Table 2), but when mean biovolume was considered there were no differences between 1980 and 1981 in any study sites (Fig. 3a–c). Sites U and O showed a significant difference between the pollution period (1981) and the time after factory closing (1991) (Fig. 3a,c) but there were no such significant difference between 1981 and 1991 at site M. There was, however, a significant difference between 1980 and 1991 at site M. At site O the only difference was found between the pollution period (1981) and the period after factory closing (1991). At site U there was a further significant difference between body size in 1991 and 1996. Body size declined faster in site U than in the other sites and the smallest individuals across the whole study area were found at site U in both 1991 and 1996. In 1991 the species size was at its smallest in site U, this increased at site M but then returned in site O to a mean biovolume similar to site U. In 1996 species size at site U was again the smallest, species size increased in site M and remained at this level in site O.

There was a significant negative correlation (Fig. 4a,b) between mean biovolume and the number of individuals ($r^2 = 0.37$, $F_{1,10} = 5.82$, $P = 0.04$; Fig. 4a) and species ($r^2 = 0.79$, $F_{1,10} = 37.76$, $P = 0.0001$; Fig. 4b), and a significant positive correlation between the effective diversity of detectable ground beetles and the number of plant species ($r^2 = 0.52$, $F_{1,7} = 7.66$, $P = 0.03$; Fig. 4c).

There were also changes in ground beetle assemblages. Only a few species were lost over the whole study period (Fig. 5a); in 1991 eight species of the 1981 fauna were lost and by 1996 a further two species had been lost. The lost species were always larger (Fig. 5b) and mostly brachypterous species (Fig. 5d). On the other hand, new species recorded in 1991 were very small and most were macropterous (Fig. 5c) and imaginal hibernators (Fig. 5f). The numbers of larval hibernators ($n_{1991} = 9$) and brachypterous ($n_{1991} = 7$) species were very low in 1991 but had increased by 1996 ($n_{1996} = 22$, $n_{1996} = 9$ respectively). The decreased mean biovolume recorded in 1991 may be explained by the presence of new immigrant species, rather than by the emigration of larger animals. While the number of macropterous species increased markedly with decreasing pollution, brachypterous species only increased marginally compared with the total number of species.

Table 1. Comparison of both immersion and digital–optical biovolume measurements for three reference species ($n = 20$).

	Immersion volume (mm^3)	Digital ellipsoid volume (mm^3)	Error (%)
Amara plebeja	19.10 ± 3.51	20.29 ± 3.01	8.35
Anisodactylus binotatus	83.75 ± 8.51	88.84 ± 9.82	9.24
Abax paralellepipedus	280.17 ± 28.84	323.10 ± 32.37	13.13
Mean error (%)			10.24

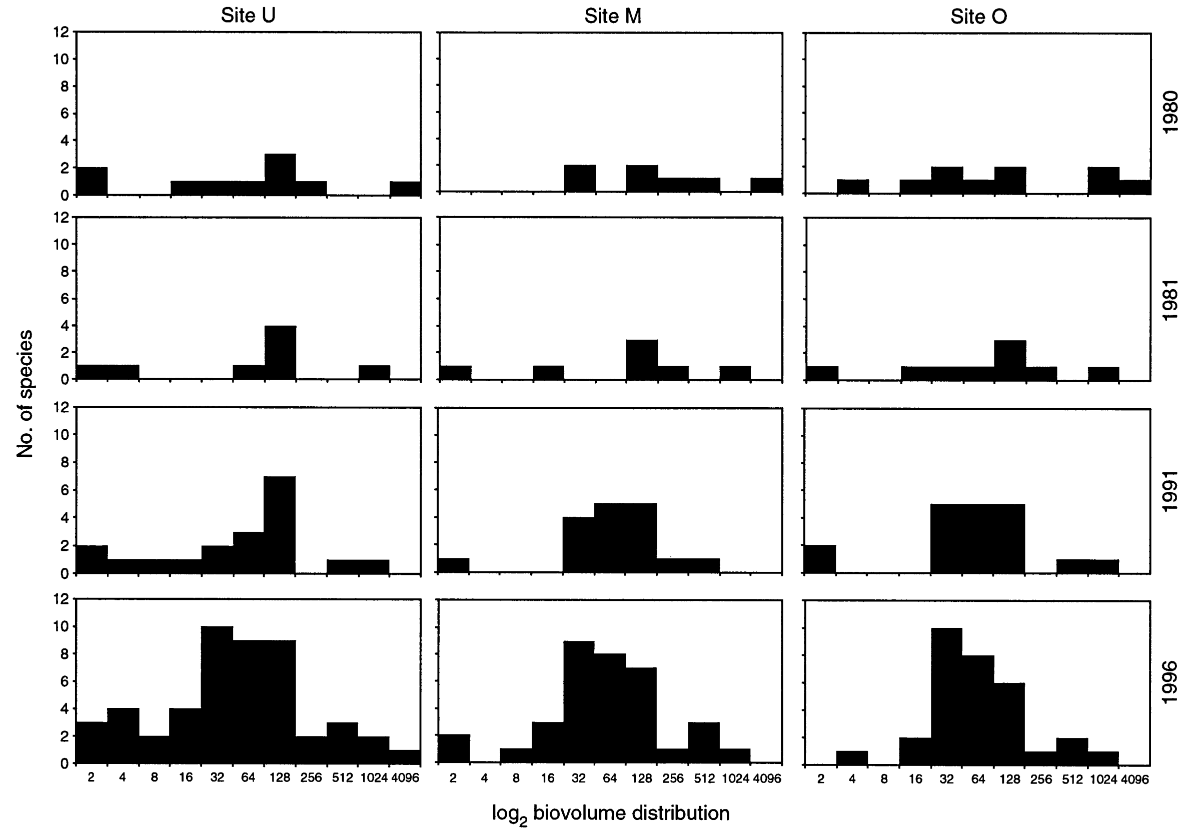

Fig. 2. Distribution of species number on a biovolume (mm^3) $\log_2$ scale (Preston, 1948); each species was classified into its own biovolume class. The number of species for each year and site are presented.

Discussion

There was a significant decrease in average ground beetle body size over the period 1980–1996. It is believed that the main causal factor, albeit indirectly, was ecological succession after factory closure in 1990. The similarity of results between 1980 and 1990 may be explained by the constant pollution experienced between these years (Metzner *et al.*, 1997); the 1980/81 data can be taken to be representative of pre-closure 1990. After factory closure in 1990 there was a noticeable increase in the number of individuals in all three sites (Fig. 1). This was especially true in site U where there was a marked increase in the number of individual beetles, although the relatively smaller increase in number of species suggests that high numbers tended to occur in only a few species. Site U, with the highest pollution before 1990, exhibited very fast succession; most landscape faces on this area were completely vegetation-free during the pollution era. After factory closure, and subsequent reduction in pollution, a few stress-tolerant, ruderal plants quickly formed a new, low diversity, high density lawn (Heinrich *et al.*, 2001). The first consequence of this new growth was a marked increase in primary production (Schäller *et al.*, 1987) followed by a high herbivore immigration (Perner *et al.*, 2003). Such a high herbivore density provides prey for a similarly high density of carnivore predators (Peters, 1983). Furthermore, two of the most dominant species in site U (*Anisodactylus binotatus* (F.) and *Harpalus affinis* (Schrk.)) are know as facultative seed feeders. This flexible foraging behaviour may explain both their fast response and their high density, particularly after factory closure in 1991. Together with *Amara plebeja* (Gyll.) both species are well adapted to the relatively high temperatures and ruderal conditions experienced in site U (Barndt *et al.*, 1991), which may be an additional reason for their high abundances.

Table 2. Results of the one-way ANOVA of sites U, M, and O. The sum of squares (SS type III), the degrees of freedom (d.f.), test statistic (*F*) and the significance level (*P*) are given.

Sites	Source	SS type III	d.f.	*F*	*P*
Site U	Year	79.20	3	93.46	<0.001
	Error	1078.13	3817		
Site M	Year	7.28	3	16.02	<0.001
	Error	71.14	470		
Site O	Year	4.58	3	9.41	<0.001
	Error	118.14	729		

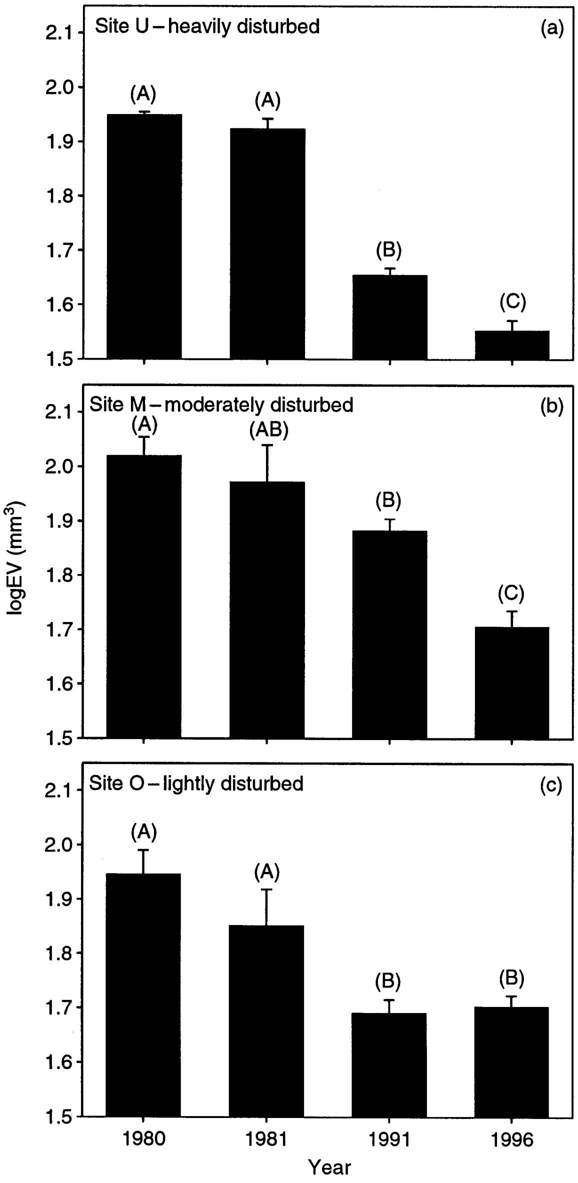

Fig. 3. The mean biovolume with standard error for 1980, 1981, 1991, and 1996 at (a) site U, (b) site M, and (c) site O. The decimal logarithm was taken for all biovolume values (mm^3). Different letters represent differences at the $P < 0.05$ significance level.

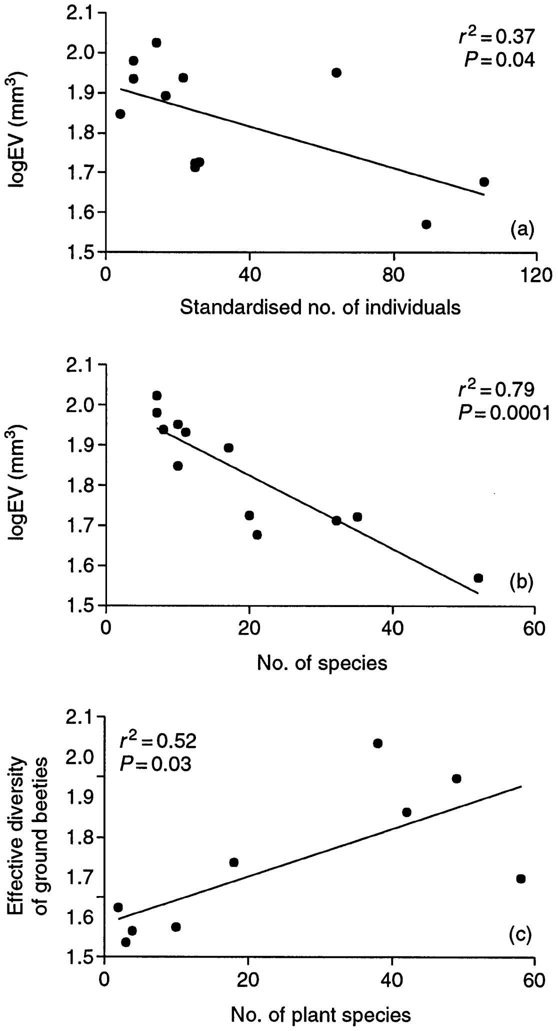

Fig. 4. The dependence of mean biovolume (mm^3) on (a) standardised number of individuals and (b) the number of species. (c) The relationship between the effective diversity of ground beetles and the number of plant species. The equation of linear regression, r^2 and the significant level (P) are presented.

There were also increases in species and individual numbers in both sites M and O but, at individual level, the latter was as low as a third of that found at site U.

Only in 1996 was a clear unimodal pattern obvious when body size distribution was investigated on a $\log_2$ distribution (Fig. 2). Most species occurred at the median body size class (Peters & Wasserberg, 1983; May 1986; Siemann *et al.*, 1996). Peters (1983) and May (1986) postulated that this unimodal relationship between body size and number of species suggested a trade-off between several species' characteristics, for example between metabolic efficiency and reproductive rate (Brown & Marquet, 1993). A shift of average body size from the higher to a lower biovolume class illustrates that the spectrum of characters in the ground beetle assemblage changed with time. The large body size found in 1980 and 1981 can be explained by the ground beetle assemblage being adapted to the polluted environment arising from the factory activity of 20 years ago (Sander, 1984), as indeed were the herbivore and plant communities (Heinrich, 1984; Köhler, 1984; Peter, 1984). Plant diversity was low during this period (Heinrich, 1984) and herbivore diversity decreased as a consequence (Tilman, 1986; Buse, 1988; Hunter & Price, 1992). Thus it is assumed that in 1980 and 1981, a few herbivore species

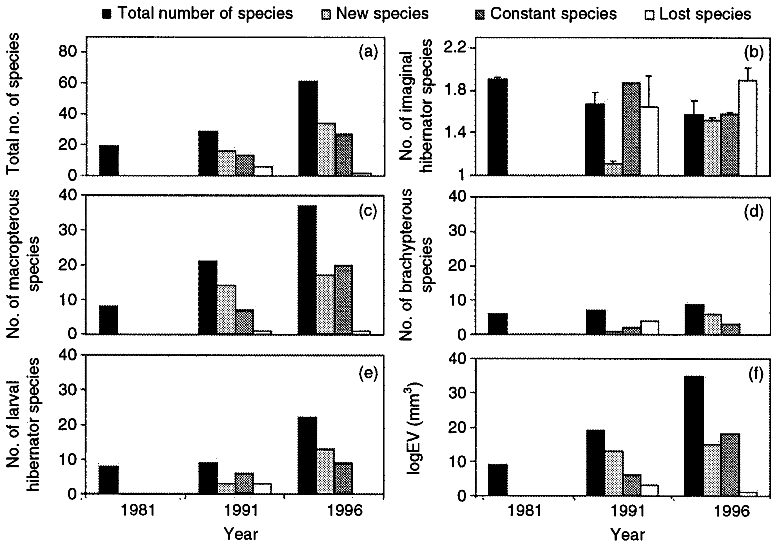

Fig. 5. Species turnover from 1981 to 1991 and 1991 to 1996; (a) total species turnover, (b) mean biovolume, (c) number of macropterous species, (d) number of brachypterous species, (e) number of larval hibernator species, and (f) number of imaginal hibernator species. In (c)–(f) numbers are always in relation to the total number of species in (a). Species new in the next year are called *new species*, species constant between two years are called *constant species* and species that are lost from the past are called *lost species*.

fed on a few plants, and that these species were generalised species synonymous with the beginning of succession (MacArthur & Levins, 1967; Brown & Southwood, 1987). Other studies, for example Kitahara *et al.* (2000), have found that more generalists are found in disturbed areas, and studies have shown that in herbivore communities generalists frequently have a larger size than specialists (Basset *et al.*, 1994; Novotny & Basset, 1999). It is suggested that in 1980 and 1981 there were only a few large herbivore species present as potential prey for the carnivore ground beetles. Belaoussoff *et al.* (2003) predict that maximum relative prey size tends to increase with body size; small species (<10 mm long) are limited by their ability to catch, or chew, so feed only on prey with smaller body sizes (Loreau, 1988). In comparison, large ground beetles species (>10 mm in length) are not restricted to smaller prey and tend to have a wider prey spectrum (Rushton *et al.*, 1991). In addition, larger ground beetle species catch more, and a greater diversity of, prey so generally use a disproportionately wider share of the resources within local ecosystems (Brown & Maurer, 1986; Siemann *et al.*, 1996). Furthermore, Peters (1983) predicts a generally higher metabolic efficiency when foraging, resulting in larger species having a greater radius of foraging.

At all three sites (sites U, M, and O) the decreasing mean body size between the pollution period (1980/81) and the post-pollution period (1996) supports Siemann *et al.*'s (1999) efficiency–specialisation hypothesis (Fig. 3a–c). This hypothesis suggests that in earlier seral stages plants exhibit poor defence against herbivores (Reader & Southwood, 1981) but have a high growth rate and a low tissue C:N ratio (Tilman, 1990). Thus large herbivores outcompete smaller species as they have both greater digestive efficiency due to larger intestines and longer food retention time (Peters, 1983; Brown, 1995), and greater metabolic efficiency (Hemmingsen, 1960; West *et al.*, 1997). In later seral stages plants are less palatable (Reader & Southwood, 1981) and have a lower growth rate with a higher C:N ratio in their tissue (Tilman, 1990). Now, smaller species outcompete larger species as they can perceive a greater level of heterogeneity and specialise on those parts of the plants that give the best quality resource (Morse *et al.*, 1985; May 1986; Shorrocks *et al.*, 1991). Margalef (1968) and Odum (1969) have also postulated an increase of specialisation in animal communities in later seral stages. In this study a similar effect of body size in ground beetle assemblages has been shown. Ground beetles are mostly predators, but they do have to adapt to increasing heterogeneity in the same way as herbivores. A significant negative regression was found between the density of species and individuals, and mean body size (Fig. 4a,b). This result provides additional support for the efficiency–specialisation hypothesis of Siemann *et al.* (1999) where increasing diversity in habitat structure leads to more new species in different microhabitats (Buse, 1988). This may cause increasing competition for habitat resource and promote further niche differentiation and specialisation. Such a direct relationship between species or individual number, and the connected shift in average body size, has been formulated over a range of animal taxa by several authors, for example Peters (1983), Morse *et al.* (1988), Blackburn and Harvey (1990), and Siemann *et al.* (1996). In all cases a decrease in average body size with increasing species or individual number has been identified. Further evidence for a positive relationship between habitat structure and ground beetle body size is the positive significant regression between number of plant species and the effective diversity of ground beetles (Fig. 4c). A direct connection between the herbivore species and the ground beetles as a predator group is assumed with increasing specialisation at herbivore level automatically leading to an increasing specialisation on predator level.

Changes in habitat structure may be also affecting the average body size of ground beetle assemblages mediated through changes in foraging efficiency. Carabid foraging success, particularly as (mainly) running hunters, is linked with vegetation structure and density (e.g. discussed in Ribera *et al.*, 2001). Early succession and open structured vegetation will favour larger species that are more efficient at travelling larger distances in a patchy environment. In later seral stages with denser vegetation structure, however, smaller and more agile species may be favoured. In this case finding resources is more important than 'getting' to them.

The extreme decrease in mean body size at site U compared with the comparable, much less marked, decrease at both sites M and O can not only be explained by the efficiency–specialisation hypothesis, but additionally adds support to the hypothesis of Blake *et al.* (1994). After the fertiliser factory was closed in 1990 a marked decrease of the pollution residuals in top soil, especially in the heavily polluted site U, was observed (Metzner *et al.*, 1997; Perner *et al.*, 2003). Although still the most polluted site, contaminant foods fall below a particular threshold level in 1991 to promote an immigration of a few macropterous species with numerous individuals into the site [see Sustek (1987), Blake *et al.* (1994), and Niemalä and Kotze (2000) for such effects in urban and agricultural ecosystems]. Species turnover analyses (Fig. 5b,c) enlighten us further. In site U three medium-sized species were dominant (*A. binotatus*, *H. affinis*, and *A. plebeja*). By comparing differently managed (disturbed) sites, Blake *et al.* (1994) found a smaller mean body size of ground beetles in the more disturbed habitats. They suggested that this arose from the quicker growth and the better dispersal of small macropterous ground beetles. Larger ground beetles have a longer juvenile period, are mostly brachypterous, and exhibit less dispersal. Blake *et al.* (1994) also found that smaller ground beetles were mostly imaginal hibernators with quick-growing larvae and a high density in the summer. Large ground beetles (e.g. *Carabus* sp.) that are larval hibernators have perennial larval development and life-history strategies that demand a stabilised habitat with high food resources. The present species turnover data support this; in 1991 species were mostly small, macropterous, and imaginal hibernators. In 1991, species immigrating into site U could be characterised as pioneer colonists. These species show a better fitness (van Huizen, 1990; Aukema, 1991; Turin, 2000) in a rapidly changing habitat. However, at site M there was a smaller (not significant) decrease of mean body size in the ground beetle assemblage between 1981 and 1991. This suggests that such *rapid immigration effects* driven by the level of disturbance play only a minor role in the less polluted site M, and that the body size shift over time is dominated by more gradual succession effects. This seems to be particularly true for the moderately degraded site O. Although in 1991 the mean body size of the ground dwelling assemblage was there similar to that of site U, the similarity is almost certainly not due to the immigration effects mentioned above. It is known that because of the lower pollution effects in site O the regeneration processes in plants and animals start earlier here than in sites U and M. This suggests that the mean body size shift in site O seems to be mainly due to succession-dependent mechanisms.

Carnivorous ground beetles are significantly smaller in later succession than in earlier seral stages, and seem to be more specialised in later seral stages. This supports the hypothesis of Siemann *et al.* (1999). Furthermore, the analyses of the mean body size during transition (1991) from pollution to post-pollution period demonstrate that the hypothesis of Blake *et al.* (1994) is also partly supported and may overlay the effects driven by succession. It is concluded that both hypotheses may be used to explain not only the change in body size from a highly polluted to a less-polluted area but also the relationship between habitat structure and predatory ground beetles.

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Appendix

Table A1. Species composition, biovolume (BV), hibernation type [L, larval; (L), predominantly larval; I, imaginal; (I), imaginal including autumn stock], wing morphology (ma, macropterous; s, sporadic fliers; br, brachypterous; di, dimorphic) and number of individuals per site. The standardised number of individuals is determined by dividing total number of individuals and number of pitfall traps per site. Nomenclature used follows Köhler and Klausnitzer (1998).

Species	BV (mm^3)	Hibernation type	Wing morphology	U80	U81	U91	U96	M80	M81	M91	M96	O80	O81	O91	O96
Abax parallelepipedus (Pill. Mitt., 1783)	322.6	(L)	br	0	0	0	2	0	0	0	1	0	0	0	8
Amara aenea (DeGeer, 1774)	25.6	I	ma	0	0	0	0	0	0	2	5	0	0	1	2
Amara apricaria (Payk., 1790)	24.7	(L)	ma	0	0	0	1	0	0	0	0	0	0	0	0
Amara aulica (Panz., 1797)	99.9	L	ma (s)	0	0	1	13	0	0	19	7	0	0	7	3
Amara bifrons (Gyll., 1810)	14	L	ma	0	0	0	9	0	0	0	0	0	0	0	0
Amara communis (Panz., 1797)	23	(I)	ma (s)	0	0	0	0	0	0	0	4	0	0	0	1
Amara convexior Steph., 1828	23.7	I	ma (s)	0	0	0	2	0	0	0	21	0	0	6	26
Amara convexiuscula (Marsh., 1802)	75.9	L	ma	0	0	0	67	0	0	0	1	0	0	0	2
Amara equestris (Duft., 1812)	53.4	L	ma (s)	0	0	0	1	0	0	2	1	0	0	1	0
Amara familiaris (Duft., 1812)	18.8	I	ma	0	0	0	1	1	0	1	5	0	0	4	2
Amara ingenua (Duft., 1812)	62.4	I	ma	0	0	0	50	0	0	0	1	0	0	0	3
Amara lunicollis Schdte., 1837	29.5	I	ma	0	0	0	0	0	0	0	10	1	0	0	2
Amara montivaga Sturm, 1825	40.3	I	ma	0	0	0	0	0	0	0	0	0	0	0	1
Amara ovata (F., 1792)	64.6	(I)	ma	0	0	0	2	0	0	0	2	0	0	0	0
Amara plebeja (Gyll., 1810)	19.2	I	ma	2	0	249	4	0	0	1	0	0	0	2	1
Amara similata (Gyll., 1810)	43.6	I	ma	0	0	0	4	0	0	1	2	0	0	2	1
Anisodactylus binotatus (F., 1787)	90.4	(I)	ma	619	167	773	51	57	21	45	0	57	7	10	0
Badister bullatus (Schrk., 1798)	8.2	I	ma	0	0	0	1	0	0	0	0	0	0	0	1
Bembidion lampros (Hbst., 1784)	2.3	I	di	0	0	0	1	0	0	0	0	0	0	0	1
Bembidion properans (Steph., 1828)	3.1	(I)	di	0	0	0	0	0	0	0	0	1	0	0	0
Bembidion quadrimaculatum (L., 1761)	1.9	(L)	ma	2	2	0	0	0	1	0	0	0	1	0	0
Bradycellus csikii Laczo, 1912	3	(L)	di	0	0	0	7	0	0	0	0	0	0	0	0
Bradycellus harpalinus (Serv., 1821)	4.5	(L)	di	0	0	0	13	0	0	0	1	0	0	0	0
Bradycellus verbasci (Duft., 1812)	5.9	(L)	ma	0	0	1	1	0	0	0	0	0	0	0	0
Calathus fuscipes (Goeze, 1777)	89.9	(L)	di	0	0	2	19	0	0	11	1	0		80	1
Calathus melanocephalus (L., 1758)	23.7	(L)	di	0	0	16	183	0	0	6	51	2	2	63	42
Calathus mollis (Marsh., 1802)	27.7	(L)	di	0	0	0	7	0	0	0	1	0	0	0	2
Carabus auratus L., 1761	688.5	I	br	0	1	0	0	0	0	0	0	1	0	0	0
Carabus cancellatus Ill., 1798	589.6	I	br	0	0	0	3	0	0	0	0	1	1	0	0
Carabus convexus F., 1775	297.8	I	br	0	0	1	20	0	0	2	28	0	0	2	22
Carabus coriaceus L., 1758	2351.2	(L)	br	2	0	0	2	2	0	0	0	2	0	0	0
Carabus nemoralis Müll., 1764	644.8	(I)	br	0	0	1	1	0	3	0	1	0	0	1	2
Cychrus caraboides (L., 1758)	292.3	I	br	0	0	0	2	3	0	0	10	0	0	0	0
Cymindis humeralis (Geoffr., 1785)	34.5	L	br	0	0	0	3	0	0	3	4	3	1	5	22
Dromius linearis (Ol., 1795)	3.5	(I)	di	0	0	0	1	0	0	0	0	0	0	0	0
Harpalus affinis (Schrk., 1781)	63.1	I	ma	1	1	448	28	0	0	2	4	0	0	1	4
Harpalus atratus Latr., 1804	81.4	I	ma	1	1	5	0	0	0	0	0	0	0	0	0
Harpalus distinguendus (Duft., 1812)	33.1	(I)	ma	0	0	0	2	0	0	0	0	0	0	0	0

Table A1. Continued

Species	BV (mm^3)	Hibernation type	Wing morphology	U80	U81	U91	U96	M80	M81	M91	M96	O80	O81	O91	O96
Harpalus honestus (Duft., 1812)	35.9	I	ma	0	0	7	0	0	0	0	0	0	0	0	2
Harpalus latus (L., 1758)	44.6	I	ma (s)	0	0	0	66	0	0	0	13	0	0	1	24
Harpalus rubripes (Duft., 1812)	71.4	(I)	ma	0	0	3	6	0	0	6	9	0	0	102	60
Harpalus signaticornis (Duft., 1812)	19	I	ma	0	0	0	1	0	0	0	0	0	0	0	0
Harpalus tardus (Panz., 1797)	49.5	(I)	ma	0	0	3	73	0	0	0	4	0	0	0	7
Leistus ferrugineus (L., 1758)	16.8	L	br	0	0	0	26	0	0	0	3	0	0	0	6
Leistus spinibarbis (F., 1775)	40	(L)	di	0	0	0	1	0	0	0	0	0	0	0	0
Microlestes maurus (Sturm, 1827)	0.8	I	di	0	0	34	115	0	0	0	2	0	0	11	0
Microlestes minutulus (Goeze, 1777)	1.5	I	ma	1	0	97	60	0	0	1	1	0	0	2	0
Ophonus azureus (F., 1775)	26.7	I	br	0	0	0	1	0	0	0	0	0	0	0	0
Ophonus nitidulus (Steph., 1828)	49.8	I	ma	0	0	0	0	0	0	2	1	0	0	0	0
Ophonus puncticeps (Steph., 1828)	25.3	(L)	ma	0	0	0	1	0	0	0	0	0	0	0	0
Panagaeus bipustulatus (F., 1775)	21.1	I	ma	0	0	0	12	0	0	0	8	0	0	0	28
Poecilus cupreus (L., 1758)	88	I	ma	2	1	4	23	1	7	21	23	2	12	10	24
Pseudoophonus griseus (Panz., 1797)	67.1	(L)	ma	0	0	0	1	0	0	0	0	0	0	0	0
Pseudoophonus rufipes (DeGeer, 1774)	101	(L)	ma	0	1	2	466	0	1	0	9	0	0	0	11
Pterostichus melanarius (Ill., 1798)	175.9	L	di	1	0	0	2	5	2	1	4	0	2	0	2
Pterostichus ovoideus (Sturm, 1824)	15.6	I	br	0	0	0	0	0	0	0	1	0	0	0	0
Stenolophus teutonus (Schrk., 1781)	14.8	I	ma	0	0	3	2	0	0	0	0	0	0	0	0
Stomis pumicatus (Panz., 1796)	12.2	I	br	1	0	0	0	0	1	0	2	1	2	0	0
Syntomus foveatus (Geoffr., 1785)	2	(I)	di	0	0	0	1	0	0	0	0	0	0	0	0
Synuchus vivalis (Ill., 1798)	20	L	di	0	0	0	0	1	0	0	1	0	0	0	2
Trechus quadristriatus (Schrk., 1781)	2.5	(L)	ma	0	2	3	1	0	0	0	0	0	0	0	0
Zabrus tenebrioides (Goeze, 1777)	229.1	L	ma	0	0	0	1	0	0	0	0	0	0	0	0
No. of species				10	8	19	48	7	7	17	35	10	9	19	31
No. of individuals				632	176	1653	1360	70	36	126	242	71	36	311	315
No. of pitfall traps				10	10	17	17	5	5	10	10	10	10	13	13
Standardised no. of individuals				63.2	17.6	97.2	80	14	7.2	12.6	24.2	7.1	3.6	23.9	24.2

8. Manuskript VII

Köhler, G., Perner, J. & Schumacher, J. (1999)
Grasshopper population dynamics and meteorological parameters –
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Grasshopper population dynamics and meteorological parameters – lessons from a case study

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Köhler, G., Perner, J. and Schumacher, J. 1999. Grasshopper population dynamics and meteorological parameters – lessons from a case study. – Ecography 22: 205–212.

Population dynamics of grasshoppers differing in phenology were analysed on a xerothermic meadow in central Germany. The study was based on standardized annual sweep net samples in relation to meteorological factors (mean and maximum temperature, rainfall, sunshine) from May through September of current and previous year, respectively. Three grasshopper species, the early hatching *Euthystira brachyptera*, the phenologically intervening *Stenobothrus lineatus*, and the late hatching *Gomphocerus rufus*, were investigated over ten years during three periods: 1971–74, 1983–85, 1987–89. By means of stepwise linear regression and a cross-validation procedure a subset of meteorological parameters was extracted which best described the field sampling data of the grasshoppers. This subset of variables was then used in multiple linear regression analyses in order to model the long-term population dynamics of the grasshoppers from 1971 to 1990. The selected variables for each species revealed different influences of meteorological parameter combinations reflecting the different phenologies. The dynamics of the three gomphocerine species modelled for 20 yr (1971–1990) differed both with maxima and minima in different years and in the fluctuation factors from 29 (*E. brachyptera*) to 155 (*S. lineatus*). In comparison with fluctuation trends in populations of other sites within the region some species-specific and habitat-specific population dynamics must be assumed. There were no significant correlations between annual aridity (precipitation-temperature)-indices and densities of the three populations studied.

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Grasshopper population fluctuations of the northern Hemisphere are generally dependent on climate and weather, followed by predators and effects of density-dependence. A warm, dry season increases a population's survival rate, developmental velocity and fecundity, while the population suffers during a cold, wet season. Rainfall also influences the growth of fresh food-plants and humidity stimulates the development of the eggs. Furthermore, predators can drastically reduce the populations. These complex relations explain why grasshopper populations are rather sensitive to climate and seasonal changes in weather (summarized in Dempster 1963, Uvarov 1977, Joern and Gaines 1990). Several studies from North America were analysing densities of rangeland grasshoppers as pest species in relation to weather data often about several decades, mainly to predict outbreaks (e.g. Edwards 1960, Gage and Mukerji 1977, Fielding and Brusven 1990). The processes underlying these correlations are very complex, hence new predictive models were developed using catastrophe theory (Lockwood and Lockwood 1991). The main aim of these studies was to detect key factors in the dynamics of high-density grasshopper populations. Moreover, the investigations do also provide the forecasting of grasshopper outbreaks and demarcating of potential outbreak areas by climate (e.g. Rubtzov 1935, Capinera and Horton 1989).

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In Europe, effects of meteorological parameters on population dynamics of non-pest grasshoppers are seldom studied, with data sets of up to five years only (Richards and Waloff 1954, Dreux 1962, Bradley 1985, Köhler and Brodhun 1987, Berger 1988). Mass multiplications of species like *Calliptamus italicus*, *Dociostaurus brevicollis*, and *Chorthippus biguttulus* in southern Europe are discussed only in relationship to aridity (Dempster 1963, Nagy 1995). Altogether, results are still rather inconsistent, indicating more subtle relationships between local populations and meteorological parameters as a complex of radiation, temperature, and precipitation (for Central Europe reviewed in Ingrisch and Köhler 1998).

The present study on low-density grasshopper populations arises from monitoring programmes on a xerothermic study site to investigate the dynamics in arthropod communities (following Müller et al. 1978). Out of about a dozen grasshopper species (Köhler 1987b) three gomphocerine species were selected because of their differing phenology. We studied dynamics for two reasons, to test the hypothesis that in Central Europe grasshopper population dynamics and meteorological factors are generally correlated and if so to model unknown population fluctuations in the past using meteorological parameters. In accordance with key factor analysis (Samietz et al. 1996) we correlated densities with meteorological parameter combinations of the present and the previous year, respectively. Moreover, as a much more simple approach a relationship between annual aridity indices (for grasshoppers according to Rubtzov 1935) and density ratings was examined.

Material and methods

Study site

Field studies were conducted in the 'Leutratal' nature reserve (50°52'N, 11°34'E) near Jena, Thuringia/Germany. The study plot (100 × 20 m) was located in the upper part of an exposed southern limestone slope (700 × 80 m) ca 340 m a.s.l., with an average inclination of 30°, where a rather homogeneous semiarid grassland (Teucrio-Seslerietum) with a vegetation cover between 50 and 60% had developed (Müller et al. 1978, Perner 1993). Such slopes are characteristic for the regional landscape along the Central Saale river valley. Structural constancy over time had been detected by using a continuous square sampling technique (Böhnert and Reichhoff 1978); therefore, an influence of vegetation succession has been ignored here. The study plot was isolated from neighbouring habitats by mixed-forest formations, so dispersal of grasshoppers between local populations was unlikely.

Sampling procedure

Grasshoppers were sampled using standardized sweep net sampling during three periods: 1971–74, 1983–85, and 1987–89 (for details see Müller et al. 1978, Köhler 1988, Perner 1993). In these ten years, samples were taken within the same long plot (100 × 20 m) in two- to three-week intervals from late April through late October, resulting in ten samples per year. On each sampling date, ten sub-samples in ten double swings each were taken, with every sub-sample on a line transect of ca 20 m. These 100 double swings per date and 1000 double swings per year, respectively, represented our sampling data. These annual sample sizes are designated in the text as 'density ratings'. Field work was carried out on dry, sunny days with little or no wind. Insects were swept, put into plastic bags, treated with ethyl acetate, and stored in a fridge. The following day they were placed in 70% ethyl alcohol and later examined to determine species, instar and sex. Adult grasshoppers were identified to species, while larval determination followed Oschmann (1969) and personal experience (Köhler unpubl.). Thereafter, we selected three phenologically different species of grasshopper: *Euthystira brachyptera* (Ocskay), *Stenobothrus lineatus* (Panzer), and *Gomphocerus rufus* (L.).

Meteorological parameters and statistical treatments

Sampling data of the ten years were used as response variables, and meteorological parameter combinations throughout the vegetation period as independent (predictive) variables. Daily values of four parameters in order to calculate the monthly means or totals from May to September were obtained from the Jena Meteorological Station (ca 6 km N of the study plot): mean temperature, mean maximum temperature, rainfall and sunshine. The data from individual months resulted in five values (May–September) per parameter, all the possible combinations of successive months (May–June, May–June–July...August–September) in ten values per parameter. So each of the four meteorological parameters was calculated for 15 periods, resulting in 60 values per year. Using 60 values from current and 60 from previous year, altogether 120 combinations of meteorological parameters were introduced into stepwise linear regression analysis for each grasshopper species. The months included represent main phenological periods (juvenile stages, adults) of the grasshopper species (see Fig. 1). Furthermore, an influence from the reproductive success of the former generation on current population dynamics (e.g. Berger 1988, Samietz and Köhler 1998) should also be assumed, using previous year parameters as well.

The process of selecting a set of independent variables best explaining the observed population dynamics consisted of two steps. First, a stepwise linear regression procedure was used to select a set of six variables best describing the observed variation of the response variables. Hence the best predicting independent variable (density ratings from altogether ten years of *E. brachyptera*, *S. lineatus*, *G. rufus* each) was entered into the equation first, the independent variable that added the next largest amount of information was entered second, and so on. Since prediction of population density ratings during intervening years was a main target of our analysis, in a second step we used a cross-validation criterion to decide on a subset of these six independent variables to be included in the model. The general paradigm of cross-validation procedures is to split the dataset into a training set (used to form the prediction rule) and an assessment set (used to evaluate the predictive power of the rule). Following the guidelines given in Davison and Hinkley (1997) we used the K-fold adjusted cross-validation algorithm, where the data set was randomly split into five groups of size two. The observed values in each group were then compared with the predicted values resulting from linear regressions based on the remaining four groups. Averaging the squared differences between actual and predicted values yields an estimate of aggregate prediction error. It is a measure of how well the prediction rule does when values in the assessment group are predicted from the rest of the data (training set) and summarizes accuracy of prediction across a range of values of the independent variables (selected meteorological parameters), using a given regression model (see Davison and Hinkley 1997). The set of independent variables was chosen to minimize the estimated aggregate prediction errors.

Finally, an aridity index was calculated for both the region and every year of study using the formula

$$A = r\,(t_{iv\ ix} - 36)$$

where r is the annual rainfall (in mm) and $t_{iv\ ix}$ the sum of mean monthly temperatures from April to September. The denominator is the sum of mean temperatures > 6°C (developmental threshold) for the six effective months (according to Rubtzov 1935, and quoted in English by Uvarov 1977).

Results

Effects of species phenology

The species investigated are seasonal, with an obligate embryonic diapause, and differ in their phenology covering the vegetation period from April through November (Fig. 1). *Euthystira brachyptera* hatches in the second half of April, and the main adult period being at the beginning of July. However, some adult females can still be found as late as August. *Stenobothrus lineatus* is also in its first larval instar in late April, but the instar peak does not occur until mid-May, while its adult peak is not until mid-July. In contrast to both of these species, *Gomphocerus rufus* hatches late in the season, beginning after mid-May and reaching its first larvae peak in the middle of June. Its adult period culminates in late August and early September, although the rufous grasshopper can sometimes still be found in November (Fig. 1). Depending on the year, population phenological shifts of up to two weeks can be observed for each species (Perner 1993, Samietz 1998).

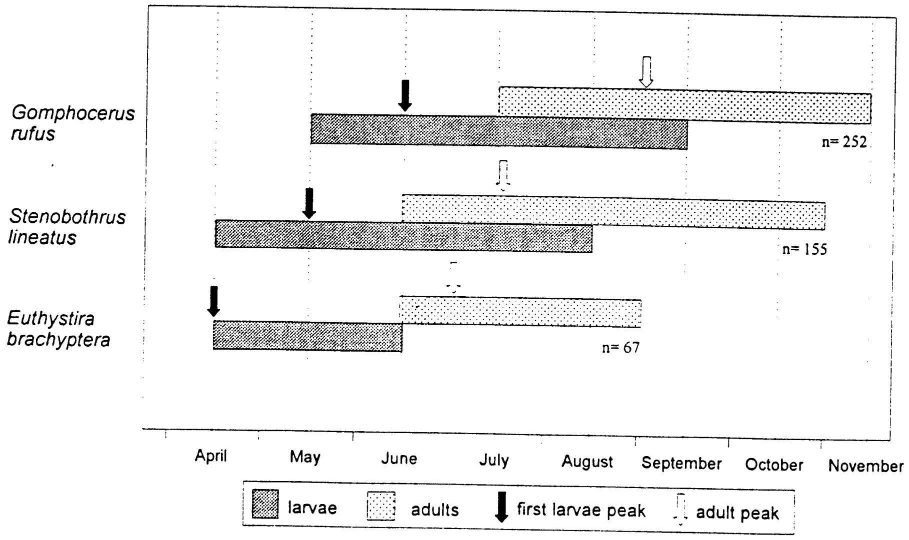

Fig. 1. Phenologies of grasshopper species studied, based on sweep net samples on the study plot, 1987–1989.

Table 1. Order of the meteorological parameters as selected by the stepwise regression procedure. r^2 = coefficient of determination based on multiple linear regression including all parameters selected. S – monthly mean period of sunshine. T – monthly mean temperature. Tx – monthly mean maximum temperature, R – monthly sum of rainfall. l – value of previous (last) year.

Euthystira bracyptera		*Stenobothrus lineatus*		*Gomphocerus rufus*	
Parameter	r^2	Parameter	r^2	Parameter	r^2
l S Jun–Jul	0.35	T Jun	0.36	S Aug–Sep	0.53
l R May–Jul	0.69	Tx Jul	0.57	T Aug–Sep	0.83
S Jun	0.82	l R Jun	0.84	R Sep	0.86
R Jun	0.97	l R May–Jul	0.86	l R Jun–Jul	0.93
l R Jun	0.99	R Jun	0.92	l T Jun–Aug	0.94
l S Jun	0.99	S Jun–Jul	0.93	l Tx Jun–Aug	0.94

The six best meteorological parameters affecting each species dynamics as selected by the stepwise linear regression procedure are given in Table 1. It is striking that in the earlier species *E. brachyptera* and *S. lineatus* parameters from May–July dominate, and in the late *G. rufus* those of July–September. Furthermore, the species evince several differences with respect to important parameters. In *E. brachyptera* sunshine and rainfall are important, in *S. lineatus* temperature and rainfall, and in *G. rufus* a complex of sunshine, temperature, and rainfall is of greatest importance. Besides some expected trends, due to species phenology, these results indicate that any single meteorological factors cannot explain sufficiently the fluctuations in grasshopper population dynamics. The correlations with parameters of the present and the previous year also changed with the species. Thus in *E. brachyptera* four, in *S. lineatus* two, and in *G. rufus* three meteorological parameters (out of six) of the previous year could be noticed (Table 1).

Modelling population dynamics

For modelling population dynamics, the used formula parameters as results of the multiple linear regression analyses are given in Table 2, and the estimated aggregate prediction errors for models including one to six independent variables are shown in Fig. 2. The prediction errors are minimized when four (*E. brachyptera*), three (*S. lineatus*) or two independent variables (*G. rufus*) are included in the linear regression model. For *E. brachyptera* the parameters sunshine (S) of June–July and rainfall (R) of May–July in the previous (last) year (l S Jun–Jul, l R May–Jul) as well as sunshine and rainfall of June in the current year (S Jun, R Jun) are highly significant and allow a good estimation of dynamics. The fluctuations of *S. lineatus* were predicted well with the parameters T Jun (temperature of June in the current year), Tx Jul (maximum temperature of July in the current year) and l R Jun (rainfall of June in the previous year). Only two current-year parameters, sunshine and temperature of August–September (S Aug–Sep, T Aug–Sep), are sufficient to estimate the dynamics of *G. rufus* (Table 2).

Based on these parameters the dynamics of the three gomphocerine species were modelled over 20 yr continuously (1971–1990, Fig. 3). Certain general patterns appear in the three population curves. Low population levels dominate in the first half of the seventies, in 1972 (all species), 1975 (*S. lineatus*), and again in 1985 (*S. lineatus*, *G. rufus*). From 1977 to 1984 most of the values are considerably higher, although the curves peaked in different years: *E. brachyptera* (1978, 1981), *S. lineatus* (1979), and *G. rufus* (1977, 1984). From that period through 1990 the populations were rather irregular, but in general increasing. As far as population fluctuations are concerned, the great differences between modelled maximum and minimum sample sizes are striking, with factors amounting to 29 (*E. brachyptera*), 101 (*G. rufus*), and 155 (*S. lineatus*). The zero values in the curves (Fig. 3) indicate density ratings too low for the sampling method used but not extinction events of the populations.

To fit these results roughly, trends in modelled density ratings from year to year, resp. generation to generation (increasing vs decreasing), can be compared with trends in populations of the same species, but from different sites of the region (compare Table 3 with Fig. 3). From 1971 to 1974 similar trends in all three species occurred in a neighbouring habitat (Leutratal M) with isolated populations ca 0.3 km further down slope in the Leutra valley. In contrast to more distant populations (4.0–13.3 km), the modelled populations of *S. lineatus* and *G. rufus* did not follow the overall tendencies from 1981 to 1984, whereas from 1987 to 1988 the increase in *E. brachyptera* and the decrease in *S. lineatus* and *G. rufus* are striking again in the modelled population curves. So far, the trends of the population fluctuations throughout the region (Table 3) show some species-specific and habitat-specific characteristics.

Aridity indices and sample sizes

Any simple meteorological index will be of interest to estimate rapidly a phenology period as favourable or unfavourable for the grasshopper population dynamics. With an index of 11.6 in the study area the regional aridity is between oceanic (high value) and continental (low value) influence. However, considerable differences between years occurred, ranging from 6.5 (in 1982) to 16.9 (in 1977). From 1971 to 1990 nearly half of the annual indices produced values < 10 and half > 10, signifying dry warm or wet cold years in irregular intervals. Between 1971 and 1977, a low index often alternated with a high one, but exclusively high indices occurred during the period from 1977 to 1981 and again from 1986 to 1988. However, with supposed linear regression we could not detect any significant correlation between the annual aridity indices and observed density ratings, in any of the three grasshopper species: *E. brachyptera* ($r = 0.155$, $p = 0.671$), *S. lineatus* ($r = 0.055$, $p = 0.891$), *G. rufus* ($r = 0.263$, $p = 0.464$).

Discussion

Factors influencing grasshopper population dynamics in Central Europe are still not well understood, despite the fact that biotic influences like density-dependent processes due to food limitation and drastical population reductions by predators (Belovsky and Slade 1995) often can be neglected (Richards and Waloff 1954). Climate in general will affect ecologically similar species in similar ways. However, there are several exceptions from this rule. Our study with gomphocerine species differing in phenology gives some new insights. Relating to single meteorological factors, the special importance of insolation on grasshopper development has been shown experimentally by Begon (1983) in *Chorthippus brunneus*, whereas Samietz and Köhler (1998) stressed its influence on reproductive rates in *S. lineatus*. These ecophysiological results generally correspond with correlations from several field studies. In populations of *Chorthippus parallelus* (and *C. brunneus*) in England, radiation had the highest positive correlation with regard to field data of egg-pod density, number of females emerged, and pods per female over five years (Richards and Waloff 1954). In Marburg, Central Germany, Berger (1988) calculated correlations between July-densities of grasshoppers (mainly *C. parallelus*) and 42 combinations of meteorological data sets obtained over five years (1982–1986). Here sunshine and temperature yielded high positive correlations and rainfall high negative ones. This holds true also for North American melanopline species and perhaps for Ensifera. In the Saskatchewan grasshopper survey the relationships between four melanopline species and weather data over 32 yr were investigated. Referring to density ratings, positive correlations could be found to heat units and heat-precipitation ratios, and negative ones to precipitation (Gage and Mukerji 1977). In southern Idaho (1950–1980) densities of rangeland grasshoppers mostly correlated positively with mean monthly temperature, but also with precipitation variables (Fielding and Brusven 1990). Some conflicting results concerning rainfall must be interpreted as both direct influences on egg and instar mortality of grasshoppers and indirect ones on their food-plants. Within a bush-cricket population (*Decticus verrucivorus*) in England, observed over 18 yr, the abundance of adults was found to be highly positively correlated with total number of sunshine hours two years ago (in accordance with an obviously two-year-cycle), whereas nearly all other correlations were insignificant (Haes et al. 1990). In *Melanoplus* species (Canada), corresponding with our findings in *E. brachyptera*, the maximum correlation coefficients tended to occur with the previous year's weather, but in contrast to our results, actual densities were highly auto-correlated with those of the previous year (Gage and Mukerji 1977).

Grasshopper population dynamics has been modelled by means of meteorological parameters hitherto for pest species, namely North American rangeland

Table 2. Statistics of multiple linear regression procedures of the populations of three grasshopper species (VIF – Variance Inflation Factor is a measure of multicollinearity; all values here indicate low levels of multicollinearity).

Parameters	coefficients	SE	t	p	VIF
Euthystira brachyptera					
constant	113.925	7.802	14.602	<0.001	
1 S Jun–Jul	−0.178	0.0319	−5.595	0.003	2.057
1 R May–Jul	−0.415	0.0447	−9.282	<0.001	1.526
S Jun	−0.166	0.0236	−7.024	<0.001	1.637
R Jun	−0.191	0.0360	−5.295	0.003	2.782
Stenobothrus lineatus					
constant	−127.661	91.441	−1.396	0.212	
T Jun	29.823	6.179	4.826	0.003	1.352
Tx Jul	−10.831	3.174	−3.412	0.014	1.403
1 R Jun	−0.571	0.176	−3.241	0.018	1.045
Gomphocerus rufus					
constant	−179.626	140.595	−1.278	0.242	
S Aug–Sep	−1.718	0.311	−5.531	<0.001	1.126
T Aug–Sep	32.208	9.289	3.467	0.010	1.126

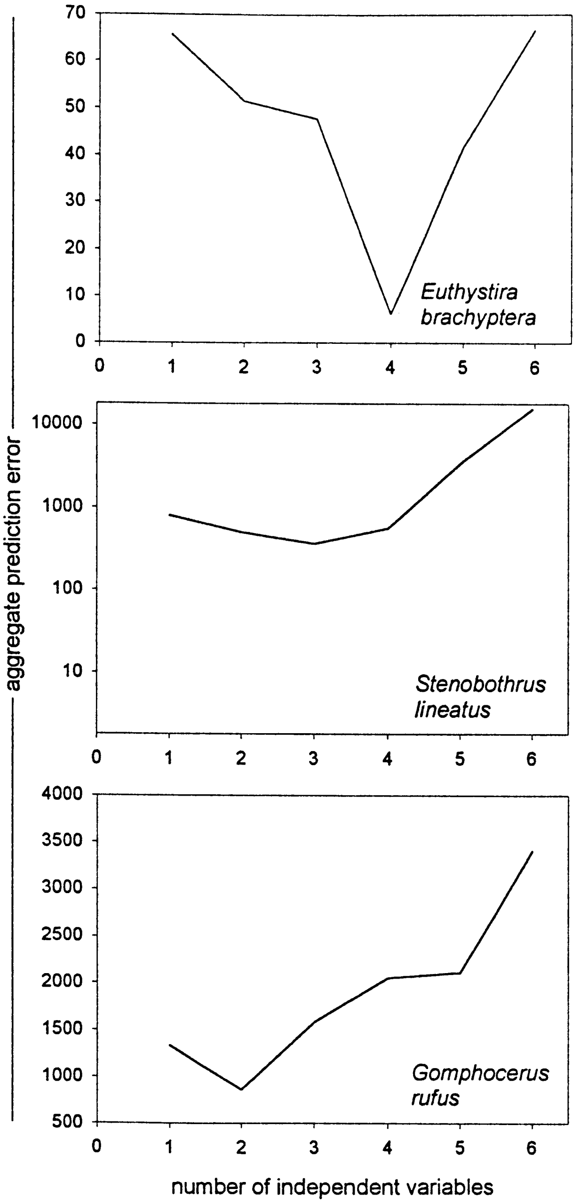

Fig. 2. Aggregate prediction error estimates for sequence of models fitted to the three grasshopper species data with the six best independent variables (meteorological parameters, see Table 1). Among the models with the same number of independent variables only the values for the best predicting model are shown.

grasshoppers (e.g. Gage and Mukerji 1977, Rodell 1977, Lockwood and Lockwood 1991). In Europe, only Berger (1988 on *C. parallelus*) focused on this problem. Grasshopper density for the next year (1987) could be forecasted with deviations up to 20% with the best values of multiple linear regression analyses. Data gathered from May to June in the previous year and from May to July in the current year yielded the best correlations. Now our results indicate distinct species-specific models due to different phenologies of grasshoppers. Furthermore, a different habitat use can also explain the differing amounts of error bars in the population curves, with lowest values in *E. brachyptera* and highest ones in *G. rufus*. In the rufous grasshopper it results from the preference of marginal areas of open grassland with shrubs and bushes instead of central areas, followed by more irregular density ratings in comparison with the two other species. In our study, density-dependence regulation has been ignored for three reasons.

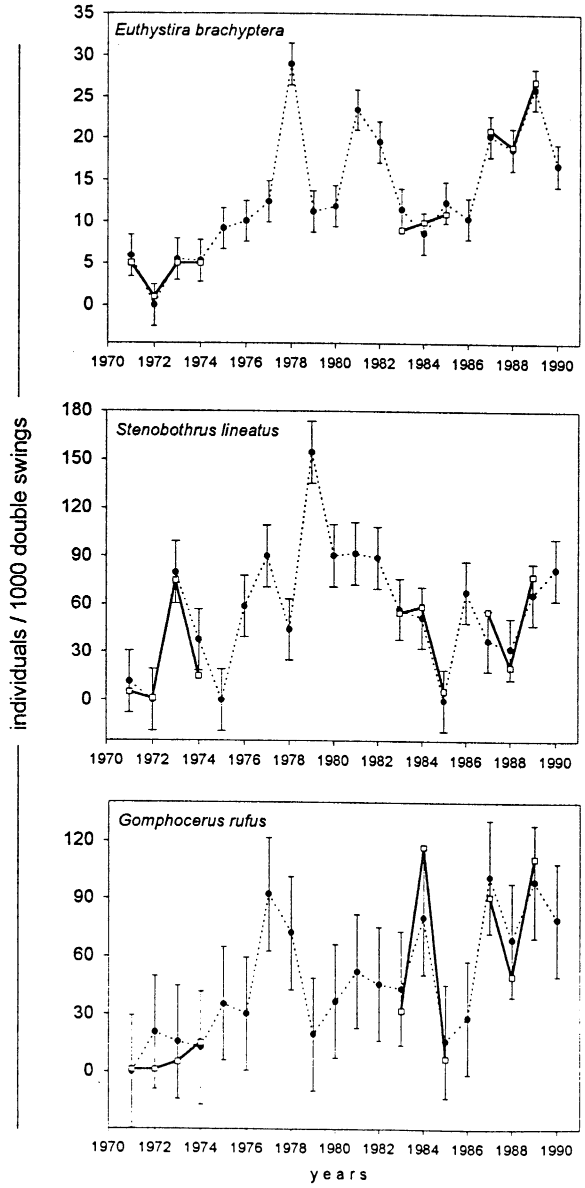

Fig. 3. Population dynamics (1971–1990) of three grasshopper species: observed (black line between empty squares) and predicted sample sizes (dotted line between filled circles). Presented error bars are square roots of the estimated aggregate prediction errors in Fig. 2.

Table 3. Comparison of densities between consecutive years from several xerothermic meadows near Jena Thuringia, Germany. See also modelled densities of the study plot in Fig. 3.

Species	site	distance from study plot (km)	sampling method	annual densities compared	source
Euthystira brachyptera	Leutratal (M)	0.3 SE	sweep net	1971 > 72 < 73 > 1974	Müller et al. (unpubl.)
	Johannisberge	4.0 NE	sweep net	1987 < 1988	Perner (1993)
Stenobothrus lineatus	Leutratal (M)	0.3 SE	sweep net	1971 < 72 = 73 > 1974	Müller et al. (unpubl.)
	Dohlenstein	8.0 SE	biocoenometer	1981 < 82 < 83 > 1984	Köhler (1988)
	Hausberg	7.3 NE	biocoenometer	1981 < 82 < 83 > 1984	Köhler (1988)
	Sonnenberge	7.3 N	biocoenometer	1981 < 82 < 83 > 1984	Köhler (1988)
	Lobdeburg	4.0 NE	biocoenometer	1981 < 82 = 83 < 1984	Köhler (1988)
	Johannisberge	4.0 NE	sweep net	1987 > 1988	Perner (1993)
Gomphocerus rufus	Leutratal (M)	0.3 SE	sweep net	1971 > 72 < 73 < 1974	Müller et al. (unpubl.)
	Lobdeburg	4.0 NE	biocoenometer	1981 > 82 < 83 > 1984	Köhler (1988)
	Gleisberg	13.3 NE	biocoenometer	1981 > 82 < 83 > 1984	Köhler (1988)
	Kernberge	4.7 NE	biocoenometer	1981 > 82 < 83 < 1984	Köhler (1988)
	Sonnenberge	7.3 N	biocoenometer	1981 < 82 < 83 > 1984	Köhler (1988)
	Hausberg	7.3 NE	biocoenometer	1981 < 82 > 83 < 1984	Köhler (1988)
	Johannisberge	4.0 NE	sweep net	1987 > 1988	Perner (1993)

First, the densities of these isolated populations calculated from the maximum sample sizes, by using a correction factor (Köhler 1987a), were rather low, amounting to 0.6 individuals m^{-2} (*E. brachyptera*), 1.2 ind. m^{-2} (*G. rufus*), and 1.8 ind. m^{-2} (*S. lineatus*). Effects of density-dependence on fitness parameters occur at considerably higher levels (Wall and Begon 1986, 1987). Second, no food limitation causing intraspecific competition, had been observed in the different years, what contrasts with results in *Melanoplus* species (Belovsky and Slade 1995). Third, we were unable to find correlations between previous- and current-year densities as shown in rangeland grasshoppers (e.g. Kemp and Dennis 1993).

Few attempts to use meteorological indices as rough indicators for grasshopper population dynamics are available. For grasshopper densities in the Maritime Alps (France), an index in relation to altitude was identified by Dreux (1962). He used an aridity index with yearly rainfall and yearly mean temperature, but also discussed the possibility of a restricted July-index as valuable. For Central Russia. Rubtzov (1935) proposed an aridity index suitable both for outbreak areas of gomphocerine species (such as *Chorthippus albomarginatus* and *Aeropus sibiricus*) and for developmental periods. Therefore, we used this index for Central European gomphocerine populations, too. According to Rubtzov (1935) outbreak areas had low aridity indices ranging between 8–10, whereas for Jena the index calculated from long-term averages (1951–80) is around 12. However, locally there is broad variation between years, so any relationship to successive grasshopper generations should be expected. Our results indicate for the three grasshopper species no correlations between aridity indices of single years and current-year population density ratings, respectively. Perhaps it is a problem of scale, with an aridity index as a rough formula valid at the zoogeographical level but not for explaining local population dynamics.

The implications of our results for forecast and conservation of low-density grasshopper populations in Central Europe are sobering. First, any index of meteorological parameters probably fails to explain the dynamics. Second, according to species phenology the obviously affecting weather parameters change. Third, between populations within the region also habitat-specific dynamics occur.

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9. Manuskript VIII

Voigt, W., Perner, J., Davis, A.J., Eggers, T., Schumacher, J., Bährmann, R.,
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TROPHIC LEVELS ARE DIFFERENTIALLY SENSITIVE TO CLIMATE

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Abstract. Predicting the response of communities to climate change is a major challenge for ecology. Communities may well not respond as entities but be disrupted, particularly if trophic levels respond differently, but as yet there is no evidence for differential responses from natural systems. We therefore analyzed unusually detailed plant and animal data collected over 20 years from two grassland communities to determine whether functional group climate sensitivity differed between trophic levels. We found that sensitivity increases significantly with increasing trophic level. This differential sensitivity would lead to community destabilization under climate change, not simple geographical shifts, and consequently must be incorporated in predictive ecological climate models.

Key words: arthropods; climate sensitivity; community; functional groups; grasslands; plants; trophic levels.

INTRODUCTION

Climate is a major driver of organism distributions and species life histories and, therefore, affects population dynamics, community composition, and the ecosystem services arising from them (Harrington and Stork 1995, Institute of Biology 1999, Lawton 2000, Parmesan et al. 2000). Consequently, predicting community responses to climate change and their impacts on human welfare is an important area of global change ecology and one of its major challenges. Nevertheless, the potential effects on complete communities are still unclear (May 1998, Harrington et al. 1999, Lawton 2000, IPCC 2001), although considerable progress has been made in understanding the responses of model systems (Ayres 1993, Jones et al. 1998, Petchey et al. 1999, Cramer et al. 2001). There is considerable evidence, however, that species respond individualistically to climate (Parmesan et al. 1999, Lawton 2000, Pimm 2001, Thomas et al. 2001, Bale et al. 2002, Watt and McFarlane 2002). Because of this, communities will be disrupted by climate change (Walther et al. 2002) since differential species responses will inevitably disrupt species interactions (Davis et al. 1998, Harrington et al. 1999, Penuelas and Filella 2001, Visser and Holleman 2001). Particularly strong disruption is likely if the average sensitivity of species differs systematically between trophic levels since, in this case, trophic interactions will be fundamentally altered. This kind of differential trophic sensitivity to climate has not yet been demonstrated in field communities because of the great difficulty and expense of long-term studies of multispecies assemblages, trophic groups, or entire communities. Some studies have, however, implicitly invoked interactions (Ives and Gilchrist 1993, Root and Schneider 1995, Fox and Morin 2001) or experimentally manipulated communities in the laboratory (Harrington and Stork 1995, Jones et al. 1998, Petchey et al. 1999, Fox and Morin 2001) or in the field (Brown et al. 1998, Grime et al. 2000, White et al. 2000). Simply scaling up the results of small-scale experiments is insufficient since real communities contain so many organisms with a multitude of complex interactions (Scholes 1990, Peters 1992, Root and Schneider 1995, Harrington et al. 1999, Lawton 2000). Nevertheless, the available evidence from short-term model systems (Jones et al. 1998, Petchey et al. 1999) indicates that such differential sensitivity exists.

We therefore analyzed extensive long-term field data on plants and animals from a real ecosystem including several functional groups on three trophic levels to determine whether trophic levels differed systematically in their sensitivity to climate variations. We used a statistical approach to assess the degree of correlation between the variation in species abundance and natural climatic variation and examined patterns in the strength of these correlations between trophic levels.

METHODS

The species data were gathered over two decades from xerothermic calcareous grassland habitats at two different sites near Jena, Germany (50.9° N, 11.6° E,

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TABLE 1. The numbers of species and individuals within sites, trophic levels, and functional groups.

Site, trophic level, and functional group	Collection method				
	Cover–abundance (No. species)	Sweep-net		Pitfall trap	
		No. species	No. individuals	No. species	No. individuals
Leutratal					
Producers					
Annual forbs	18				
Grasses	18				
Mosses	40				
Perennial forbs	86				
Woody plants	31				
Herbivores					
Cell-tissue suckers		72	16 864		
Lifetime chewers		11	4 832		
Miners		115	5 622		
Stage-specific chewers		217	22 173		
Vascular suckers		101	38 350		
Carnivores					
Attacking chewers		5	488		
Biting suckers		100	1 236		
Parasitoids		31	131		
Sucking hunters		11	296		
Steudnitz					
Producers					
Annual forbs	30				
Grasses	17				
Mosses	16				
Perennial forbs	36				
Woody plants	14				
Herbivores					
Miners		92	28 436	32	1760
Stage-specific chewers		144	2 977		
Vascular suckers		84	68 549		
Carnivores					
Biting suckers		93	6 954	77	2780
Chewing hunters		74	1 160		
Web-spinners		87	12 794		

Note: The total number of species recorded was 1295, of which 254 (193 in Leutratal [L], 113 in Steudnitz [S]) were producers, 656 (L = 518, S = 325) herbivores, and 385 (L = 147, S = 295) carnivores.

145 m above sea level). One site, Leutratal (south of Jena), is a nature reserve of seminatural calcareous grassland dominated by the grass species *Bromus erectus* Huds., *Brachypodium pinnatum* (L.) P.B., and, in the drier parts, *Sesleria varia* (Jacq.) Wettst. The other site, Steudnitz, 18 km further north, is similar but was heavily disturbed in the past by industrial air pollution. Both sites are described in detail elsewhere (Heinrich 1998, Heinrich et al. 2001; also see Appendix I).

These data derive from 254 producer species (vascular plants and mosses), 656 species (189 563 individuals) of arthropod herbivores, and 385 species (25 839 individuals) of arthropod carnivores (Table 1, Appendices A–C, H) and represent a substantial part of the whole grassland community. Plant species abundance was assessed by the Braun-Blanquet method (Kent and Coker 1994), a combined cover–abundance estimation technique. Invertebrate abundance was determined by collections from regularly maintained pitfall traps and by standardized sweep-net sampling every two weeks throughout the annual period of vegetation growth.

Data preparation

The arthropod data were standardized to unit sample vector length (sample norm) to adjust for different sample sizes:

$$x'_{ij} = \frac{x_{ij}}{\left(\sum_{j=1}^{r} x_{ij}^2\right)^{1/2}}$$

where x_{ij} is the original abundance of species i in sample j (for r sampling years). Logarithmic transformation was applied where necessary to improve normality of variances and avoid distortions (Fig. 1). Rare species of invertebrate taxa (≤5 individuals) were omitted to reduce noise. Likewise, two data sets for the parasitoid Diptera, both from Steudnitz, were also excluded because of the very low abundances of the few species

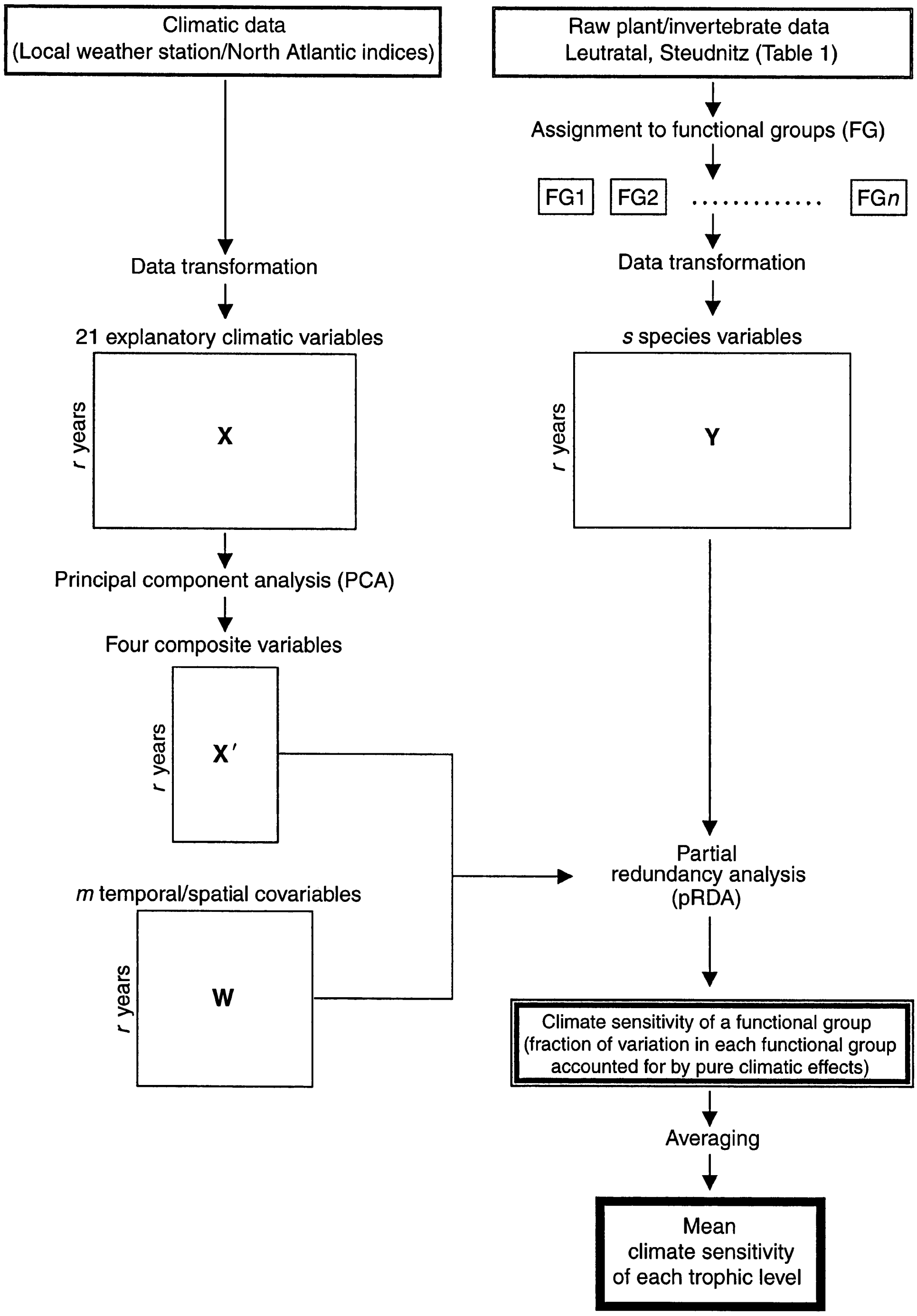

FIG. 1. Organization of data analysis (**W**, **X**, **Y**, **Z** denote data matrices).

they contained. Standardization of plant data was unnecessary because of the uniform sample size and the relative abundance scale used (Braun-Blanquet method; Kent and Coker 1994).

The climate sensitivity of multispecies groups spanning several trophic levels can only be adequately assessed by calculating an index that encapsulates the long-term overall response of the assemblage. We

TABLE 2. Original climatic variables used to produce four explanatory composite variables by a standardized principal component analysis.

No.	Name of variable	Description
1	Tav1-12	mean air temperature, whole year
2	Tav1-3	mean air temperature, January–March
3	Tav4-6	mean air temperature, April–June
4	Tav7-9	mean air temperature, July–September
5	Tav10-12	mean air temperature, October–December (of previous year)
6	Tmax	maximum air temperature (yearly average)
7	Tmin	maximum air temperature (yearly average)
8	dTmax >30	no. days with maximum temperature >30°C
9	dT <0	no. days with minimum temperature <0°C (preceding winter)
10	dT <−10	no. days with minimum temperature <−10°C (preceding winter)
11	dTmax <−10	no. days with maximum temperature <−10°C (preceding winter)
12	PRsum	annual precipitation (mm)
13	PRJanMar	precipitation (mm), January–March
14	PRAprJun	precipitation (mm), April–June
15	PRJulSep	precipitation (mm), July–September
16	PROctDec	precipitation (mm), October–December (of preceding year)
17	SunHour	annual number of sun hours
18	NLI1-3	North Wall Index (mean latitude of Gulf Stream) January–March
19	NLI7-9	North Wall Index (mean latitude of Gulf Stream) July–September
20	NAO11-3	North Atlantic Oscillation (mean November (previous year)–March)
21	EA9-4	East Atlantic Pattern (mean September (previous year)–April)
22	EAJET4-8	East Atlantic Jet (mean April–August)

Note: These variables comprised local meteorological data (University Weather Station, Jena, Germany), three North Atlantic climate indices (NAO, EA, EAJET; Climate Prediction Center, Camp Springs, Maryland, USA) and the mean quarterly latitude of the Gulf Stream (NLI, also called North Wall Index; Marine Laboratory, Plymouth, UK [Taylor 1996]).

therefore assessed the effect of climate fluctuation on long-term changes in species abundances within functional groups (i.e., the interannual variation of functional groups) so as to capture changes in species abundance due to species interactions within groups of ecologically similar species, as well as those due to direct responses to climate. Changes due to species interactions within functional groups would be hidden in background variance if only single species responses were examined. Thus, using functional groups directly links ecological characteristics to climatic sensitivity. We combined species into functional groups, depending on their growth form and life history (producers) or their foraging behavior (herbivores and carnivores), within each site and assigned the groups to trophic level (Table 1 and Fig. 1: FG1 . . . FG*n*; see also Appendices A–C). The producers were grouped as mosses, grasses, woody plants, annual forbs, and perennial forbs; the herbivores were grouped as vascular suckers (e.g., Auchenorrhyncha), cell-tissue suckers (e.g., Heteroptera), life-time chewers (e.g., Orthoptera), stage-specific chewers (e.g., Coleoptera), and miners (e.g., Diptera); and carnivores were grouped as chewing hunters (e.g., Coleoptera), attacking chewers (e.g., carnivorous Orthoptera), biting-suckers (e.g., Diptera), sucking hunters (e.g., Heteroptera), parasitoids (e.g., Diptera), and web-spinners (e.g., Araneae). Because collections were made over different periods within the 20 years of research and not all species were collected over the whole period, the species composition of functional groups varied with year.

Climatic data were derived from 22 variables including both local and global meteorological indices (matrix **X** in Fig. 1; Table 2). By including many climate measures we greatly reduce the possibility of omitting signals that are weak but biologically important (Taylor et al. 2002). To condense these data and to avoid nonorthogonality, we summarized these climatic variables as the four major axes (matrix **X**′ in Fig. 1) of a standardized principal component analysis (PCA). Since PCA axes are, by definition, orthogonal and so independent of one another, this procedure creates composite independent climate variables and so avoids the danger of spurious correlations (i.e., multicollinearity) inherent in a multivariate design using nonorthogonal climate factors. Very little information was lost by this process since the first four PCA axes explained nearly all of the total variance in the original climate data (mean 93.7%, range 81–100%, $n = 9$; i.e., nine different year-sequences for which PCA axes were calculated). All further analyses therefore were carried out using the combined and condensed climate information represented by the interannual fluctuations of these four axes. These composite variables fluctuated widely over time and showed no particular long-term trends (Appendix D). The principal component coefficients (loadings) for all the standardized original climatic variables (Table 3) show that the first PCA axis primarily represents temperature (many temperature variables, number of hours of sunshine, and the winter signal of the North Atlantic Oscillation [NAO]) but the second PCA axis mainly represents the interannual var-

TABLE 3. The eigenvector coefficients (loadings) of a standardized principal component analysis of original climatic variables for the entire period 1970–1996.

No.	Climatic variable	Axis 1	Axis 2	Axis 3	Axis 4
1	Tav1-12	**−0.9509**	0.1687	0.1043	0.0736
2	Tav1-3	**−0.8021**	0.1912	0.3772	−0.3433
3	Tav4-6	−0.1724	**0.4766**	**−0.5625**	−0.0937
4	Tav7-9	**−0.7523**	−0.0127	−0.3489	0.1989
5	Tav10-12	−0.2237	−0.0049	0.3026	**0.7233**
6	Tmax	**−0.9562**	−0.0054	−0.0506	0.0547
7	Tmin	**−0.5802**	−0.1280	**0.6287**	0.1848
8	dTmax >30	**−0.6741**	−0.1350	−0.3200	−0.0630
9	dT <−10	**0.6843**	−0.0463	−0.4180	0.4371
10	dTmax <−10	0.1892	**0.6100**	−0.3638	−0.0154
11	dT <0	**0.7650**	−0.0497	−0.4556	0.1617
12	PRsum	0.3306	**0.8506**	0.2630	−0.0341
13	PRJanMar	0.0861	0.4151	0.2448	**0.5937**
14	PRAprJun	0.2404	0.3627	0.2367	−0.1865
15	PRJulSep	0.4415	**0.7329**	0.0215	−0.2592
16	PROctDec	0.0845	**0.6990**	0.2354	−0.1260
17	SunHour	**−0.6888**	−0.3695	**−0.5307**	−0.0878
18	NLI1-3	−0.3253	**0.5829**	−0.1000	−0.1995
19	NLI7-9	−0.2545	**0.5965**	−0.2915	−0.0107
20	NAO11-3	**−0.5975**	0.3733	−0.3842	−0.0669
21	EA9-4	−0.3672	**0.6018**	0.2283	0.3795
22	EAJET4-8	−0.2371	0.3656	−0.4294	**0.4709**

Note: The eigenvalues of the first four axes are: axis 1 = 0.2981, axis 2 = 0.1920, axis 3 = 0.1227, and axis 4 = 0.0838 (sum = 70% of total variance explained). Loadings >0.45 are shown in boldface type to highlight the meanings of the respective axes. A mean eigenvalue sum of 0.94 (93.7% variance explained) was calculated for the shorter periods during which organism abundance was recorded within the total 26-year study (see *Methods: Data preparation*).

iation of local precipitation and the impact of general weather processes (North Wall Index [NLI], East Atlantic Pattern [EA]). PCA axis 3 accounts for the effects of spring temperature (Tav4–6) and cold weather in general (Tmin), number of hours of sunshine, and the impact of East Atlantic Jet [EAJET], but axis 4 predominantly represents the winter temperature of the preceding year (Tav10–12), as well as spring precipitation (PRJanMar) and the effect of EAJET.

Data analysis

We derived a measure for climate sensitivity of each functional group as the percentage of its total species variation explained by the four composite climatic variables (PCA axes) by partial redundancy analysis (pRDA; Jongman et al. 1995, Legendre and Legendre 1998; performed with CANOCO 4.5, Ter Braak and Smilauer [2002]). RDA is a canonical extension of PCA that uses, instead of the original values (matrix **Y** in Fig. 1), the fitted values of a multiple linear regression of each species data on the set of explanatory variables (here the composite climate variables). As it combines PCA and multiple regression analysis, the axes extracted by RDA are linear combinations of the explanatory variables involved (matrix $\mathbf{X}'$ in Fig. 1), and so the amount of species variation accounted for by this model is restricted solely to that fraction explained by the four composite climate variables (the sum of the canonical eigenvalues; Jongman et al. [1995]). Partial RDA controls for the effects of one or more covariables and is comparable to partial correlation or partial regression techniques. In our pRDA analysis, we constructed two covariables reflecting differences in species composition and abundance that arise, even if climate is invariant, merely from the arrangement of the collections. These covariables represent either spatial position, which might give rise to small topographical differences (e.g., the relative position in the study site) or the temporal sequence of collections, which might show successional changes (e.g., sampling years). The remaining variance is that due predominantly to climatic effects. All the functional groups were significantly associated with climate (at $\alpha = 0.05$, Monte Carlo permutation test) except Steudnitz mosses, Leutratal annual forbs, and chewing hunters. All the functional groups were then grouped by trophic level, and trophic climatic sensitivity was derived as the mean climate sensitivity of all the functional groups within a particular trophic level (Fig. 1).

ANOVA models could not be appropriately used to analyze differences in sensitivity between trophic levels because normal distributions and homogeneity of variances were neither present nor could they be satisfactorily achieved by data transformation. We therefore applied a Jonckheere-Terpstra trend test (Jonckheere 1954, Sachs 1999; in SPSS 10.0; SPSS, Chicago, Illinois, USA) to test for trends in the sensitivity to climate across trophic levels. This test is a powerful k-sample extension of the Mann-Whitney U test, a more

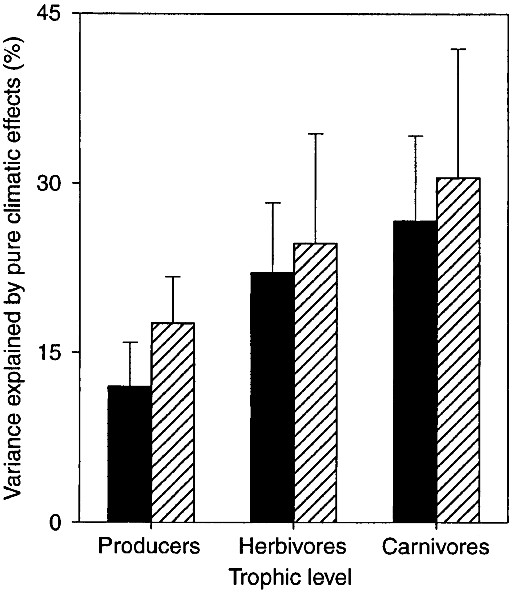

FIG. 2. Climatic sensitivity of different trophic levels at two separate grassland sites (solid bars, Leutratal; hatched bars, Steudnitz; means + 1 SD). Sensitivity is the mean temporal variation (averaged over functional groups within trophic levels) in organism abundances explained by climate (four major axes of a principal component analysis [PCA] based on 21 local and global climatic indices; for more details see *Methods: Data analysis*).

appropriate alternative to the Kruskal-Wallis test when assuming an a priori rank order in the data.

To exclude the possibility that trophic sensitivities resulted from differences in mean species richness of functional groups within trophic levels, we conducted a Jonckheere-Terpstra trend test on the size of functional groups within trophic levels. In addition, we used a model I regression to test whether functional group sensitivity was related merely to group size. Sensitivities in species-rich functional groups might be higher because large groups are more likely to contain strongly responding species or lower because of statistical averaging, the reciprocal canceling out of individual species fluctuations (Doak et al. 1998), the effects of which are greater the greater the number of species a functional group contains.

To indicate the relative importance of each of the four axes, and thus the relative importance of different aspects of climate, we also calculated the functional group sensitivity to each of the axes separately.

RESULTS

Different trophic levels had different sensitivities to climate (Fig. 2), and these sensitivities were highly significantly ordered with increasing trophic rank (producers < herbivores < carnivores: Jonckheere-Terpstra (J-T) trend test, two-tailed $P = 0.001$, $n = 27$, Monte-Carlo significance based on 10 000 samples). The differences were the same in both sites (Fig. 2) and the sensitivity trend in Leutratal was also highly significant (J-T test, two-tailed $P < 0.002$, $n = 14$), although that in Steudnitz was not (J-T test, two-tailed $P = 0.075$, $n = 13$). There was no significant tendency in the species richness of functional groups across the three trophic levels (J-T test, two-tailed $P = 0.11$, $n = 28$, Monte-Carlo significance based on 10 000 samples) and the ordering of mean species richness (producers < herbivores > carnivores) was not the same as the ordering of climatic sensitivities. There was also no significant relationship between sensitivity and group species richness (model I regression, total data, $r^2 = 0.06$, $P = 0.21$; Leutratal, $r^2 = 0.03$, $P = 0.55$; Steudnitz, $r^2 = 0.16$, $P = 0.18$; Fig. 3).

Within trophic levels, each of the four climatic variables explains ~25% of the total climatic variance (Appendix E). However, the relative sensitivity to each of the four axes separately differed between functional groups but the differences showed no particular pattern with respect to trophic level except that producers might be more affected by local precipitation and Gulf Stream impact (axis 2) than by temperature (axes 1 and 3; Appendix F). For individual response of species to composite climatic variables, see RDA triplots in Appendix G.

DISCUSSION

The differential sensitivity of trophic levels to climate will have profound effects on the way in which these xerothermic grassland communities respond to climate change. More importantly, however, the differential trophic sensitivities to climate that we found may indicate a general phenomenon in trophic systems, and finding the same differences in sensitivity at both the sites studied strengthens this contention. The species responses at each site are independent because individual arthropod species were not sampled synchronously between sites and because population syn-

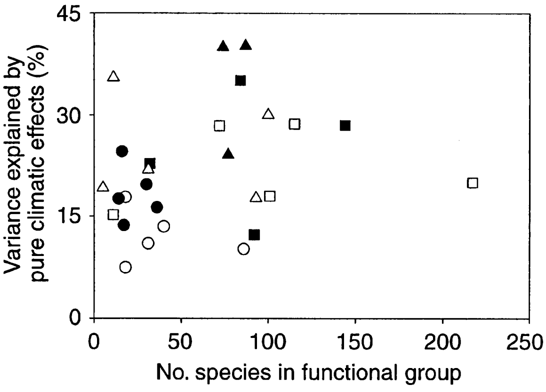

FIG. 3. Relationship between climatic sensitivity in terms of explained variance and species number of functional groups (circles, producers; squares, herbivores; triangles, carnivores; open symbols, Leutratal; solid symbols, Steudnitz).

chronization between sites through the migration of organisms is prevented by the town of Jena and the considerable distance (18 km) that separate the sites. The generality of differential trophic response is also supported by the similar results from controlled aquatic microcosm experiments on the effects of elevated temperatures (Petchey et al. 1999). Furthermore, our data derive from a frequent ecosystem type that is in no way unusual, and it is unlikely that the trophic structure and interactions of other systems differ greatly from those of our grasslands. Differential responses to climate between trophic levels may therefore be widespread.

Our results are likely to be the direct results of climate since we can exclude alternative, nonclimatic causes of differential trophic responses. Differences between trophic levels might arise if each level were represented by few taxa because small groups of taxa might have differences in sensitivity to climate by chance. This phenomenon cannot affect our findings, however, because our data derive from large numbers of species in each level and from a substantial part of highly diverse and real grassland ecosystems. Neither can they be attributed to purely taxonomic effects, as could be the case if the species analyzed were largely taxonomically similar within, but taxonomically distinct between, trophic levels. This is not the case since at Leutratal and Steudnitz the "producers" include a wide range of plant species from different taxa as, similarly, the "herbivores" and "carnivores" include a wide range of arthropod species. In addition, at both sites, the "herbivores" and "carnivores" are not taxonomically distinct since they contain representatives of the same taxonomic groups (e.g., Coleoptera, Diptera, Heteroptera). Differences in plant generation time or arthropod voltinism are also unlikely to be the cause of the differences we report although short-generation organisms might be expected to respond more quickly to climatic changes. The distribution of generation times is similar for the "carnivores" and the "herbivores" but we did find that short-generation plants, i.e., annual forbs, had higher climate sensitivity (Leutratal [Lt], 17.8%; Steudnitz [St], 19.7%) than the mean of all plant functional groups (Lt, 12.0%; St, 17.6%). Nevertheless, these values for short-generation plants are still well below the mean sensitivity of herbivores (Lt, 21.5%; St, 23.6%) so the generally low climate sensitivity of the producers cannot be attributed merely to the inclusion of long-generation, i.e., perennial, plants in this trophic level. There are also no consistent differences in voltinism between the herbivore and carnivore arthropods, each arthropod functional group consisting of both univoltine and multivoltine species with diverse overwintering modes.

We can also exclude the possibility that differential climate sensitivity arises because there are different numbers of species within functional groups (McArdle et al. 1990) since there is no relationship between these two quantities (Fig. 3). Furthermore, the variation explained purely by climate is a fraction of the total variation in the data. There is no reason to believe that the size of this fraction should be determined by the number of species within the functional group from which it was derived even if the total variation (from climate and all other causes) were to be so. In addition, our results do not arise because of statistical averaging because group species richness does not decrease systematically with trophic rank and, in consequence, higher sensitivity to climate is not associated with species-poor groups.

Why trophic levels generally, or only in our grasslands, should be differentially sensitive to climate variation cannot be determined at this stage. It may be possible that differential sensitivity to climate is due to functional groups in different trophic levels responding to different elements of climate. Other possible explanations and foci for further research may lie in different degrees of density dependence, differences in metabolic rates, or in varying resource availability. Populations with weak density dependence are expected to be more sensitive to climate than those with overcompensatory dynamics (Ives and Gilchrist 1993), and this mechanism could operate if density dependence differed systematically between trophic levels. The "carnivores" may be generally more active foragers and so have intrinsically higher metabolic rates than "herbivores," and these in turn, since they have to forage among, and select from, the available vegetation, may have higher metabolic energy expenditure than "producers" (Pianka 1981, Townsend and Hughes 1981). It is also conceivable that response to climatic variations in one trophic level causes the resource availability to vary for the level above. This increased extrinsic uncertainty in resource availability might be amplified along trophic chains causing a reciprocal cascade. Differential sensitivity to climate may be a specific manifestation of the general observation that sensitivity to disturbance of any kind often increases with trophic level (e.g., Morris and Rispin 1987, 1988, Eyre and Rushton 1989, Eyre et al. 1989, Rodriguez et al. 1998, Cagnolo et al. 2002).

Whether caused by intrinsic or extrinsic mechanisms, our findings, from detailed and abundant long-term field data, indicate that different trophic levels respond differently to climate fluctuations and suggest that differential trophic responses are likely to be a common, widespread, and important phenomenon. Communities are, therefore, unlikely to respond as discrete entities to climatic changes, and climate change is likely to disrupt trophic relationships between organisms, prompting trophic cascades (Jones et al. 1998, Petchey et al. 1999). Changes in the trophic structure of communities will affect ecosystem processes such as nutrient cycling and thereby the services these systems provide (De Angelis 1992, Jones et al. 1998) although the proximal mechanisms for these differential sensitivities to climate are still under study. Differential response of trophic levels will substantially increase the ecological disruption to be expected under global climate change and must therefore be incorporated into existing models (Root and Schneider 1995) if the prediction of ecosystem responses to climate change is to be adequate.

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APPENDIX A

A list of identified plant species and their classification into functional groups is available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A1.

APPENDIX B

A list of herbivore species caught and their classification into functional groups is available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A2.

APPENDIX C

A list of carnivore species caught and their classification into functional groups is available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A3.

APPENDIX D

A figure showing the fluctuations of four PCA axes (composite climatic variables = sample scores) over the total study period is available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A4.

APPENDIX E

Figures providing the distribution of variance explained by PCA axes (composite climatic variables) for each trophic level are available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A5.

APPENDIX F

Figures providing the distribution of the fraction of variance, standardized to 1, independently accounted for by the four composite variables (PCA axes) for all functional groups of different trophic levels are available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A6.

APPENDIX G

Redundancy analysis (RDA) triplots for all functional groups analyzed are available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A7.

APPENDIX H

Literature used in Appendices A–C is available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A8.

APPENDIX I

A map and pictures of Leutratal and Steudnitz study sites are available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A9

10. Manuskript IX

Perner, J. & Voigt, W.
Measuring the complexity of interaction webs
using the vertical connectance of functional groups.
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Measuring the complexity of interaction webs using the vertical connectance of functional groups

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Abstract

Interaction web models of community networks contain not only trophic interactions and competitive-facilitation effects but also non-trophic and non-competitive effects. These are common in natural communities but have largely been ignored in food-web studies because such complex interaction patterns are difficult to analyze. Ecological insights into the usually high complexity of interaction webs demand a simplification of their structure to concentrate on the most important interactions within a community. One way to achieve this goal is to use functional groups (FGs). Using simple and partial Mantel tests we studied the vertical interactions between FGs from different trophic levels (producers-herbivores-carnivores) both at a disturbed grassland site and at a similar but undisturbed site. The resulting interaction structures of both ecosystems were compared. Irrespective of the significance level adopted, we found: (i) an approximately 30% - 40% higher vertical FG-connectance in the undisturbed than in the disturbed grassland; (ii) a much higher percentage of significant correlations between FGs in the undisturbed system; and (iii) that the disturbed grassland was characterized by more simply structured patterns of biotic interaction. From these results we conclude that (a) Mantel tests are a useful tool for detecting significant interaction patterns (web links) between FGs, and that (b) FG-connectance is a powerful measure of complexity and functional diversity of communities.

Introduction

Complexity is an inherent property of ecological communities. It is usually measured "...as the number of species, the number of interactions between species, the average strength of interaction, or some combination of these..." (Forbes 1998: 149). Although species number gives only partial information about community complexity, it is often used as an integrated measure because it is reasonably easy to obtain in the field. The concept of ecological community in the strict sense, however, includes various taxa of different trophic levels, and so the determination of species numbers alone can be an expensive job. The effort increases dramatically, and makes great demands on the technical and analytical abilities of ecologists, when interactions between multitudes of species are the purpose of the study. The reward, however, is an enormous gain of information about the degree of community complexity.

Food web models are very useful tools that can help to provide abstractions of complexity within natural communities based on trophic links (e.g. Berlow 1999, Dunne and Martinez 2002). However, interactions between community elements comprise a variety of relationships, some of which go beyond the scope of food webs. Price (2002) listed seven major factors that are basic to terrestrial food webs founded on living plants: plants as food; plants as habitat; physical properties of plants; adaptations of insects to the plant habitat and food; chemical constituents of plants; induced chemical reactions of plants; and landscape and biogeographic variation in vegetation types and food web richness. This wide range of plant factors suggests that 'food web' is much too narrow a term to encompass all of the processes which may be present. Many other factors besides trophic interactions can, directly or indirectly, influence the patterns observed. Price supported the use of an alternative term 'interaction web', first mentioned by Menge and Sutherland (1987). This term captures not only trophic-interaction and competitive-facilitation effects but also the non-trophic and non-competitive effects which are common in natural ecosystems (Ohgushi 1997, Price 2002). These more complex interactions are difficult to detect by classical food web methods and have therefore largely been ignored.

To understand the usually high complexity of interaction webs demands a simplification of their structure which concentrates on the most important interactions within a community (Hall and Raffaelli 1997). A more holistic way to reduce the dimensionality of complex data is the assignment of species into a number of functional groups (FGs). These are aggregated units of species that share an important ecological characteristic and play an equivalent functional role in the community. To a first approximation, these groups are assumed to respond as a unified whole to their environment (Colasanti et al. 2001, Blondel 2003), though substitutions between members of the same group can occur in response to subtler influences. Because FGs are independent of particular species compositions they confer a high degree of comparability between different communities (Simberloff and Dayan 1991).

The pros and cons of various FG classifications have been widely discussed for both plants and animals and the choice of system usually depends upon the questions being asked and upon the level of species-specific information available (Simberloff and Dayan 1991, Blondel 2003). In spite of some arbitrariness, the classification of species into FGs appears to be an efficient way to analyze web interactions (Bengtsson 1998). For example, Hall and Raffaelli (1991) and Sugihara et al. (1997) analyzed the effects of taxonomic and trophic group aggregation on web properties and found that the most links between different trophic levels survived even after they were aggregated into coarser classes.

To retain the most detailed information on species composition and dominance structures requires the use of data matrices, not simply a lumping together of species abundances. Consequently, different species of the same FG should comprise the vectors (quantitative variables) of FGs within the same matrix. Based on this approach we have analyzed the number of interactions between different FGs across three trophic levels by simple and partial Mantel test procedures (Mantel 1967, Smouse et al. 1986). This multivariate symmetrical correlation method analyses the relationship between matrices on the basis of previously calculated resemblance matrices. Although this general approach is now increasingly common in ecology, it has not so far been applied to analyze interaction patterns between different trophic levels.

Using this approach we investigated the main hypothesis, deduced from species-based food web analyses, that disturbed ecosystems are more simply structured and less linked than undisturbed systems (O'Neill et al. 1986, Townsend et al. 1998, Post 2002, Schmid-Araya et al. 2002). For this test we compared vertical-interaction web structures between FGs of different trophic levels (producers-herbivores-carnivores) in related examples of disturbed and undisturbed grassland ecosystems. To describe community complexity in terms of vertical interactions, we calculated the *vertical connectance* of interaction webs in both grassland ecosystems adopting the term "connectance" originally used in food-web ecology. Vertical connectance may be defined as the ratio between the potential number of interactions (links) between FGs in different trophic levels and the number of significant interactions actually found. Here we disregard possible (horizontal) interactions, e.g. competition, between FGs within the same trophic levels, as they are small in magnitude in resource-driven terrestrial webs compared to vertical interactions that control ecosystem processes (Price 2002, Blondel 2003; see also discussion).

Material and Methods

Grassland sites

We chose two extensive, long-term datasets originating from disturbed and undisturbed grasslands on Triassic limestone near Jena, Germany (11.6°E, 50.9°N, 145m above sea level). The two sites have similar geologies and topographies but different management histories. Previous studies have demonstrated low species diversity in the disturbed grassland (Heinrich et al. 2001, Perner et al. 2003) and rather high diversity in the undisturbed grassland (Heinrich et al. 1998). Based on this difference in community structure we assumed that these datasets were contrasted sufficiently in complexity to test our main hypothesis.

One site is an exposed slope of ESE aspect near the village Steudnitz, 18 km north of Jena. Until 1990 it was heavily disturbed by air pollution from a nearby phosphate fertilizer factory. After the factory closed in 1990, a rapid, unassisted vegetation recovery was noted. We refer to the Steudnitz site as our 'disturbed grassland'. The second grassland site is S-facing exposed slope in a nature reserve south of Jena in the Leutratal valley. This semi-natural grassland, managed for hay a long period, was abandoned in 1970. After this a natural succession to scrub and woodland started. We refer to the Leutratal site as our 'undisturbed grassland'. More detailed information on both sites is given by Heinrich et al. (1998), Heinrich et al. (2001) Perner et al. (2003) and Voigt et al. (2003).

Data sampling

The data used in this study were obtained by identical methods from three locations at both sites. In the *disturbed grassland*, the three sub-sites were named U in the lower region of the slope, M in the middle, and O in the upper. They had decreasing order of pollution impact along the former main gradient (Heinrich et al. 2001). In the *undisturbed grassland*, the three sub-sites (A, M, and S) lay along a gradient of increasing slope and increasing mean annual insolation (Heinrich et al. 1998).

To analyze the vegetation patterns, a systematic sampling design was developed. In each sub-site of both grasslands there was a grid of 24 permanent plots, each of size 5 × 5 m and arranged in 4 rows of 6 contiguous plots. Vegetation was assessed using the combined cover-abundance method of Braun-Blanquet (Kent and Cocker 1994). In the disturbed grassland the vegetation was sampled annually from 1990 until 1999 (Heinrich et al. 2001) and in the undisturbed grassland it was sampled every fourth year from 1972 to 1996 (Heinrich et al. 1998).

Arthropods were collected using standardized sweep-netting techniques (30 cm diameter linen net and 10 randomly-distributed sub-samples). This was done actually within, or within the immediate vicinity of, the vegetation grids. Each sub-sample consisted of 10 double swings covering approximately 8 m^2 and was conducted at midday every 2 weeks from April to October. These data were collected annually from 1992 to 1996 in the disturbed grassland and in 1972-74, 1983-85 and 1986-89 inclusive in the undisturbed grassland (Heinrich et al. 1998, Perner et al. 2003).

Classification of functional groups

In our study, a stringent numerical definition of FGs (Simberloff and Dayan 1991) was not possible. Such an approach would need detailed functional information which at present is not equally available for all species in our data sets. We therefore assigned species *a priori* to our own simple system of FGs. Plants were classified by combinations of growth habit and life history traits into mosses, grasses, annual forbs, perennial forbs and woody plants. Arthropods were grouped according to their foraging characteristics within trophic levels. This did not always follow taxonomic membership (Table 1) and species in some taxa (e.g. Diptera, Coleoptera or Heteroptera) therefore appeared in different FGs and even in different trophic levels (e.g. herbivores and carnivores). For those groups in which shifts between trophic levels occur during the life history of individuals, our classification was based on the feeding strategy of the immature stage, normally the most important stage in abundance and biomass. A detailed overview of the data and species grouping was given by Voigt et al. (2003).

Data analysis and construction of interaction webs

Abundance data were summarized for each species over the 24 plots (for plants) or across the sub-samples (temporal replications) within a year (for arthropods) for every sub-site and every collection year. As a result we derived 14 FG-based matrices for each grassland. Each matrix for each FG within each site (disturbed and undisturbed) comprised the abundance values of all individual species within the FG. This matrix had ***s*** columns (the total number of species in the FG) and ***n*** rows (the total number of sub-sites sampled over all collection years). The plant data were square-root-transformed and the arthropod data were log-transformed to secure statistical normality.

To determine links between the various FGs across different trophic levels (the vertical interactions) we correlated whole matrices of FGs (see above) by applying simple and partial Mantel tests (Mantel 1967, Smouse et al. 1986). We calculated these by means of the program of Bonnet and Van de Peer (2002). Unlike a simple correlation of two data matrices, this method is based on previously-calculated resemblance matrices (***n*** x ***n*** squares), a test of the independence of elements of two matrices. Consequently it can be used to measure the association between two matrices, i.e. the extent to which the variations in the pair wise distances/similarities of one matrix (i.e. abundance variations of all species within one FG across sub-sites and years) correspond to the variations in a second distance/similarity) matrix (of another FG). Hence, this type of matrix correlation is independent of species identity and richness. Using matrices in this way allows for the simultaneous comparison of abundance changes of numerous species even though the species numbers in the two initial matrices may be different. The calculated standardized Mantel statistic r_M for the correlation between any two FGs may be interpreted in the same way as Pearson's product-moment correlation coefficient. However, to test its statistical significance a permutation test must be used because the distances in the compared matrices are not independent variables. Mantel tests are rather robust to such autocorrelation patterns because they are based upon resemblance matrices, the cells that correspond exactly and relate to the same spatial or temporal samples (Legendre and Legendre 1998).

To clarify the vertical relationship across trophic levels between FGs, and to check for spurious correlations, it is necessary to calculate r_M between two FGs of different trophic level (e.g. herbivores and carnivores) while controlling for the effect of a third group (e.g. plants as the primary driving force for regeneration and succession). This 'partial' Mantel test is a step towards causal modeling using resemblance matrices (Legendre 1993, Legendre and Legendre 1998). Using three matrix models, and criteria given for model expectations suggested by Legendre (1993), we evaluated all possible pairs of plant-herbivore-carnivore (P-H-C) combinations. There are four potential relationship patterns between trophic levels (Fig. 1). Model characteristics, and criteria to support particular model types, can be found in Fig. 1, Legendre (1993) and Legendre and Legendre (1998).

In the present context, it is important to know that the most important criteria for accepting a specified model are: (i) value, rank and significance of $r_{M\,PH}$, $r_{M\,PC}$ and $r_{M\,HC}$ (r_M for combinations of P, H and C); (ii) decrease or increase of $r_{M\,HC.P}$ in comparison to $r_{M\,HC}$ ($r_{M\,HC.P}$ being the partial Mantel correlation between variables (matrices) H and C when controlling for their relationships with P). The possible different outcomes are: *Model 1*, an intervening sequence where there is no immediate effect of producers on carnivores, or vice versa; *Model 2*, having simultaneous effects of producers on herbivores and carnivores but no causal relationship between herbivores and carnivores; *Model 3*, having a double cause, independent relationship between carnivores and both producers and herbivores; but no correlation between producers and herbivores; and *Model 4*, with multiple causes demonstrating strong interactions between all trophic levels.

To accept a specified interaction model, and so to determine the nature of links between FGs, we chose the significance level $p < 0.05$ as the threshold criterion. To examine the sensitivity of our results in relation to the selected threshold level, and to deal with the criticism that these proportions may be due to statistical artefacts, we additionally used the marginal significance level of $p < 0.1$ and the Bonferroni adjusted significance level of $p < 0.005$ (Bonferroni procedure: 0.05 / 9 or 10 $\approx$ 0.005), which is very stringent and conservative. Using all significant vertical links between FGs, interaction webs for both the disturbed and undisturbed grassland communities were constructed.

We quantified and standardized the extent of vertical interactions within each web by calculating its connectance, defined as the number of actual links in a food web divided by the total number of possible links (Lincoln et al. 1998). As explained in the Introduction, we intentionally use the term 'interaction web' here. To describe the connectance between FGs of different trophic levels (vertical) we calculated a '*vertical FG-connectance*' as:

C(FG) = L(FG) / potential vertical links

where L(FG) represents the number of significant vertical links between FGs which follow one of the four models listed above (the same links occurring in different models were only counted once) and potential vertical links are the sum [No. of plant FGs × No. of herbivore FGs] + [No. of plant FGs × No. of carnivore FGs)] + [No. of herbivore-FGs × No. of carnivore FGs].

Results

In total, 267 plant species and 1049 arthropod species (686 herbivores and 363 carnivores) were included in our analyses (Table 1). The results of simple Mantel test procedures between matrices of all the functional groups (FGs) of different trophic levels available for both grasslands studied are presented in terms of Mantel correlation coefficients (r_M) in Tables 2a-b. The percentage of significant and highly significant correlations is much higher in the undisturbed system than in the disturbed (68% and 41% respectively). Further, we evaluated all possible vertical pairs of plant-herbivore-carnivore combinations and compared the calculated simple and partial Mantel correlation coefficients using the model criteria given in Fig. 1. Only if all the criteria listed for a model in Fig. 1 were fulfilled ($p < 0.05$) was that model type used in Fig. 2 to define the type of interaction present. Fig. 2a shows that, in general, relatively few significant correlations were detected in the disturbed grassland. Most cases of FG interactions follow Model Type 1 and few can be classified as Types 2 or 4. However, in the undisturbed grassland a large number of significant correlations follow Model Types 1 or 2, and mostly Type 4 (Fig. 2b). Interestingly, almost all plant FGs occur in interaction patterns in all three model types (the exception is that PAF is not represented in Model Type 2). Further, all consumer FGs are included at least in one of the three model types supported by analyses of the undisturbed grassland. However, in neither grassland was an interaction pattern meeting the criteria of Model Type 3 detected.

We also identified model types by relaxing the marginal significance level to $p < 0.1$. Whereas the change from $p < 0.05$ to $p < 0.1$ increased the proportion of interactions supporting Model Type 1 in the undisturbed grassland, it increased the proportion of interactions following

Type 4 in the disturbed grassland (Fig. 3a, b). However, we found a much higher percentage of significant interactions generally in the undisturbed compared with the disturbed grassland at the more relaxed level. This difference has the effect of keeping nearly constant the very conservative Bonferroni corrected significance level ($p < 0.005$) as a threshold criterion. Although, under Bonferroni, the total number of supported models decreases considerably in both grasslands, a much higher percentage of supported interaction models remains in the undisturbed system (Fig. 3c).

To quantify the extent of the interaction web complexity we analyzed the vertical FG-connectance for both grasslands at different levels of significance (Fig. 4). Independently of significance level we found approximately 30% - 40% higher vertical FG-connectance in the undisturbed compared with the disturbed grassland.

The ranges of FGs within each trophic level are nearly identical between both sites. However, for reasons of logistics the HLC and CAC groups are not available within the disturbed grassland, nor the CCH or CWS groups in the undisturbed grassland (Table 1). So we repeated the analysis of vertical FG-connectance using only those FGs that are present in both systems. Though reduced in scope, this approach rigorously compares identical sets of FGs from the two systems. No major differences were found between the results of the reduced and the complete analyses. Also, the reduced approach showed a vertical FG-connectance for the undisturbed site (0.81 at $p < 0.05$) that was more than twice as great as the value for the disturbed site (0.30 at $p < 0.05$).

Discussion

This case study

By whatever approach we took we found a much higher percentage of significant vertical correlations between FGs in different trophic levels in the undisturbed than in the disturbed grassland (Appendix 1). In particular, all FGs at the producer and herbivore levels were significantly associated in the undisturbed site in what seems to be an expression of strong interaction between trophic levels. In comparison, the amount of significant relation between FGs of herbivore and carnivore levels is much lower in both grasslands. However, partial Mantel correlations between herbivore and carnivore FGs when statistically controlled by producer FGs are higher than the simple Mantel correlations between the FGs of herbivores and the carnivores alone, especially in the undisturbed site. This indicates that the upper relationship is affected by the lower processes. Analyses of simple FG-correlations are therefore insufficient to understand fully such interaction patterns.

To disentangle these vertical relationships, and to permit a stepwise causal modeling of our data (sensu Legendre 1993 and Legendre and Legendre 1998), the comparisons of simple and partial Mantel test results with logically-deduced model criteria were indispensable (Fig. 1). The fact that we found a 30% - 40 % lower vertical FG-connectance in the disturbed grassland than in the undisturbed one (Fig. 2a-b) does not depend upon the level of significance applied (Fig. 3, Fig. 4). Three of the four model types are supported in both systems. Only Model Type 3, which assumes that both plants and herbivores independently affect carnivores without correlations existing between plants and herbivores themselves, was not found in either grassland. Because it hardly represents a plausible pattern, the absence of a verified Type 3 model is not surprising (Duffy 2002, Post 2002).

In the disturbed grassland system most of the vertical FG-interactions which were detected follow Model Type 1 (Fig. 2a, Fig. 3a). This linear interaction model includes four producer FGs (PGR, PMO, PPF, PWP), three herbivore FGs (HCW, HTS, HVS) and only two carnivore FGs (CSH, CWS). It is obvious that Model Type 2, which describes a double effect of plants on both herbivores and carnivores and Model Type 4, which points to interactions between all trophic levels, both depend upon only one producer group: PGR (grasses) in Type 2 and PPF (perennial forbs) in Type 4. Further, there is no significant relationship between annual forbs (PAF) and any invertebrate consumer group in the disturbed system. However, in the undisturbed grassland every FG is part of at least one of the models and is significantly linked with one FG within another trophic level (Fig. 2b). Model Type 4 shows particularly developed interactions in this respect.

The distinctions we found between the two grasslands are not due to methodological differences (Closs and Lake 1994) because we investigated both ecosystems with the same techniques and used the same analyses. Nor can the distinctions arise from differences in the identities of the FGs analyzed since they are largely the same in both systems. Ensuring similarity between the groupings from both systems was, indeed, one of the reasons for using FGs rather than individual species as the units of analysis. There is no difference between the implications of the reduced and the complete analysis and both lead to the same conclusions (see last paragraph in Results section).

Another reason for a higher FG-connectance in the undisturbed grassland may be due to higher species diversity (Table 1), with the exception of annual forbs which are more abundant in the disturbed site. This may cause a higher over-all degree of connectance between producers, invertebrate herbivores and carnivores. Having more species in any FG could increase the chance of finding a suitable resource species in the trophic level below (Lawton and Brown 1994, Naeem and Li 1997). However, this hypothesis could not be tested directly using our data. In our approach, degree of connectance was established from the degree of matrix correlation between FGs. If a higher amount of species richness were to produce higher FG-connectance, this should be detectable in the form of a positive relationship between the sum richness of all FG-pairs and the standardized Mantel statistic (r_M). However, no significant correlations of this type were detected, either for plant-herbivore or herbivore-carnivore combinations, or for plant-carnivore combinations in the case of data from disturbed and undisturbed systems tested together (Appendix 2). We therefore conclude that the differences in connectance between these two grasslands cannot be attributed to the differences in species richness alone.

There is a long standing and somewhat controversially conducted debate about the relationship between species richness, connectance and interaction strength (Cohen and Newman 1988, Bengtsson 1994, McCann 2000). Our negative results concerning the relation between richness and connectance support the findings of Dunne et al. (2002), highlighting that robustness of food-web structures increases with connectance but appears independent of species richness. This indicates a certain degree of species redundancy. Dunne et al. (2002) observed from their simulation experiments on 16 food webs from terrestrial and aquatic ecosystems that selective removal of those species with the most trophic links to other species influences food-web structure significantly. Therefore, the potential to find correlations between species richness and connectance (i.e. here between species richness and r_M) seems to be dependent on the structure of the interaction web itself (Williams and Martinez 2000, Dunne et al. 2002, Duffy 2002).

This may also explain the different results we obtained (Appendix 2) when both grassland systems were analyzed separately. Whereas no significant correlations could be found between species richness of the FG-combinations and the standardized Mantel statistic (r_M) for the disturbed grassland, significant relationships were detected for the plant-herbivore- and the herbivore-carnivore combinations of FGs in the undisturbed system. We interpret this as an indication of an increased degree of host plant or prey specialization to resources over a long period of low disturbance, and consequently a higher degree of interaction between species of different trophic levels. By contrast, the disturbed system seems to be characterized by more generalist herbivores and predators with a higher degree of functional redundancy which leads to weaker interactions between FGs at different trophic levels.

The disturbed grassland experienced a rapid increase in plant species richness (and change of community structure) since 1990. This could especially be seen in the two higher-lying sub-sites (U and M) and was due to an attenuation of pollution residuals (Heinrich et al. 2001, Perner et al. 2003). The period 1990-1999 was probably too short for the establishment of any complex vertical interaction patterns (Fig. 1, Fig. 2a). In particular, the presence of many annual species (PAFs) appears to be rather episodic. Because of such a rapid turnover of species, the PAF group lacks significant interactions with consumer groups. More simply-structured biotic interactions (i.e. simple correlations between FGs, see Appendix 1) between producer groups and herbivores, or between herbivores and carnivores, seem to be the source of the considerably higher consumer diversity shown by this disturbed grassland (Perner et al.

2003). Studies of food webs in disturbed habitats have shown that the mean chain length in the web may be reduced by disturbance (Pimm et al. 1991, Townsend et al. 1998, Post, 2002). Although this possibility could not be tested here because of the design of our study, the low number of complex interactions (Fig. 2a) and the reduced number of (significant) simple FG-correlations (Appendix 1) seems to support the idea of reductions in path length and complexity being caused by disturbance.

By contrast, in the undisturbed system the plant species richness (and composition) changed only slowly in all three sub-sites between 1972 and 1996 (Heinrich et al. 1998). So gradual successional changes in composition and structure at the producer level, which may be caused by cessation of management (mowing or grazing), may only gradually change any pre-existing horizontal and vertical interactions between FGs and trophic levels. The high correlation values between the FGs within their respective trophic levels indicate that a very similar (balanced and proportional) temporal pattern is being followed by each of these groups (Appendix 1). This concordance decreases with increasing trophic rank because fluctuations within different consumer levels are driven in different directions by abiotic conditions, e.g. climate (Voigt et al. 2003). These are partially caused by autogenic succession processes (e.g. alteration of microclimate by vegetation height or density).

The functional group approach and mantel test procedures

The effects of taxonomic and trophic aggregation on food web properties have been rigorously discussed in literature. Some criticize the aggregation of species into larger groups because this reduces much important trophic information (e.g. Paine 1988, Abarca-Arenas and Ulanowicz 2002). Hall and Raffaelli (1991) studied the effects of taxonomic resolution on estuarine web properties. They found that food-chain length is sensitive but that linkage density (i.e. number of trophic links per species) and ratios between different trophic levels were insensitive to taxonomic resolution. Sugihara et al. (1997) found that most food web properties stayed unchanged after both taxonomic and trophic group aggregation. In contrast to the taxonomic or trophic aggregations mentioned above, in our Mantel test approach the grouped species are not lumped together with a loss of species-level information. All the species comprising any one FG contribute to the information included in the distance matrix. In extreme cases, the correlation patterns thus obtained could be due to a few strong links (e.g. among dominant species) or to many weak links (e.g. among a higher number of subordinate species). Our approach, therefore, also considers the effects of weak interactions, even though these, though widespread, are sometimes difficult to detect (e.g. Berlow 1999, McCann 2000).

In our study the primary data are temporally auto-correlated. This is often problematic, especially in the case of comparative examinations of interaction patterns (Bengtsson 1994). It may cause Mantel tests to be too liberal, i.e. to reject a true null hypothesis (no relationship between two FGs). However, partial Mantel tests appear to be rather robust even in the presence of such autocorrelations (Oden and Sokal 1992, Legendre and Legendre 1998). Thus the comparison of interaction webs between the two sites with regard to their complexity should be unbiased. Partial correlations between FGs while controlling for the effects of climate (Voigt et al. 2003) and temporal development resulted in only a slight modification of single correlation values between FGs but not in a change of total web structures and proportions of vertical interactions.

Because our focus has been on interactions between different trophic levels we intentionally neglected horizontal interactions. Actually, correlation between FGs of the same trophic level turned out to be substantially mediated by relations to other trophic levels. For example, a high correlation between FGs of herbivores drops if the effects of various FGs of plants on them are statistically controlled for (e.g. in the undisturbed grassland r_M between HVS and HCW dropped from 0.8 to 0.53 if controlled for the effects of PGR).

A high positive correlation between two FGs (e.g. grasses and vascular suckers) should not necessarily be interpreted as a high degree of trophic association (e.g. herbivory) but rather as a concordant temporal or spatial pattern. In consequence, r_M measures the interaction pattern between members of two FGs; this should be understood as an average value caused by two sets of biotic and abiotic factors (see Price 2002).

Not all important invertebrate groups could be considered in our studies (e.g. Hymenoptera, aphids, molluscs and others), so we have been not able to evaluate and test these groups' interrelationships within our grassland communities. Also, the recently much-acknowledged, strong and important links between trophically-different above- and below-ground components of ecosystems (e.g. Bradford et al. 2002, Gange and Brown 2002) have had to be neglected here. Nevertheless, we believe that these differences in vertical FG-connectance between disturbed and undisturbed grasslands have uncovered general and system-inherent patterns. Further, we think that the FG-connectance of such interaction webs can be regarded as a very useful measure encompassing complexity, functional diversity and stability of communities (see reviews by O'Neill et al. 1986, Bengtsson 1998, McCann 2000). From our point of view the simple and partial Mantel tests we used seem to be an excellent tool to detect significant interaction patterns between FGs and are worthy to be explored by analysis of additional data sets.

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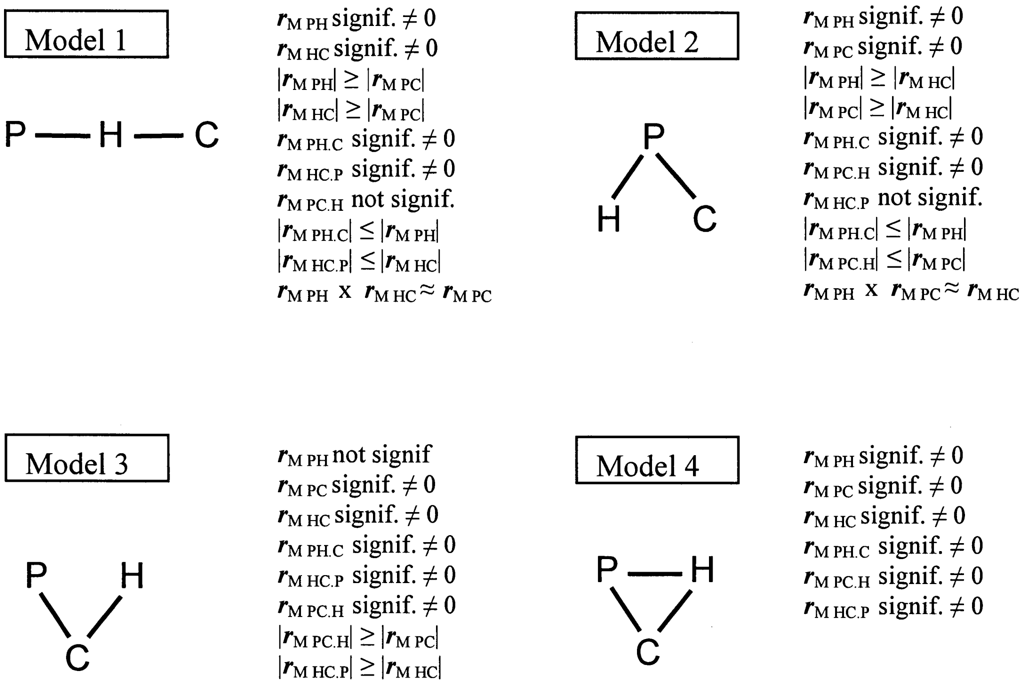
Table 1. The functional groups (FGs) and the numbers of species and individuals collected in the disturbed (Steudnitz) and undisturbed (Leutratal) grasslands. In total, 267 plant species and 1049 arthropod species (686 herbivores and 363 carnivores) were collected. For Diptera and Coleoptera only imagines were used. Detailed overviews of these data are given by Voigt et al. (2003)

[1] including the tissue sucking species of the Typhlocybinae. [2] including the ambushing species of the Salticidae and the Thomisidae

Trophic level	Code	Functional group (FG)	Taxon	Steudnitz		Leutratal	
				Species	Indiv.	Species	Indiv.
Producers				***132***		***193***	
	PAF	annual forbs	Spermatophyta	38		18	
	PGR	grasses	Spermatophyta	17		18	
	PMO	mosses	Bryophyta	18		40	
	PPF	perennial forbs	Spermatophyta	44		86	
	PWP	woody plants	Spermatophyta	15		31	
Herbivores				***348***	***44.642***	***544***	***95.214***
	HCW	stage-specific chewers	Coleoptera	144	2.977	217	22.173
	HLC	lifetime chewers	Caelifera			11	4.832
	HMI	miners	Diptera	67	9.751	134	6.461
	HTS	cell-tissue suckers	Heteroptera	60	5.287	72	16.864
	HVS	vascular suckers[1]	Auchenorrhyncha	77	26.627	110	44.884
Carnivores				**245**	**17.992**	***168***	***3.173***
	CAC	attacking chewers	Ensifera			5	488
	CBS	biting suckers	Diptera	56	2.957	119	2.087
	CCH	chewing hunters	Coleoptera	74	1160		
	CPA	parasitoids	Diptera	17	145	33	302
	CSH	sucking hunters	Heteroptera	11	936	11	296
	CWS	web-spinners[2]	Araneae	87	12.794		



Model 1

$r_{M\,PH}$ signif. $\neq 0$
$r_{M\,HC}$ signif. $\neq 0$
$|r_{M\,PH}| \geq |r_{M\,PC}|$
$|r_{M\,HC}| \geq |r_{M\,PC}|$
$r_{M\,PH.C}$ signif. $\neq 0$
$r_{M\,HC.P}$ signif. $\neq 0$
$r_{M\,PC.H}$ not signif.
$|r_{M\,PH.C}| \leq |r_{M\,PH}|$
$|r_{M\,HC.P}| \leq |r_{M\,HC}|$
$r_{M\,PH} \times r_{M\,HC} \approx r_{M\,PC}$

Model 2

$r_{M\,PH}$ signif. $\neq 0$
$r_{M\,PC}$ signif. $\neq 0$
$|r_{M\,PH}| \geq |r_{M\,HC}|$
$|r_{M\,PC}| \geq |r_{M\,HC}|$
$r_{M\,PH.C}$ signif. $\neq 0$
$r_{M\,PC.H}$ signif. $\neq 0$
$r_{M\,HC.P}$ not signif.
$|r_{M\,PH.C}| \leq |r_{M\,PH}|$
$|r_{M\,PC.H}| \leq |r_{M\,PC}|$
$r_{M\,PH} \times r_{M\,PC} \approx r_{M\,HC}$

Model 3

$r_{M\,PH}$ not signif
$r_{M\,PC}$ signif. $\neq 0$
$r_{M\,HC}$ signif. $\neq 0$
$r_{M\,PH.C}$ signif. $\neq 0$
$r_{M\,HC.P}$ signif. $\neq 0$
$r_{M\,PC.H}$ signif. $\neq 0$
$|r_{M\,PC.H}| \geq |r_{M\,PC}|$
$|r_{M\,HC.P}| \geq |r_{M\,HC}|$

Model 4

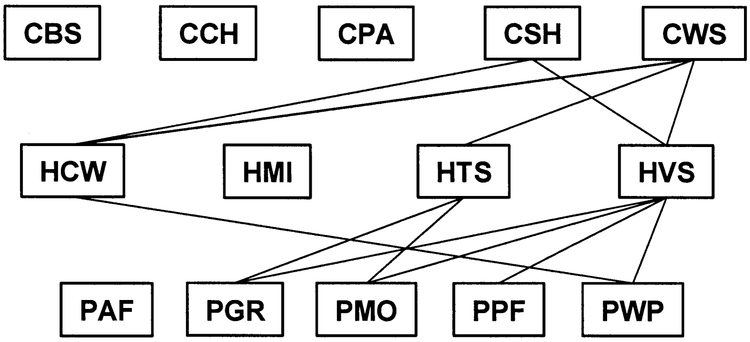
$r_{M\,PH}$ signif. $\neq 0$
$r_{M\,PC}$ signif. $\neq 0$
$r_{M\,HC}$ signif. $\neq 0$
$r_{M\,PH.C}$ signif. $\neq 0$
$r_{M\,PC.H}$ signif. $\neq 0$
$r_{M\,HC.P}$ signif. $\neq 0$

Figure 1. Criteria for the four possible models of correlative relationships between functional groups of the three trophic levels (producers, P; herbivores, H; carnivores, C) in terms of the expected values for the simple and partial standardized Mantel statistic r_M (after Legendre and Legendre 1998). Model Type 4 is supported even if one, but only one, of both $r_{M\,PC}$ and $r_{M\,HC}$ are not significant.

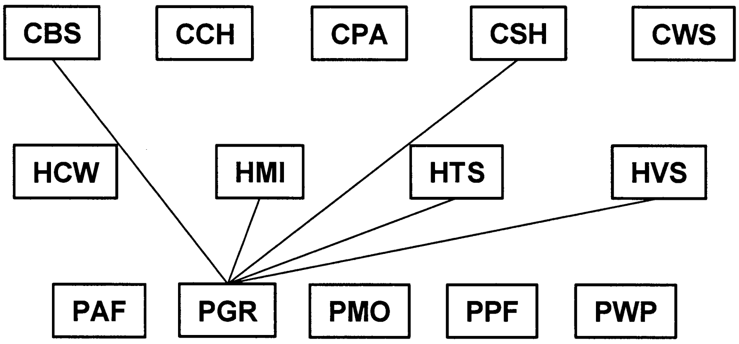
Figure 2

(a) Disturbed grassland

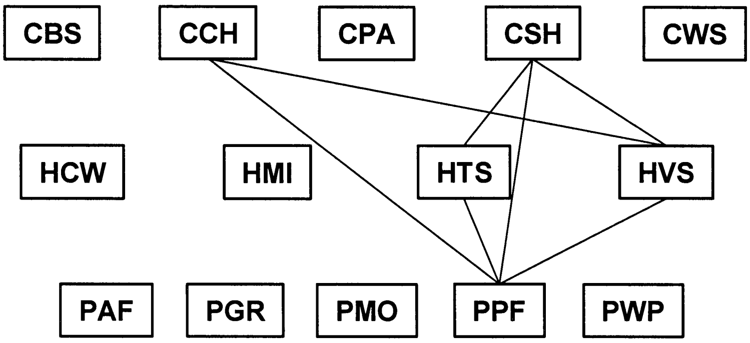
Model 1



Model 2

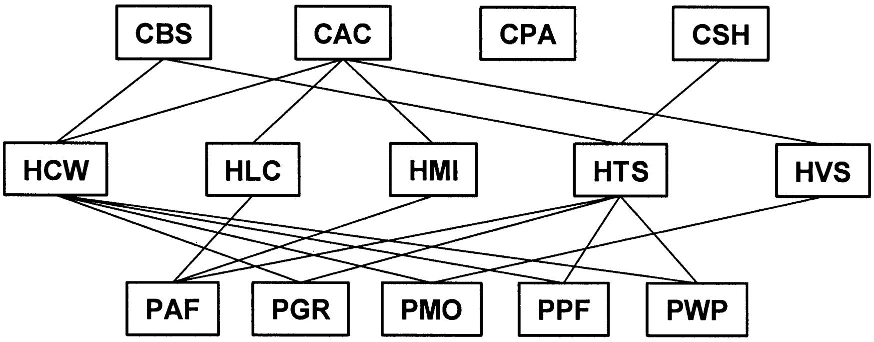


Model 4

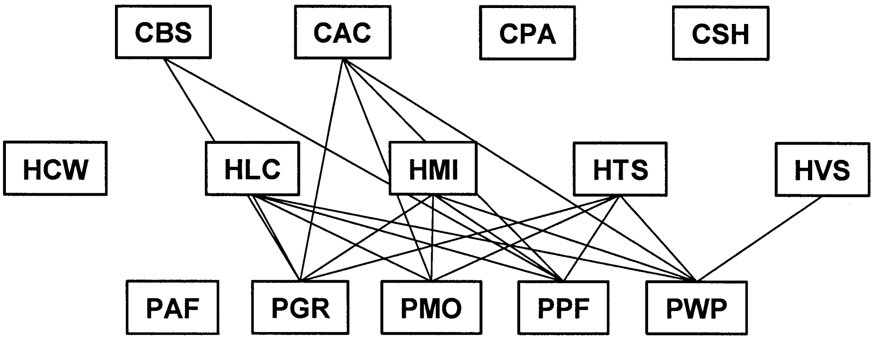


(b) Undisturbed grassland

Model 1



Model 2



Model 4

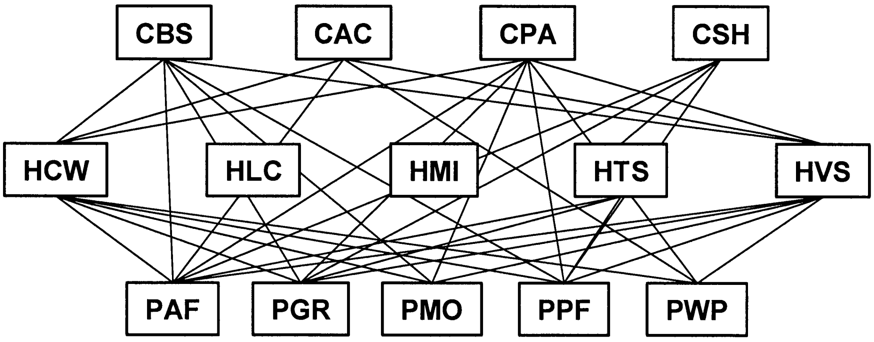


Figure 2. Vertical interaction web diagrams linking the functional groups (FGs) of different trophic levels separately for the models supported in the disturbed (a) and undisturbed grassland (b). Model Type 3 (compare with Fig. 1) was never supported. For explanations of FG-codes see Table 1.

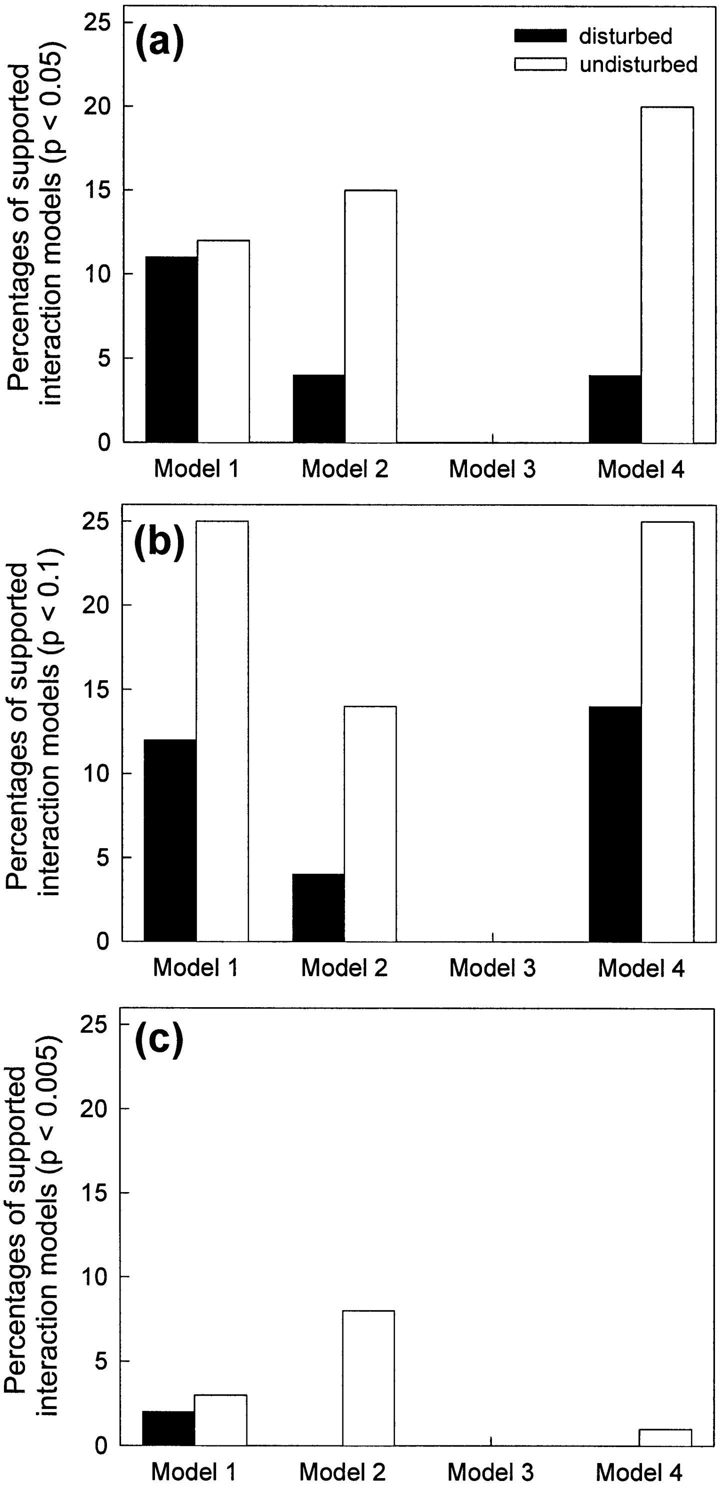


Figure 3. Percentages of significant interaction links between functional groups analysed separately for the models supported in both grasslands (filled bars, disturbed; empty bars, undisturbed). (a) significance at $p < 0.05$; (b) marginal significance at $p < 0.1$; (c) Bonferroni adjusted significance at $p < 0.005$.

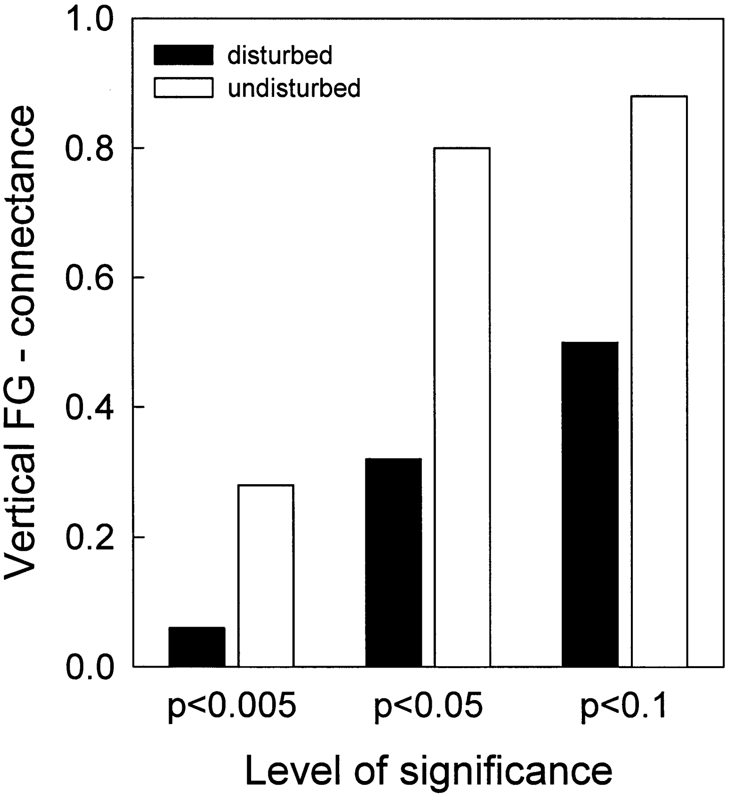


Figure 4. Vertical connectance of functional groups (FGs) for both grasslands (filled bars: disturbed; empty bars: undisturbed) and different levels of significance.

Appendices

Appendix 1

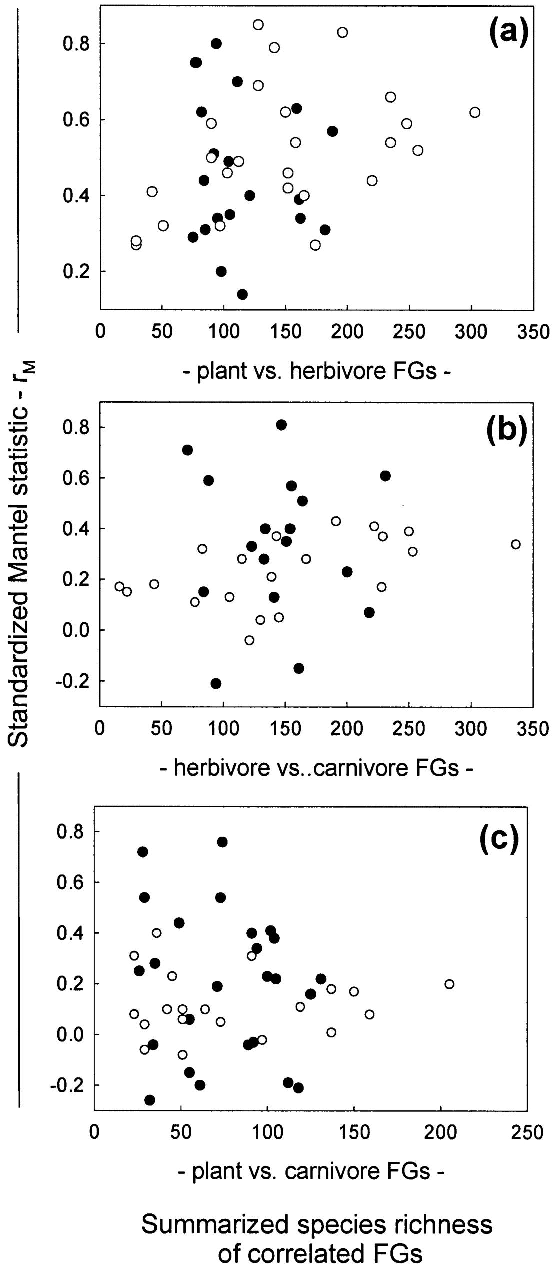
The standardized Mantel statistic r_M for correlations between the functional groups. (a) disturbed grassland (n.p.= calculations not possible, no corresponding years available) and (b) the undisturbed grassland

(a)	PAF	PGR	PMO	PPF	PWP	HCW	HMI	HTS	HVS
HCW	0.31	0.39**	0.34	0.57*	0.63***				
HMI	0.35	0.44**	0.31	0.70**	0.62**				
HTS	0.20	0.75**	0.75*	0.49*	0.29				
HVS	0.14	0.80***	0.34**	0.40***	0.51***				
CBS	0.34	0.54***	0.76***	0.23	0.19	0.23	0.33	n.p.	0.28
CCH	-0.19	0.40**	-0.03	-0.21	-0.04	0.07	0.13	0.40	0.35**
CPA	-0.14	-0.04	0.28	-0.20	-0.26	-0.15	0.15	n.p.	-0.21
CSH	0.44	0.72**	0.54*	0.06	0.25	0.57*	n.p.	0.71***	0.59**
CWS	0.16	0.38***	0.22	0.22	0.41**	0.61***	0.40	0.81***	0.51***

(b)	PAF	PGR	PMO	PPF	PWP	HCW	HLC	HMI	HTS	HVS
HCW	0.54***	0.66***	0.52***	0.62***	0.59***					
HLC	0.27**	0.28***	0.32**	0.32***	0.41***					
HMI	0.42***	0.47***	0.27***	0.44***	0.40***					
HTS	0.59***	0.50***	0.49***	0.54***	0.46***					
HVS	0.69***	0.85***	0.62***	0.83***	0.79***					
CAC	0.08	0.31***	0.23**	0.31***	0.40***	0.41***	0.17*	0.21*	0.11	0.28*
CBS	0.01	0.18**	0.08	0.20**	0.17**	0.34**	0.04	0.31*	0.43**	0.37***
CPA	-0.08	0.10	0.05	0.11*	0.10	0.39**	0.18	0.28	0.13	0.37**
CSH	0.04	-0.06	0.06	-0.02	0.10	0.17	0.15	0.05	0.32**	-0.04

Appendix 2

Scatter plot of the r_M – coefficients from the simple Mantel tests (standardized Mantel statistic) vs the summarized species richness of functional groups (FGs) for (a) producers and herbivores (total: $r^2 = 0.06$, $p = 0.09$; disturbed: $r^2 = 0.02$, $p = 0.52$; undisturbed: $r^2 = 0.18$, $p = 0.04$), (b) herbivores and carnivores ($r^2 = 0.04$, $p = 0.26$; disturbed: $r^2 = 0.0004$, $p = 0.94$; undisturbed: $r^2 = 0.27$, $p = 0.02$) and (c) producers and carnivores ($r^2 = 0.005$, $p = 0.66$; disturbed: $r^2 = 0.02$, $p = 0.53$; undisturbed: $r^2 = 0.002$, $p = 0.89$). Filled circles: disturbed grassland; Empty circles: undisturbed grassland.



11. Manuskript X

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Reliability characteristics of natural interaction webs.
Evolutionary Ecology Research, in press

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Reliability characteristics of natural functional-group interaction webs

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ABSTRACT

We compare the reliability of interaction webs for functional groups derived from extensive field data. Reliability is the probability of continued web function despite the failure of one or more functional groups. Interaction webs are diagrams of all the trophic and non-trophic relationships between groups. Functional groups are suites of species with similar ecosystem roles, and importantly mediate the diversity/ecosystem-function relationship. How they interact will thus have major ecological consequences. We reveal interactions between groups by simple and partial Mantel tests. Link type is then determined by applying sets of logical rules to the Mantel test results. We calculated the reliability of the resulting interaction webs. We also derived the reliabilities for webs of different link types because web topology affects reliability, not just the number of groups and links. Using the qualities of sink webs derived from these interaction webs, we illustrate the overall patterns in the relationships between reliability and other web characteristics. We compare these with the relationships in food-webs. We demonstrate the relation of reliability to principal components representing the information common to web characteristics other than reliability. We show that reliabilities for functional group interaction webs are very high, at least as high as those for food-webs, and that they show similar relationships to other web characteristics. Nevertheless, in our natural setting, the number of groups and the number of links a web has most affects reliabilities. However, they also differ more between webs of different link types, where topology differs, than between sites. Thus, in nature, the reliability of functional group interaction webs will depend on both web size and topology. This means that their contribution to mediating the biodiversity-ecosystem relationship will do so too.

INTRODUCTION

We examine the reliability of functional group networks. This is just part of our interest in the inter-relationships of functionally defined species groups. We want to detect how these relationships differ between habitats and ecosystems (Perner, *et al.*, 2003; Voigt, *et al.*, 2003; Voigt and Perner, 2004; Perner and Voigt *submitted*). Functional groups are important. They mediate relationships between diversity and ecosystem function (Bengtsson, 1998). There is no direct link between these phenomena. But the link is perhaps through organism function (*cf* Jones and Lawton, 1995; McCann, 2000). Implementing a functional group approach is particularly important because of current global environmental change effects on ecosystem structure and function (Blondel, 2003).

Functional groups

Functional groups are polyphyletic suites of species (Steneck, 2001) carrying out the same ecosystem process (Blondel, 2003). The same processes operate in most ecosystems of similar type. Using functional groups frees comparison of system behavior from dependence on species presence. Functional groups allow comparison between sites with different species compositions. They even allow comparison between biogeographic regions with no species in common.

Many criteria can be used for assigning species to groups. They may include ecosystem engineering processes as well as feeding mechanisms and morphology (Anderson, 1995; Woodward and Cramer, 1996). The exact choice of criteria depends on the questions asked (Körner, 1994). It also depends on the information available for species. But stringent mathematical or statistical definitions (Martinez, 1996; Bengtsson, 1998; Blondel, 2003) are often impossible. This is because the detailed information necessary is unavailable for all species in multispecies data sets. These data need not be ignored or discarded. Ecologists can define functional groups *a priori* and examine their interactions for meaningful and useful patterns.

Interaction webs

Interactions between species, or groups, produce networks. Among networks food-webs are familiar ecological examples. However, food-webs contain only trophic interactions. These are the influence of natural enemies and their victims on each other's abundance. Interaction webs are networks that capture other links. They include not only trophic interaction and competitive-facilitation effects (Paine, 1980), but also the effects that species exercise as ecosystem engineers (Anderson, 1995). Such non-trophic, non-competitive, effects are common (Ohgushi, 1997; Price, 2002) but ignored by food-web studies. Some lepidopteran larvae roll up leaves and so provide refuges from predators for other species. Leaf rolls thus influence the population dynamics of these other species (Fukui, 2001). Likewise, the colonization of grassland by woody perennials provides anchorage points for orb webs. This produces an increase in the abundance of the spider species that produce webs (Borges and Brown, 2001).

We know that our webs omit potentially important groups. This is true despite their including large numbers of species. However, no webs are all-inclusive, even those containing hundreds of species (Müller, *et al.*, 1999; Schönrogge and Crawley, 2000; Henneman and Memmott, 2001; Lewis, *et al.*, 2002). All webs are also necessarily based on temporally and spatially limited data. They are nevertheless useful. They describe and visualize patterns within and between ecosystems.

It is very difficult to observe the links between numerous functional groups directly. This is especially so when each group contains very many species. But many large sets exist of long-term population abundance data for numerous species. These are valuable compilations of how population abundances vary and co-vary. Such datasets were not assembled for producing webs. Identifying interactions from them thus requires complex statistical techniques. We use simple and partial Mantel tests to detect similarity in the patterns of abundance change (Mantel, 1967; Legendre and Fortin, 1989; Legendre and Legendre, 1998). We then apply sets of logical rules to the Mantel test results (Legendre and Troussellier, 1988; Legendre, 1993). Using matrices in this way has the advantage of simultaneously comparing abundance changes in numerous species.

Reliability

Reliability is a static property of networks. It depends on topology, on how groups join together. It differs fundamentally from properties derived only from the numbers of nodes and links, such as connectance. Reliability theory originated in engineering and process management. It deals with the determinants of successful operation of complex systems (Barlow and Proschan, 1965; Aggarwal, 1993; Molnár, 1995). Buildings, production lines and power distribution all form networks composed of nodes (structural elements, factories, or power producers and consumers). Links between these nodes represent flows (stress, product, and electricity). Reliability analysis determines the probability of continued network function when failure of one or more nodes interrupts flows.

In ecological networks, nodes are species or species groups. Links represent various influences between these nodes. In food-webs, links represent matter and energy flow between species. Food-webs are the only ecological networks so far analyzed for reliability (Jordán and Molnár, 1999; Jordán, *et al.*, 1999; Jordán, *et al.*, 2003). But links can also be invoked whenever one species, or functional group, affects another. We are interested in the inter-relationships of functional groups. We therefore apply reliability analysis to networks in which the nodes are functional groups. The links are the mutual influences on population abundances between groups. There are thus two ecological equivalents of node failure. The first is the weakening of the interaction between groups to a value below a given threshold. The second is the disappearance of the species in the group by extinction or phenology. We investigated whether functional group interaction webs have high or low reliabilities similar in size to those for food-webs (Jordán and Molnár, 1999). We also examine whether reliabilities for our webs relate to other web characteristics in the same way as for food-webs. We discuss the major influences on these relationships. We determine how different types of links affect reliability. And we examine whether web reliabilities differ between sites or are related to ecological differences.

METHODS

Sites and species

The data came from two grasslands on Triassic limestone near Jena, Germany. These sites are at 11.6°E, 50.9°N and 145m above sea level. Leutratal is dominated by the grasses *Bromus erectus* Huds., *Brachypodium pinnatum* (L.) P.B. *Sesleria varia* (Jacq.) Wettst. is abundant in the dryer parts. Steudnitz is 18km further north. It is similar to Leutratal but subject to industrial pollution until 1990. Heinrich, *et al.* (1998) and Heinrich, *et al.* (2001) give detailed descriptions of both sites. Müller, *et al.* (1978), Heinrich (1984) and Perner (1997) report the considerable research at these sites.

Species abundance data came from collections made by colleagues and students. These collections cover several years within a 24-year period. They were made at three locations within each of the two sites. Plant species abundance was assessed by the Braun-Blanquet method (Kent and Coker, 1994) on a regular program (Heinrich, *et al.*, 1998; Heinrich, *et al.*, 2001). Arthropod abundance was determined by standardized sweep net sampling (Köhler, 1987) on a similar program (Heinrich, *et al.*, 1998; Perner, *et al.*, 2003). We included all available data in the analysis.

Functional groups

We uniquely assigned species to ecologically defined functional groups using readily available information (Perner, *et al.*, 2003; Voigt, *et al.*, 2003; Voigt and Perner 2004). We classified producers by combinations of growth habit, structure, and life span. Invertebrates were grouped according to their foraging characteristics (Table 1). Some species fall into different categories at different stages of development (Steneck, 2001). These species we placed in the group that had the greatest influence on the local ecosystem. Thus, Tachinidae

(Diptera) were placed with 'parasitoids'. Their larvae are likely to have greater local effects than the mobile adults. In addition, the diets of some species vary with place or opportunity. We therefore classified these species according to their predominate foraging behavior in the collection sites. We classified Ensifera species as 'attacking chewers' although some can be somewhat omnivorous. This classification into functional groups disrupts taxa. Species of the same taxon may well fall into different functional groups. Species of the same taxon can also fall into different trophic levels.

Interaction webs

We constructed webs from interaction links between functional groups identified in the abundance data. We used a statistical technique that successfully reveals such relationships (Voigt and Perner, 2004; Perner and Voigt *submitted*). We improved normality of variances of the plant data by square root transformation. Arthropod data was log transformed. We then tabulated these data for each functional group within each site. The rows of the table represent collection locations and years. The columns give the abundance measures for each species within the functional group. Each cell of this table therefore records the abundance of a single species, year, and collection locality within one of the sites. We then calculated a matrix of dissimilarities between the rows of the table based on species abundances in the columns. This matrix represents the pattern of abundance changes over locations and years for all the species in the group.

To determine the existence of a link we applied simple and partial Mantel tests (Mantel, 1967; Legendre and Legendre, 1998; Fortin and Gurevitch). A link between two functional groups exists whenever $p<0.05$ for the Mantel correlations ($\boldsymbol{r}_{\mathrm{M}}$) between their matrices (Voigt and Perner 2004; Perner and Voigt *submitted*). If $\boldsymbol{r}_{\mathrm{M}}$ between two functional groups is high, their species abundances change in similar ways over locations and years. The value $p=0.05$ is a useful threshold value. It is not part of null-hypothesis testing. There is thus no need to use a correction for multiple comparisons.

Simple Mantel correlations do not fully characterize a link, however. This is because relationships between groups may arise for several reasons. And each set of reasons produces a different relationship type. A link may exist between groups A and B because one directly affects the other. Alternatively C may affect both A and B, and other pathways exist. We distinguished these link types by using partial Mantel tests and applying four sets of logical rules (Legendre and Troussellier, 1988; Legendre, 1993; Voigt and Perner, 2004; Perner and Voigt *submitted*). Partial Mantel tests determine the significance of interactions between two groups holding constant the influence of a third (analogous to partial Pearson or Kendal correlations). The logical rules derive from the value, rank and significance of two sets of correlations. The first is $\boldsymbol{r}_{\mathrm{M\ PH}}$, $\boldsymbol{r}_{\mathrm{M\ PC}}$ and $\boldsymbol{r}_{\mathrm{M\ HC}}$ ($\boldsymbol{r}_{\mathrm{M}}$ for all pair-wise combinations of functional groups from producer (P), herbivore (H) or carnivore (C) categories). The second is the values of $r_{\mathrm{M\,HC}}$ relative to $r_{\mathrm{M\,HC.P}}$, $r_{\mathrm{M\,PC}}$ to $r_{\mathrm{M\,PC.H}}$ and $r_{\mathrm{M\,PH}}$ to $r_{\mathrm{M\,PH.C}}$. The notation XY.Z means the partial effect of X on Y while controlling for their relationships with Z. Each of the four sets of logical rules defines a possible link type or model.

Links can belong to more than one type just as it is possible for partial correlations to be high in more than one direction. This would occur when groups B and C greatly affect group A. We omitted horizontal links because the sets of logical rules based on Mantel-like comparisons of more than three matrices (*e.g.* Manly, 1986) are highly complex and occasionally ambiguous. Horizontal links are rarely included in food-web studies.

We constructed webs using the links identified. Each web was of a single type because it included only links that fit a certain model. Some of the links in such webs may also fit other models (Voigt and Perner, 2004; Perner and Voigt *submitted*). Analysis of these webs allowed us to examine how different link types affect reliability. Together, webs compiled from links of different types show all the interactions stronger than our threshold. The real ecosystem contains all such links. They must all be included in order to examine the reliability of the complete system. Therefore, we combined all the links into a single complete web for each site (the two webs analyzed in Voigt and Perner, 2004; Perner and Voigt *submitted*). All these webs are related because the complete web contains no more links than those in constituent webs. They might thus be expected to have similar properties. But, despite their origins, their reliabilities may differ if they have different topologies. Even webs with the same number of nodes and same connectance have widely divergent reliabilities (Jordán and Molnár, 1999). We tested this possibility since it would be of great ecological importance if true. It suggests that the reliabilities of natural functional-group interaction webs depend on the number and particular arrangement of the different link types they contain. This, in turn, would change their role in diversity/ecosystem function mediation. For simplicity and to avoid confusion, we refer to eight 'models'. These eight are collectively the webs derived from different models and their associated complete web from each site.

To characterize the models fully, we compiled all their constituent sink webs. These are webs where only one species or group ultimately receives all flows (Cohen, 1978). The sink is a top carnivore or herbivore without predators. Sink webs were also necessary in order to compare the reliabilities of functional-group interaction webs with those for food-webs. Only Jordán and Molnár (1999) have derived food-web reliabilities. They did so only from sink webs.

Sink webs characterize the model from which they are constructed. However, those from the same model need not have the same structure or reliability (Jordán and Molnár, 1999). The difference between sink webs reflects the size and structural diversity of the original model. It is itself a model character. All the sink webs are related because our models share functional groups between sites. For the same reason they are also mutually related within sites. A consequence of this relatedness is that some sink webs from different models are structurally identical. They nonetheless characterize different models. Deleting these identical sink webs is thus invalid. To do so would remove model similarities. It would artificially inflate differences between models. Minimizing differences is conservative. It ensures that any differences we find occur despite model relatedness.

Reliability

The reliability of a network is the probability that sinks remain connected to at least one source if nodes randomly fail with a certain probability. We assumed that sinks do not fail (Jordán and Molnár, 1999). Webs with a single sink disconnect as soon as the links break between the single sink and the producers because of the failure of a base, or intervening, node. In webs with more than one sink, different definitions are possible. The weak definition is that webs fail when only one sink is disconnected. The intermediate that failure occurs when 50% or more sinks detach. The strong definition is that webs fail only when all sinks become detached. We used the strong definition under which web failure is least likely. This represents a true, complete, failure.

In principal, each web node has its own failure probability. But computational difficulties currently prevent calculation of reliabilities on this basis. We therefore used fixed and equal failure probabilities for all nodes (Jordán and Molnár, 1999). To be able to compare interaction web reliabilities with those for food-webs we used the same failure probability p=0.01 (Jordán and Molnár, 1999). However, reliabilities tend to be very high with this value. They therefore do not fall accurately into size categories. The category widths are not much bigger than the rounding errors of individual values. To avoid this problem we also used failure probabilities of 0.1 and 0.3. These two values reveal more clearly the relationships between reliability and other web characteristics.

Link directedness is a key distinction between food- and interaction-webs. In food-webs, matter and energy flow in a single direction to a defined sink (*e.g.* a top predator). Flows in interaction webs are practically undirected. Reliable flows are much more difficult to define. They might be determined between several sets of nodes but this is a large and complex subject. Therefore, we assumed trophic flow to enable comparison with food-web reliabilities. We calculated the trophically directed component of reliability by the equation:

$$R = 1 - \sum_{i=1}^{n-1} \binom{n-1}{i} p^i q^{((n-1)-i)} F_i$$

The value p is the failure probability (=0.01, 0.1 or 0.3) and q the probability of not failing (= 1-p = 0.99, 0.9 or 0.7). The total number of nodes is n (and n-1 is thus the number of deletable nodes). F_i is the 'fatal ratio', the ratio of the number of sets of i deleted points that result in disconnection between sources and sinks to the total number of sets of i deleted points (Jordán and Molnár, 1999; Jordán *et al.*, 2003).

Analysis

We compared the patterns of reliability in functional group interaction webs and in food-webs. To do this we plotted the values of various web characteristics against reliability classes (Jordán and Molnár, 1999). Calculation of web characteristics used conventional definitions. But we also calculated vertical, as well as normal, connectance because our webs omit horizontal links. Vertical connectance is unbiased by the omission of horizontal links. It equals the number of links existing as a proportion of all possible vertical links. For functional group webs, the "predator-prey ratio" is the ratio of groups with only links to lower trophic groups to those that have links upwards. This is the ratio of the numbers of groups with only in-degrees to the number with out-degrees (*cf* Jordán and Molnár, 1999). It measures how much groups at the top of the web interact with species in more than one lower group. The proportion of "specialists" equals the proportion of groups having an "in-degree" of one. Such groups have only one link to a lower trophic level. This measures the proportion of groups in which species interact with species in only one lower group. We estimated the "specialization range" as the standard deviation of the mean number of in-degrees. Webs with high specialization-ranges have more varied structure than those with low values. We derived reliability classes of <0.9, 0.901-0.96, 0.9601-0.97, 0.9701-0.98, 0.9801-0.99 and 0.9901-1.00 using only the reliabilities calculated with a 0.3 failure probability. This gave the greatest separation of reliability values. The two lowest classes are broad in order to avoid many non-empty classes with small numbers of values.

We examined the null hypothesis of no relationship between reliabilities and each of the other web characteristics. We used Kendal rank correlations because reliability and many of the web characteristics are proportions. They are therefore non-normally distributed. Multiple pair-wise correlations of these data are misleading. Most web characteristics ultimately derive from the number of nodes and links. In consequence, the measures are not independent of each other. To escape this problem we used principal component analysis (PCA). This technique also determines the major factors influencing the reliabilities of our webs. It extracts independent axes from the primary (numbers of nodes and links) and derived web characteristics. The web characteristics were standardized. This ensured that those with quantitatively larger values (*e.g.* number of nodes) did not overly influence the analysis. We then identified the major PCA axes as those collectively explaining more than 75% of the variance in the constellation of web characteristics. Afterwards we determined the relationship of reliability to these PCA axes.

We tested the null hypothesis that reliabilities did not differ between models or between sites with a nested anova. This design was needed because sink webs are derived from site-specific models. Sink web reliabilities are thus non-independent within and between models. Standard anova therefore underestimates within-sample variance and so inflates *F* values (Underwood, 1997). We removed this effect by first calculating the residuals after multi-regression against variables denoting degree of relation between sink webs. We then carried out the anova on these residuals (Stearns, 1983).

RESULTS

Species abundances, functional groups and models

The data included the abundances of 267 producer species (autotrophs). There were 686 arthropod herbivore species (139 856 individuals). There were also 363 species of arthropod carnivores (21 165 individuals) (Table 1). Numerous species occurred in both sites. The sum of the site totals was therefore greater than the overall total. These species formed 16 functional groups. There were 14 functional groups at each site. But Leutratal had one fewer carnivore group and one more herbivore group than Steudnitz. Most of the groups at the two sites were the same. However, Leutratal had no CWS and CAC rather than CCH. Steudnitz lacked HLC. Leutratal had more significant links than Steudnitz. In both sites, the logical rules identified significant links of types one (m1), two (m2) and four (m4). No significant links fulfilled the rules for model three. Overall, most links were of type 4 (39). There were fewer model 1 (30) and model 2 (24) links.

Interaction webs

The complete model for Leutratal (l-c) was the largest. It contained 14 functional groups and 52 links (Fig. 1). The smallest was the m4 model for Steudnitz with five groups and seven links (Fig. 2). We derived 17 sink webs from the four Leutratal models and 14 from the four in Steudnitz. These sink webs are identified by a code of the form “l-m1-cac”. The first element indicates the site (l or s). The second is the model from which they are derived (c, m1, m2 or m4). The third element is the identity of the sink species. Of these 31 sink webs, nine were c, five m1, 11 m2 and 6 were m4. The largest was of 10 nodes and 29 links (for l-c-cac). The smallest had a single pair of nodes and a single link (Fig. 3).

Reliability and analysis

There was very close correlation between sink web reliabilities calculated with the three different node failure probabilities (r=0.970-0.998). We therefore only analyzed reliabilities calculated with p=0.3. This produces the clearest patterns of relationship (Table 2).

Sink webs with the highest reliabilities tended to contain more functional groups. The large webs from the Leutratal complete model occurred in the higher reliability classes (Fig. 4a). There was a similar positive relationship between the total number of links in webs and reliability class (Fig. 4b). It remained even after removing the high value of 52 links for the Leutratal complete web. High reliabilities were also associated with high link densities (Fig. 4c). There was no pattern, however, in the relationship between connectance and reliability class, despite the first column (Fig. 4d). Vertical connectance and class were also unrelated (Fig. 4e). The ratio of top groups (sinks) to others appeared least for webs in high reliability classes (Fig. 4f). This suggests a negative relationship between this ratio and reliability. However, high reliability classes had lower proportions of specialist groups (those with in-degrees of one) (Fig. 4g). Two of the Leutratal models falling in the highest reliability classes had no specialist groups at all. There was no discernable relationship of reliability class and specialization range (standard deviation of the number of in-degrees per group) (Fig. 4h). Leutratal models clustered together. They tended to occur in the higher reliability classes. Steudnitz models, however, did not cluster. They occurred across the entire range of classes.

There were highly significant Kendal rank correlations of reliability with most web characteristics. Strong positive correlations occurred with the number of functional groups, the number of links, and with link density. Strong negative correlations existed with proportion of specialists and predator-prey ratio (Table 3). Reliability did not correlate with range of specialization, or with either of the connectance values.

The first two PCA axes together explained 83.7% of all the variance in web characteristics. The remaining axes explained little additional variance. Loadings of the web characteristics on the first axis (PCA1) were all high whether positive or negative. Only link density and vertical connectance had loadings greater than 0.500 on the second axis (PCA2) (Table 4). PCA1 thus tends to represent web size. PCA2 reflects structural aspects. Reliability correlated strongly (0.756) with the first PCA axis. But it did not correlate strongly with the second (0.260).

The quantities total number of groups, number of links, and link density all correlate (Fig. 5). The ordination also indicates the correlation of proportion of specialists, predator-prey ratio, and normal connectance. But these correlate in the opposite sense. Vertical connectance, however, did not correlate closely with either of these variable groups. Reliability plots nearly parallel to the axis of the other variables except vertical connectance. This indicates its correlation with them. The majority of Leutratal sink lay in the right half of the plot. They thus associate with high values on PCA1. However, they spread over the whole range of PCA2. Most Steudnitz webs, in contrast, associate with low, negative, values on PCA2. But they extend over the range of PCA1. Sink webs from some models clustered together but others did not.

Sink reliability differed significantly between web types (F^6_{23}=2.64, p=0.04) by nested anova corrected for web relationships. Nevertheless, the overall anova was not significant (F^7_{23}=2.27, p=0.65). There were no significant differences between sites (F^1_{23}=0.13, p=0.72).

DISCUSSION

Our natural interaction webs are broadly as reliable as natural food-webs (Jordán and Molnár, 1999). This is true even though we used a higher failure probability. Interaction web reliabilities are very high using the same small failure probability of 0.01 as used for food-web studies. The most stable class contained all reliabilities. Reliabilities for our interaction webs might have been expected to be lower than for food-webs in general. This is because we omitted horizontal links, those representing competition or facilitation. But our interaction web reliabilities are not lower. This suggests that adding horizontal interactions to interaction webs will make their reliabilities greater than those for food-webs. This is probable since full interaction webs include more links that food-webs. They include all the trophic links of food-webs together with all the non-trophic interactions. Thus, for a given number of groups or species, interaction webs will usually contain more interactions than food-webs. Having more links, they will be more reliable.

We can exclude the possibility that our webs are unusual because they derive from a limited number of taxa. The webs derive from data on a large number and variety of plant and arthropod species. These species represent a substantial part of the whole grassland community.

Putting species in the “wrong” functional group could change link orientation. This would affect the web and possibly alter reliability. It is unlikely that this is a systematic problem in our webs. The presence of several species in functional groups buffers single species effects. However, wrongly placing particularly variable species might affect reliability. This possibility thus requires theoretical examination.

Interaction webs show similar relationships between reliability and other web characteristics as small food-webs (Jordán and Molnár, 1999). It is possible to compare these patterns. But direct comparison of the frequency histograms for interaction and food-webs is invalid. This is because we calculated reliability classes using a higher failure probability. Our data derive from a wider range of web sizes but do not show the relationships across a complete range of reliabilities. This is because we analyzed only those webs represented in the field data. We did not generate numerous webs of similar sizes but varied reliabilities.

In our interaction webs total number of nodes strongly influences reliability. This is not seen in food-webs (Jordán and Molnár, 1999). The difference is probably because number of nodes (functional groups) and proportion of linked nodes positively correlate in our webs. The relationship of reliability with link density shows this. Of course, larger webs must also have larger numbers of links. However, an increase in the proportion of links derives from the particular characteristics of Leutratal and Steudnitz natural interaction webs. Testing the generality of this relationship requires reliability analysis of more ecosystem webs.

There is a very clear difference between food and interaction webs. There is no relationship between reliability and connectance measures in interaction webs. This may be illusory. The data for food-webs includes all possible connectance values for the five-node webs generated (Jordán and Molnár, 1999). In contrast, our interaction webs have different sizes. Their connectances are thus not the full range of values for webs of these sizes. The Leutratal and Steudnitz data unfortunately yielded too few webs to control for the effect of different web sizes. Such a control might have revealed a relationship with reliability similar to that for food-webs.

We found the same relationships between reliability and the number of specialists and with the predator-prey ratio as in food-webs (Jordán and Molnár, 1999). However, the relationship with degree of specialization found at high connectances, but not at low, for food-webs is absent. This arises because the interaction web connectances lay in the lower part of their possible range.

There may be a simple reason for the differences we describe between food- and interaction webs. They may arise mainly because the interaction webs derive from field data. They are not all possible webs of a given size (Jordán and Molnár, 1999). These interaction webs are those possible in nature. They are a selection of those structurally conceivable (Maynard Smith *et al.* 1985). We found broad similarities between food- and interaction webs. We imagine, therefore, that ecological web reliabilities will relate similarly to other web characteristics. Interaction web reliabilities should have the same relationships to trophic chain length, compartmentalization and omnivory as food-webs (Jordán and Molnár, 1999). However, we could not test these contentions. We examined the interrelations of functional groups unambiguously assigned to discrete trophic levels. Such levels may or may not exist in species-specific food-webs (Oksanen, 1981; Polis and Strong, 1996). But defining such levels is intrinsic to the definition of functional groups. It unavoidably affects the analysis of their group interactions. The levels in our webs constrain chain lengths to either one or two. We did not divide carnivore functional groups into grades (primary, secondary or higher-grade carnivores). Not dividing functional groups into grades also restricts the identification of omnivory. Omission of horizontal links within trophic levels prevented reliable estimation of compartmentalization.

In food-webs, connectance influences relationships between reliability and other characteristics (Jordán and Molnár, 1999). The relationship is not linear, however. In our webs the relationship is different, although not significant. It is linear and negative. Reliability decreases as connectance increases. This is surprising since high connectance should mean high reliability. High connectance means more links among available groups. More groups must then fail to cause disconnectedness. Part of the reason for the difference is that the number of nodes and the number of links strongly influences connectance. Connectance will fall if the number of links falls but the number of nodes does not. Differences in web structure also affect the relationship, however. Different reliabilities of inter-related models and webs show this.

The close association of group number and reliability in ordination also reveals a strong effect of web size on reliability in our natural web data. Many of the other web characteristics align similarly with the number of groups. Web structure is also important since low reliability is associated with small numbers of upward links. That is, with high predator-prey ratios and high proportions of specialists. Without differences in structure between models, their reliabilities would be similar because of their interrelationships. Models also differ because their sink webs have different ranges of characteristics. Sink webs from the same models ordinate separately. This arises predominantly because of structural differences within models. The separation is greatest in relation to the second, structural, PCA axis. Differences in sink web size also contribute, particularly for Steudnitz models. Here the separation is in relation to PCA1. The anova shows the importance of structural differences. If models were random selections from all the links possible there would be no differences between their reliabilities. They differ between models, however. These differences are independent of web relationships. Reliabilities are also more different between models than they are between sites. The same models exist at both sites.

The assessment of reliability for ecological webs is in its infancy. Ways of improving the technique are thus not difficult to find. Among other things, failure probability of a group is not a web-wide constant as we have had to assume. Failure probabilities, in fact, will relate to the strengths of interactions. They will vary between pairs of species and with time. In conventional food-webs, failure probabilities might be estimated using the average value of the node's pair-wise interaction strengths (D_{ij}). In our interaction webs the average value of $\boldsymbol{r}_{\mathrm{M}}$ might be appropriate. It is not clear, however, whether these values and failure probability should correlate positively or negatively. Large effects might result from weak interactions (Berlow, 1999). Interaction strength variance might thus be a more suitable measure of failure probability. In addition, species turnover rates might indicate realistic failure probabilities. Web reliabilities would then relate to stated time intervals.

Interaction web analysis is also a recent development (Price, 2002). But its use will contribute greatly to understanding ecosystem stability and resilience because interaction webs encapsulate more of the links in a system than do food-webs. Interaction webs are less easily detected than the trophic interactions portrayed in food-webs, however. Many interactions do not involve matter transfer and so they cannot always be observed directly. Painstakingly detailed research reveals them (*e.g.* Fukui, 2001; Nozawa and Ohgushi, 2002ab). But such studies are logistically limited to small parts of systems. Our statistical technique detects interactions in much larger systems. It therefore provides a good overall view based on species abundance data. Time-series autocorrelation analysis (Turchin, 2003) might also produce similar overall views.

Reliabilities in functional group interaction webs resemble the available reliabilities from food-webs. They have similar sizes and relationships to other web characteristics. Using our methodology, they can assess and compare the interactions of functional groups in large, species-rich, systems. They are important measures because web structure, as well as web size, influences them. They thus reveal topological differences between otherwise similar webs. Reliabilities are therefore one measure, among others, for assessing differences in the linkage properties of different systems. The possibility of reliability differences between models indicates that functional group interaction web reliabilities will depend on the proportions of links of different types they contain. In consequence, how functional groups affect the relationship between species and ecosystems will relate to web reliability. Reliability analysis is thus an important component of our understanding of the diversity/ecosystem function-relationship.

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Table 1. The numbers of individuals and species collected in Leutratal and Steudnitz grouped into functional groups (*cf* Voigt and Perner 2004).

	Code	**Functional group**	*Steudnitz*		*Leutratal*	
			Species	**Individuals**	**Species**	**Individuals**
Trophic level						
Producers			**132**		**193**	
	PAF	annual forbs	38		18	
	PGR	grasses	17		18	
	PMO	mosses	18		40	
	PPF	perennial forbs	44		86	
	PWP	woody plants	15		31	
Herbivores			**348**	**44 642**	**544**	**95 214**
	HCW	stage-specific chewers	144	2977	217	22 173
	HLC	lifetime chewers			11	4832
	HMI	miners	67	9751	134	6461
	HTS	cell-tissue suckers	60	5287	72	16 864
	HVS	vascular suckers	77	26 627	110	44 884
Carnivores			**245**	**17 992**	**168**	**3 173**
	CAC	attacking chewers			5	488
	CBS	biting suckers	56	2957	119	2087
	CCH	chewing hunters	74	1160		
	CPA	parasitoids	17	145	33	302
	CSH	sucking hunters	11	936	11	296
	CWS	web-spinners	87	12 794		

Table 2. Reliability values for full model and sink functional group interaction webs for Leutratal and Steudnitz.

site	model	description	sink group	reliability
Leutratal	model 1	full model		0.9806
		sink	cac	0.9424
		sink	cbs	0.9054
		sink	csh	0.6943
	model 2	full model		0.9919
		sink	cac	0.9919
		sink	cbs	0.9100
		sink	hlc	0.9919
		sink	hmi	0.9919
		sink	hts	0.9919
		sink	hvs	0.7000
	model 4	full model		0.9975
		sink	cac	0.9896
		sink	cbs	0.9970
		sink	cpa	0.9975
		sink	csh	0.9862
	complete	full model		0.9975
		sink	cac	0.9975
		sink	cbs	0.9974
		sink	cpa	0.9975
		sink	csh	0.9901
Steudnitz	model 1	full model		0.9387
		sink	csh	0.8413
		sink	cws	0.9467
	model 2	full model		0.7000
		sink	cbs	0.7000
		sink	csh	0.7000
		sink	hmi	0.7000
		sink	hts	0.7000
		sink	hvs	0.7000
	model 4	full model		0.7000
		sink	cch	0.7000
		sink	csh	0.7000
	complete	full model		0.9873
		sink	cbs	0.7000
		sink	cch	0.9043
		sink	csh	0.9929
		sink	cws	0.9455
		sink	hmi	0.7000

Table 3. Kendall rank correlations between reliabilities and other web characteristics for sink functional group interaction webs for Leutratal and Steudnitz.

characteristic	Kendall's τ	p significance
number of functional groups	0.537	<0.001
number of links	0.609	<0.001
link density	0.625	<0.001
connectance – normal	-0.130	0.280
connectance – vertical	-0.050	0.680
predator-prey ratio	-0.467	<0.001
specialist proportion	-0.681	<0.001
specialization range	0.048	0.739

Table 4. The loadings on the first two axes of a PCA of the web characteristics for sink functional group interaction webs for Leutratal and Steudnitz.

characteristic	PCA 1	PCA 2
number of functional groups	0.9756	0.0754
number of links	0.8329	0.4921
link density	0.7984	0.5669
connectance – normal	-0.8139	0.3372
connectance – vertical	-0.6129	0.7335
predator-prey ratio	-0.9354	0.0069
specialist proportion	-0.8010	-0.1300
specialization range	-0.8168	-0.2156

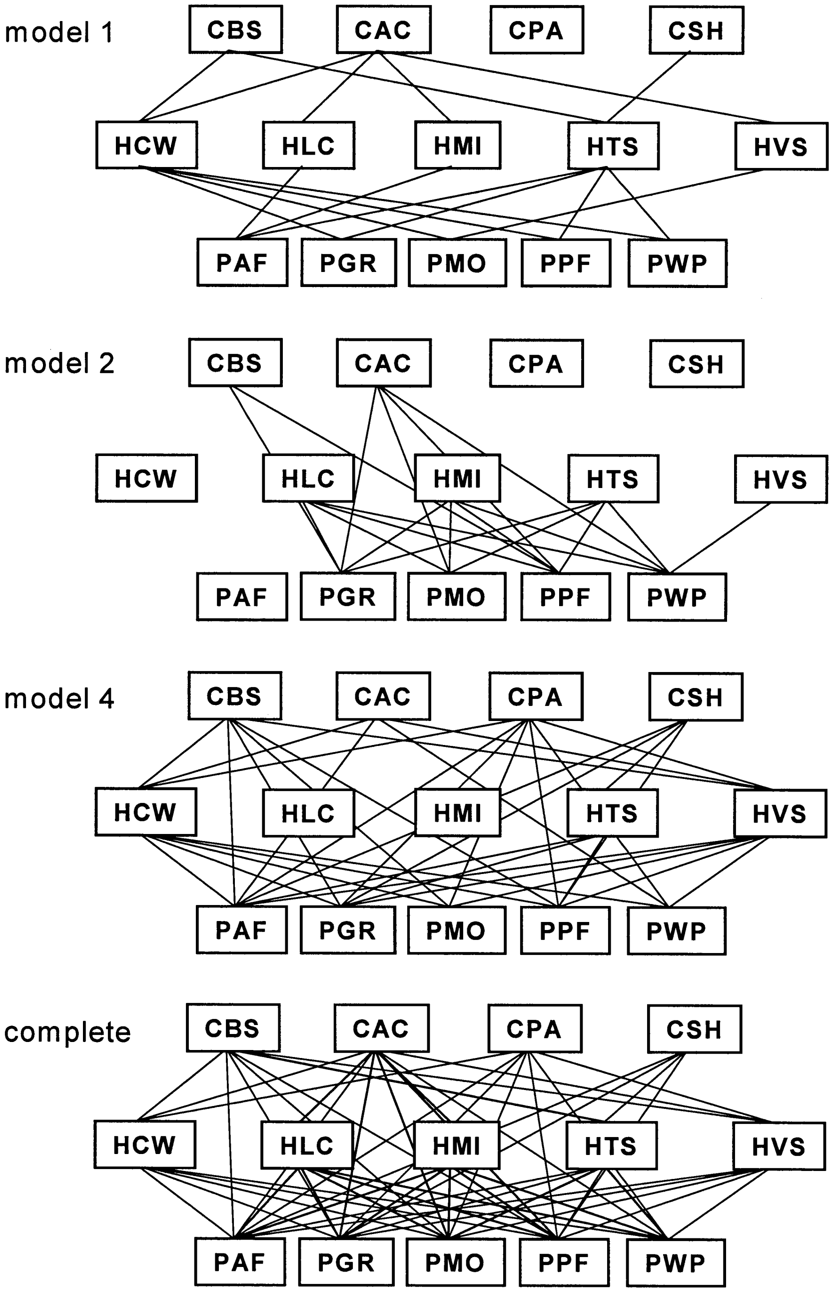


Fig. 1. Functional group interaction webs for Leutratal; Models 1, 2 and 4 and the complete web produced by combining them. (Models 1, 2 and 4 incorporated from Voigt and Perner 2004).

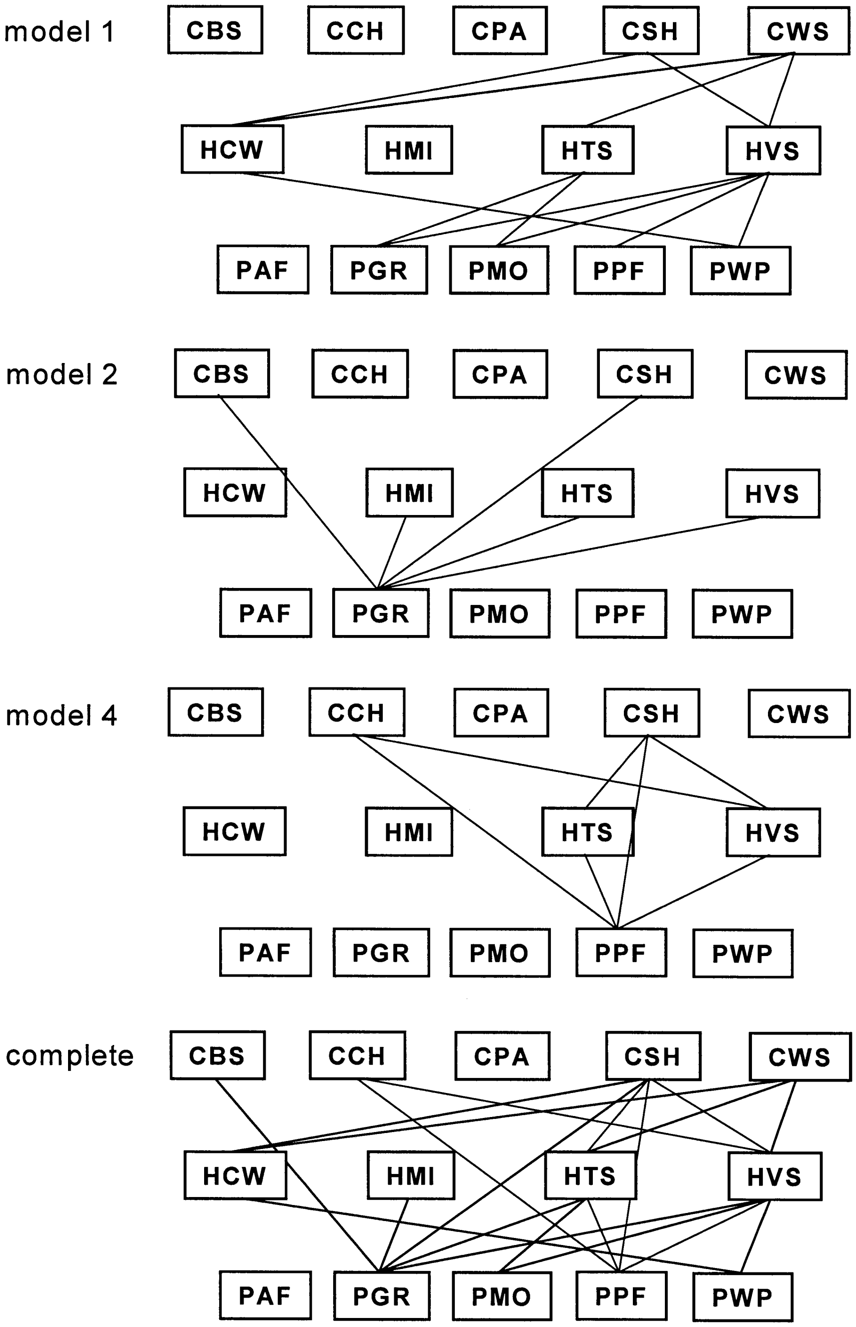
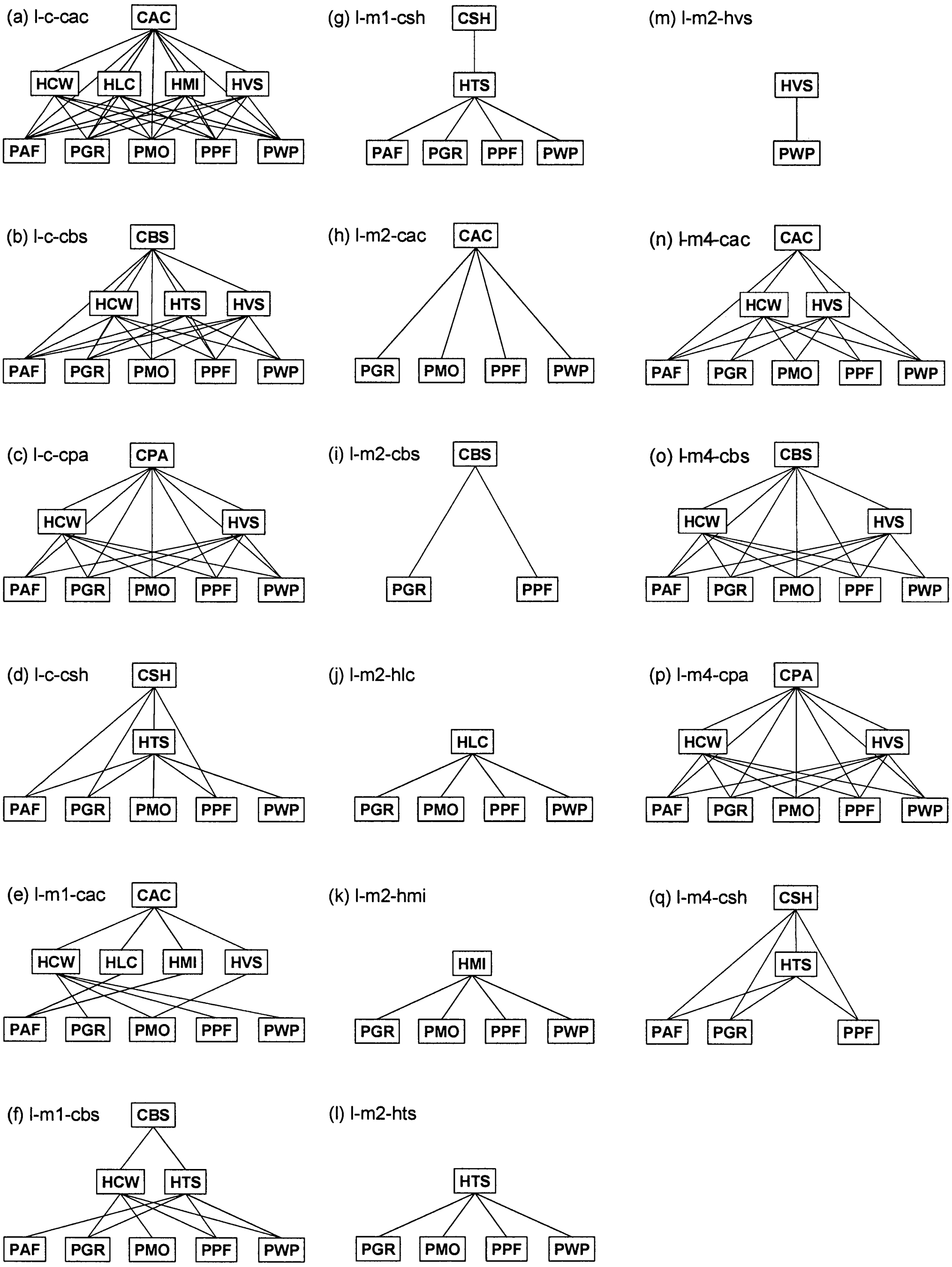


Fig. 2. Functional group interaction webs for Steudnitz; Models 1, 2 and 4 and the complete web produced by combining them. (Models 1, 2 and 4 incorporated from Voigt and Perner 2004).

Leutratal sink webs


(a) l-c-cac
(b) l-c-cbs
(c) l-c-cpa
(d) l-c-csh
(e) l-m1-cac
(f) l-m1-cbs
(g) l-m1-csh
(h) l-m2-cac
(i) l-m2-cbs
(j) l-m2-hlc
(k) l-m2-hmi
(l) l-m2-hts
(m) l-m2-hvs
(n) l-m4-cac
(o) l-m4-cbs
(p) l-m4-cpa
(q) l-m4-csh

Steudnitz sink webs

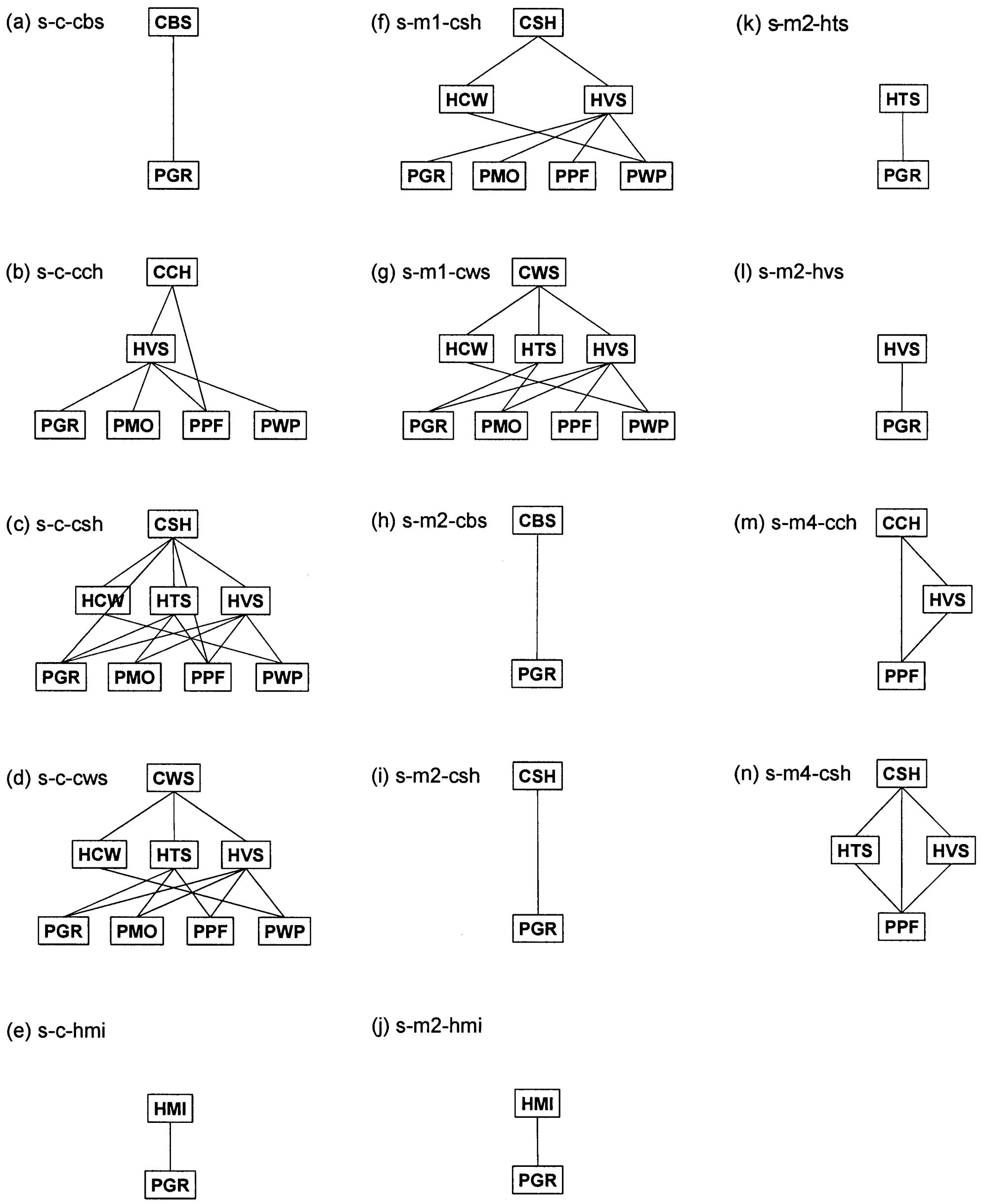


Fig. 3. All 31 sink webs derived from the four models of functional group interaction webs from Leutratal and the four from Steudnitz. (Detailed derivations in text.) (Codes: l = Leutratal, s = Steudnitz, m1 = model 1, m2 = model 2, m4 = model 4, c = complete web. Sink functional groups indicated by the three letter codes in Table 1).

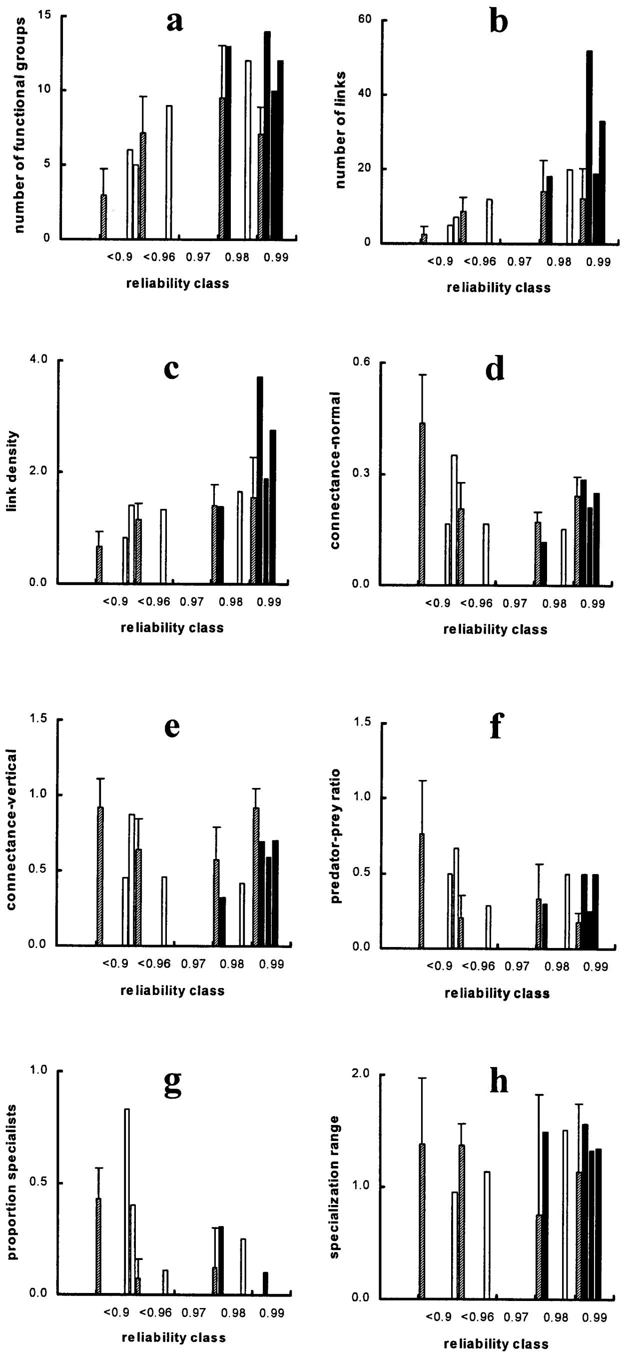


Fig. 4. The relationships between reliability classes and the other characteristics of model and sink functional group interaction webs for Leutratal and Steudnitz. Black bars indicate Leutratal models. White bars indicate Steudnitz models. Shaded bars are the means (±1SD) for sink webs from all models. Plot a, number of functional groups; b, number of links; and c, link densities. Plot d, connectance - normal; e, connectance - vertical; and f, predator-prey ratio (ratio of top groups to others). Plot g, proportion of specialist groups (those with in-degrees of one - two Leutratal complete webs in the highest reliability classes have no specialist groups. They, therefore, do not appear). Plot h, range of specialization (standard deviation of the number of in-degrees per group).

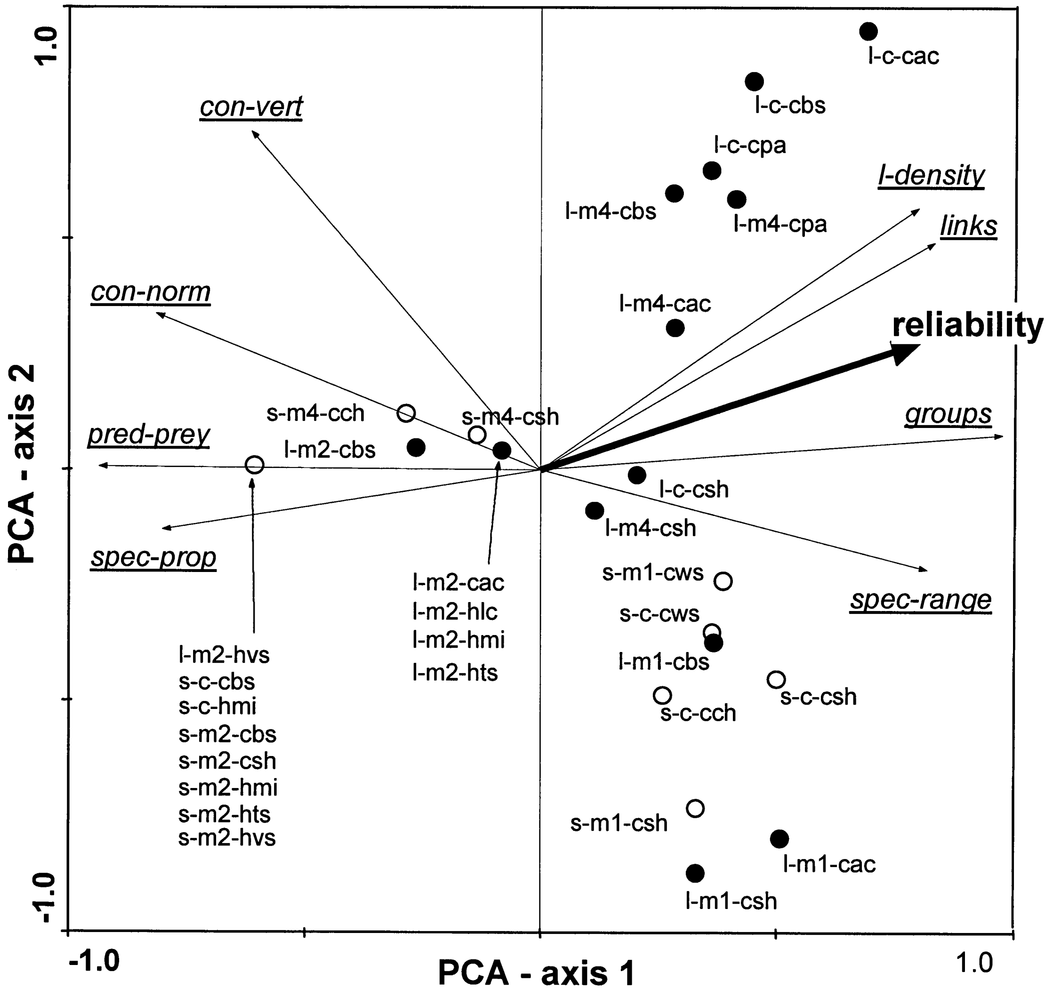


Fig. 5. PCA ordination diagram showing the relationship of reliability to the first two PCA axes and to other web characteristics. Groups = number of functional groups in the web. Links = number of links. L-density = link density. Pred-prey = predator: prey (the ratio of groups with only in-degrees to those with out-degrees). Spec-prop = proportion of specialist groups (those with only one in-degree). Spec-range = range of specialization (standard deviation of in-degree number per group). Also plotted relative to the two PCA axes are the positions of individual sink functional group interaction webs for Leutratal and Steudnitz. (Codes: l = Leutratal, s = Steudnitz, m1 = model 1, m2 = model 2, m4 = model 4, c = complete web. Sink functional groups indicated by the three letter codes in Table 1).

12. Manuskript XI

Perner, J. & Arndt, E.
Effects of native diversity and extrinsic factors on
invasibility of ground-dwelling arthropod assemblages.
Ecography, in review

ECOGRAPHY, in review

Effects of native diversity and extrinsic factors on invasibility of ground-dwelling arthropod assemblages

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Abstract

Based on data of ground-dwelling arthropods sampled in 20 different laurel forest stands of the Canary Islands, we tested the hypothesis that the proportion of aliens to the whole assemblage should be negatively related to the diversity of natives. Using generalised linear models (GLMs) this hypothesis was confirmed in all functional feeding groups studied. In some cases we found an additional significant effect of extrinsic environmental factors (e.g. climate, disturbance) on the proportion of aliens. These results support the diversity-resistance-hypothesis. We present a simple conceptual model where the negative effects of natives on the proportion of aliens might be partially caused by extrinsic factors affecting the diversity of natives and the invader success in a different extent or direction. Finally, we conclude that the proportion of aliens is a simple and robust measure that indicates ecosystem changes promoting species invasions.

Introduction

Biological invasions have become a global phenomenon stimulating intense theoretical, experimental and observational research activities in ecology. The basic theoretical concept, first summarized by Elton (1958) and supported by resource-competition theory (e.g. Elton 1958; MacArthur and Wilson 1967; Pimm 1991; Crawley et al. 1999; Tilman 1999) predicts that species diverse communities are highly competitive and less invasible ('diversity-resistance hypothesis'). However, studies exploring the validity of this hypothesis vary in their conclusions. Whereas the several results of theoretical (e.g. Case 1990; Luh and Pimm 1993) and experimental studies conducted at small spatial scales support this hypothesis (e.g. Tilman et al. 1996; Tilman 1997; Hooper and Vitousek 1998; Naeem et al. 2000; Dukes 2001) other experimental and observational studies, mostly related to regional scales, did not find any evidence for its validity in nature (e.g. Palmer and Maurer 1997, Planty-Tabacchi et al. 1996, Robinson et al. 1995, Stohlgren et al. 1999).

Recently, this disparity was attributed to the impact of extrinsic factors, such as disturbance, climate, or soil conditions, that covary with the diversity of native and alien species and might mask the effect of natives diversity (e.g. Levine and D'Antonio 1999; Naeem et al. 2000; Kennedy et al. 2002). Figure 1 depicts a conceptual model of potential impacts of extrinsic factors on the diversity of natives and the invasion success of aliens. The basic idea of Elton (1958) ignores the possible effect of such extrinsic factors and predicts a negative association between the (native) species diversity and the success of invaders (Fig. 1a). However, if extrinsic factors (e.g. climate or soil conditions) favour higher native species diversity as well as directly increase niche opportunity for invaders, a positive relationship between both might occur (Fig. 1b). Shea and Chesson (2002) analysed this discrepancy and showed that a positive relationship between alien and native species appears when data are combined on broader spatial scales. In contrast, when extrinsic factors like disturbance affect the native species and the invasion success of alien species in an opposite way (Davis et al. 2000; Petryna et al. 2002) also a negative relationship between them might be observed (Fig. 1c). Therefore, it seems that these confounding effects of covarying extrinsic factors should be controlled for in future studies (Levine 2000; Naeem et al. 2000; Shea and Chesson 2002), which requires the development of appropriate data analysis techniques (Shea and Chesson 2002). Towards this aim, we postulated that in all cases, the proportions of observed alien species should be negatively related to the diversity of natives (independent of the effects of extrinsic factors) if a diversity resistance effect really exists in nature (Fig. 1a-c).

To test this hypothesis we analysed data of ground-dwelling arthropods sampled in laurel forest of the Canary Islands. These forests are one of the species richest ecosystems of the Canarian Archipelago and only occur in the northern parts of the mountainous western islands

(Del-Arco et al. 1999; Walter and Breckle 1999). Laurel forests are characterized by 20 mainly endemic tree species and a forb-rich flora. Currently non-native species are negligible at the floristic level. However, during faunistic surveys in natural as well as anthropogenically influenced laurel forest sites, a surprisingly high percentage of non-native (alien) ground-dwelling arthropods were observed. We used this data set to assess our idea and analysed functional different ground-dwelling feeding groups. To model the effects of natives' richness and abundances on the proportional responses of aliens' richness and abundances within each functional group we used generalised linear models (GLMs) with a logit-link function (Crawley 2002; Quinn and Keough 2002). Even though both natives and aliens of the same functional group respond to extrinsic factors in the same way, there might be considerable differences in intensity of response and that might determine whether invasions were promoted or inhibited by changing extrinsic factors (Shea and Chesson 2002). Therefore, in addition to the effects of native diversity we also tested for the effects of extrinsic factors describing the climate differences and the disturbance status of sites on the invasion success.

Material and Methods

Study area and sampling sites

The Canarian Archipelago is the Central part of the Macaronesian subregion of the Mediterranean biogeographical region. Laurel forests occur there as cloud forests on the north parts of the mountainous western Canary Islands (and Madeira) at elevations between 600 and 1400 m. Because of the influence by trade winds, these forest are characterised by comparatively cool and moist conditions. Four endemic tree species of the Lauraceae, together with 16 other trees and shrubs (e.g. *Myrica faya*, *Erica arborea*, and *Viburnum rigidum*) are the dominating plants.

The study was confined to the three western islands of the archipelago though laurel forests also occur on Gran Canaria and Tenerife. However, Gran Canaria has been largely deforested (more than 99% of laurel forest disappeared) and therefore an examination of native laurel stands was impossible there. Also Tenerife has lost about 75% of their original laurel forests and remaining areas are isolated and of different historical origin.

Depending on the different extent of recent laurel forests 11 sites were selected on La Gomera, five on La Palma and four on El Hierro (Table 1). All sites were located in the so-called 'bioclimatophilous region of laurel forest' (Del-Arco et al. 1999) indicating that the central laurel zone is characterized by comparable soil conditions and potential vegetation. The sites selected include stands with natural forest structure (not or hardly influenced by human activity), as well as sites influenced by forestry, forest fire or other human activities.

It is widely accepted that a low cover of *Laurus* as well as a high cover of *Erica* and *Myrica* indicate anthropogenic disturbances in laurel forests (Del-Arco et al. 1999: 285, Hohenester and Welss 1993, Pérez de Paz et al. 1990). We used the percentage cover of those trees as surrogates for the degree of disturbance in addition to the age of forest plots (Table 1; 'disturbance parameters') and tested if the disturbance level affects the proportion of aliens. Sites dominated by *Laurus* and *Persea* represent nearly natural forests. Secondary forests however, where laurel trees were partially removed ("fayal-brezal" in Canarian terminology) are largely dominated by *Myrica*. Sites dominated by *Erica* and partly covered with *Ilex* describe young tertiary forests (15-40 years old) with pioneer vegetation (Table 1). Although, *Myrica*- and *Erica*-dominated forest sites might generally be regarded as successional stages after removing the natural laurel forest, native late successional *Myrica-Erica* stands exist on La Gomera in the upper, cooler and drier region of the laurel zone on the mountain ridges (higher than 1300 m). These native *Myrica-Erica* forest sites are very rare and the only one examined in this study is site M1G (Table 1).

To test for climatic effects on the proportion of aliens we used potential direct solar insolation (PDSI), altitude of sites and cover of tree and forb layer as well as the extent of litter layer; these are considered to be important parameters affecting the above ground climate (Table 1; 'climate parameters'). Mean daily PDSI values were calculated using mean aspect and inclination of sites (based on an algorithm by Volz 1959).

Data collection

Pit fall traps were used to collect surface-active macro-invertebrate taxa. Five traps (plastic cups, 65 mm diameter, containing a 5% acetic acid/salt mixture) were placed in a transect about 3-4 m distant from each other. The traps were open for 6 weeks during March and August 2002/03. (three weeks each in spring and in summer) and were checked weekly. Additionally 8 soil samples of 25x25x15 cm were taken per site between March and August 2002/03. All invertebrates were transferred to 70% ethanol counted and identified to species level. Based on the different foraging characteristics the following functional feeding groups were classified: carnivorous ground and rove beetles (carnivorous Carabidae and Staphylinidae), carnivorous centipedes (Chilopoda), detritivorous millipedes (Diplopoda) and detritivorous isopods (Isopoda). An overview of data collected by pitfall traps and soil samples is given in Table 2.

Data analysis

Our focus in this study was to analyse the relative differences between the natives and aliens based on abundances and species richness instead of absolute differences between study sites and species groups. For this purpose abundances as well as species richness of native and alien species were summarized separately for each functional group and both sampling methods (Table 2). The proportion of aliens (aliens / (aliens + natives)) within each functional group was modelled using the abundances as well as species richness of natives and some selected parameters describing the physical environment (climate and disturbance parameters, see above and Table 1) as independent explanatory variables. Because of data structure (no homogeneity of variances, errors not normally distributed) weighted regression models were needed and therefore generalised linear models (GLMs) were used (see e.g. Crawley 2002; Quinn and Keough 2002; Pyšek *et al.* 2003). We used a logit-link function to model the proportional responses of alien and native species within each functional group, which is appropriate for such data. In cases of overdispersion, the variance function was modelled proportional to *mu (1-mu)* (mu = mean of the distribution; using the *quasi* option in S-PLUS; see Crawley 2002). The following stepwise procedure was used in all analyses to derive the most parsimonious model that adequately describes the observed data (see suggestions of Crawley 2002: p 449). First, a basic model was fitted including only the abundances or species richness of natives. Second, the additional explanatory power of each extrinsic physical parameter was examined by sequential parameter inclusion and re-fitting of the model and the significance of the decrease in model deviance was assessed using *F*-tests. The sequential parameter inclusion was repeated until no more statistically significant improvement could be achieved; the resulting model was considered as the minimal adequate model.

Additionally, we used Pearson's correlation analysis to test for a simple (negative) correlation between species number or (log-transformed) abundances of natives and aliens originally predicted by the 'diversity-resistance hypothesis' (Fig. 1a).

Results

In both pitfall traps and soil samples (Table 2) 6,552 individuals (2,911 natives, 3,641 aliens) of 67 arthropod species (46 natives, 21 aliens) were collected. Whereas nearly all species of ground and rove beetles were natives, we found a much higher proportion of alien species in all other groups (Table 2). In particular, conspicuously high abundances of alien species were detected for the isopods and millipedes.

The results of the generalised linear model (GLM) fits are presented in Table 3. As indicated by the sign of estimated coefficients and illustrated in Figure 2, we found negative effects for native abundances or richness on the proportions of observed aliens in all cases. Furthermore, except for the abundances of centipedes (Table 3, part b) and species richness of isopods (Table 3, part l), the abundances or richness of natives caused a significant change in deviance compared to the null model (Table 3) and, induced the highest decrease in deviance compared to the contribution of the sequentially included extrinsic physical parameters. In some cases a significant decrease in deviance was reached by inclusion of altitude (Table 3 part a, f, l) or cover of the tree layer (Table 3 part i), *Erica* (Table 3 part c, j) or *Laurus* (Table 3 part b) additionally to abundance or richness of natives in model. In other cases (Table 3 parts d, e, g, h, k) no significant decrease in deviance could be observed by additional inclusion of extrinsic physical parameters.

A simple negative correlation between species richness or abundances of native and alien species was not found in any functional group. However, the species richness of native and alien centipedes were significantly positively related (r = 0.47, p = 0.04).

Discussion

Effects of native diversity and extrinsic factors on the proportion of aliens

We postulated that the proportions of observed alien species (aliens / (aliens + natives)) should be negatively affected by the diversity of natives if a diversity resistance effect really exists. Furthermore, this relationship should be robust to the covarying effects of extrinsic physical parameters (Fig. 1). Our results strongly support this hypothesis. Using data of ground-dwelling arthropods of Canarian laurel forests we have shown that native abundances or richness negatively affect the proportional alien abundances and species richness respectively, of different functional feeding groups (Table 3, Fig. 2). Basically, our findings are in agreement with the theoretical concept summarized by Elton (1958) and predicted by the resource-competition-based theory (e.g. Elton 1958; MacArthur and Wilson 1967; Pimm 1991; Crawley 1999; Tilman 1999). However, originally this concept focused on the relationship between the real observed species richness or abundances of natives and aliens which might be easily confounded by co-varying extrinsic factors (e.g. Naeem *et al.* 2000; Shea and Chesson 2002). Therefore, it was not surprising that we did not find a significant negative correlation between absolute abundance or species richness of natives and aliens in any of the functional groups studied. In contrast, we accounted for the effects of covarying extrinsic factors simply analysing the proportions of aliens using generalised linear models (GLMs). The examined arthropod data were sampled in laurel forests with considerably different extrinsic factors (different islands and different site parameters, see Table 1). If a diversity-resistance effect did not exist in our study, the observed consistent negative relation between the proportion of aliens and the diversity of natives across different functional groups would be very unlikely.

In addition to the effects of native diversity, which induced in nearly all cases the highest decrease in model deviance (Table 3), we tested the effects of extrinsic physical parameters describing climatic differences and anthropogenic disturbance on the observed proportion of aliens. Only in seven (of 12) cases was an additional significant decrease in model deviance reached (Table 3). Altitude and cover of tree layer caused significant effects as parameters describing climate conditions but with inconsistent trends between the functional groups. Whereas with increasing altitude the proportional abundance of alien ground and rove beetles increased (Table 3 part a), proportional abundance and species richness of alien isopods decreased (soil samples; Table 3 part f and l). Also proportional species richness of alien millipedes decreased with increasing cover of tree layer (pitfall trap data; Table 3 part i). From the parameters describing the disturbance status of sites *Laurus* and *Erica* cover decreased of model deviance significantly. Whereas the proportional abundance of alien centipedes (Table 3 part b) and millipedes (pitfall trapping; Table 3 part c) were positive related to the level of disturbance (decreasing *Laurus* or increasing *Erica* cover), the proportional species richness of alien millipedes increased (soil sampling; Table 3 part j) with decreasing disturbance (decreasing *Erica* cover; Table 3 part j). It has been widely accepted that the level of disturbance (Vitousek 1990; Williamson 1996; Shea and Chesson 2002) or harshness of climate (Chesson and Huntly 1997; Davis *et al.* 2000; Shea and Chesson 2002) can have considerable effects on the success of species invasions. However, as both natives and invaders might respond to climate or disturbance, it is the difference in this responses that determines whether invasions are promoted or inhibited by differences in climate or disturbance (Shea and Chesson 2002). Therefore the observed inconsistent relationship of response to both parameter groups between the functional groups examined seems to be plausible.

Compared to the decrease in model deviances caused by native abundance or species richness, the decrease in deviance caused by the climate or disturbance parameters was low (Table 3). One reason for this finding might be that the parameters used as climate or disturbance surrogates do not describe the differences concerning the climatic conditions or the disturbance level between sites precisely enough. However, more likely seems to be that the effects due to variation in native diversity might only partially be separated from the pure effects due to extrinsic factors that covary with native diversity (Naeem et al. 2000; Shea and Chesson 2002). Such variance overlaps are a well known problem in observational studies where the extrinsic factors cannot experimentally be controlled for. In the (more theoretical) case of nearly balanced (positive or negative) effects of extrinsic factors on the diversity of natives and the success of invaders, no proportional change of aliens should occur and no additional effects of extrinsic factors on the proportion of aliens should be detectable (Fig. 1b). If extrinsic factors promote or inhibit the invasion success of aliens to a stronger extent than the diversity of natives, an additional positive or negative effect of extrinsic factors on the observed proportion of aliens would be measured (Fig. 1b). However, if extrinsic factors promote or inhibit the diversity of natives to a stronger extent than the success of invaders, these effects might be partially or completely masked as negative natives' effects on the proportion of aliens (Fig. 1b). In the (also more theoretical) case that extrinsic factors promote or inhibit the invasion success of aliens to the same extent as the diversity of natives was inhibited or promoted, this effect on the proportion of aliens would be completely masked as a negative effect of native diversity on the proportion of aliens (Fig. 1c). However, if extrinsic factors promote or inhibit invader success to a stronger extent than the diversity of natives was inhibited or promoted, this effect would be only partially masked as natives' effect on the proportion of aliens and an additional positive or negative effect of extrinsic factor on the proportion of aliens would be detectable (Fig. 1c).

Based on this model, we have shown that diversity-resistance effects do exist in our system, because we detected in nearly all cases the highest decrease in model deviance due to native diversity. However, this measured negative effect on the proportion of aliens might be also partially caused by the indirect effects of extrinsic factors.

Alien ground-dwelling arthropods in an island forests ecosystem

Small islands seem to be more fragile and prone to species invasions than continental areas because of the combined effect of the special characteristics island species have evolved, and the gregariousness of invasive species (Dulloo et al. 2002). Consequently, many island studies give evidence that the ecology of such former hotspots of biodiversity has been affected by invasive alien species that have caused large-scale degradation and impoverishment of the indigenous flora and fauna (e.g. Chown et al. 2002; Dulloo et al. 2002; Jones et al. 2002; Kelly and Samways 2003). The Canary Islands are one such hotspot of biodiversity. Despite the small total area of 7447 km^2, the seven main islands harbour 1147 families, 4520 genera, and more than 12680 species of terrestrial plants and animals (Izquierdo et al. 2001 supplemented by additional unpublished data). The percentage of endemic species is about 38% in insects, 70% in millipedes, 60% in terrestrial Malacostraca, 78% in molluscs, and 26% in vascular plants (Izquierdo et al. 2001). However, the biodiversity of this archipelago is endangered by devastation of the naturally small ecosystems through anthropogenic influences like settlements (especially tourism infrastructure), agricultural plantations and clear-cutting of forests as well as by invasions of alien species. The proportions of native and alien ground-dwelling arthropods in laurel forests of the Canary Islands were studied the first time. Whereas up to now invasive species are negligible at the producer level, at the consumer level, a large proportion of aliens (species and abundances) was observed in the most of the studied arthropod groups. Several aliens were found for first time either on a particular island or in a particular site. Although previously largely ignored, recently some studies have highlighted the potential impacts of invasive soil invertebrates on ecosystem structure and function. Aliens can change, for example, soil carbon, nitrogen and phosphorus pools and can considerably affect the distribution and function of roots and microbes (Bohlen et al. 2004; Kelly and Samways 2003; Suarez et al. 2004). Crooks (2002) emphasised that the invaders that will have the largest impacts on ecosystems are those that directly modify ecosystems and thus have cascading effects for resident biota. Furthermore he argued that such invasive ecosystem engineers can facilitate further invasions by directly changing habitat characteristics (extrinsic factors). From these points of view the locally very high dominance of some invading decomposers like *Armadillidium vulgare*, *Cylindroiulus disjunctus* or *Ommatioulus moreletii*, originally distributed in the Mediterranean region, seems to be critical. Therefore, further studies in the Canarian laurel forests should focus in particular on the impacts of management and continued fragmentation of laurel forests on the diversity of natives and the changing extrinsic factors promoting the invasion of aliens.

Conclusions

We have shown that the proportion of aliens is an appropriate measure to indicate diversity-resistance effects in field studies. Analysed with generalised linear models a negative relationship between native diversity and the proportion of aliens will be observed if such effects are relevant. The negative relationship should be detectable independently of covarying extrinsic factors, even when data were combined across different spatial scales. However, as explained with a simple conceptual model (Figure 1) this observed negative effect might be partially or (in an extreme case) completely caused by extrinsic factors affecting the diversity of natives and the invasion success of alien species to a different extent or direction. We conclude that the proportion of aliens is a simple and robust measure indicating ecosystem changes promoting species invasions regardless of which forces are dominant in driving the changes: native diversity or extrinsic factors.

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Table 1. Site characteristics of the 20 investigated laurel forest stands. * Site codes are as follows: first letter indicates native forests dominated by *Laurus* and *Persea* = L, secondary forests often dominated by *Myrica* = M, or tertiary forests often dominated by *Erica* = E; middle letter counts the site type; last letter indicates the Island - La Gomera = G, La Palma = P, El Hierro = H. ** PDSI = potential direct solar insolation.

	Site code*																			
Site parameters	**L1G**	**L2G**	**L3G**	**L4G**	**L5G**	**L6G**	**M1G**	**E1G**	**E2G**	**E3G**	**E4G**	**M1H**	**M2H**	**M3H**	**E1H**	**L1P**	**L2P**	**M1P**	**M2P**	**E1P**
Tree layer in total [%]	90	75	76	80	85	90	80	60	90	75	60	60	85	85	50	80	95	85	85	80
Laurus azoica [%]	70	35	65	77	70	46	0	18	0	5	0	0	0	0	0	40	95	60	50	20
Erica arborea [%]	0	0	0	1	0	12	50	36	80	55	40	6	17	8.5	40	0	0	0	17	24
Myrica faya [%]	5	0	3	1	0	3	30	6	10	5	10	54	68	76.5	10	0	0	17	18	24
Forb layer in total [%]	35	50	50	10	5	5	75	50	80	2	5	90	85	15	30	10	10	5	30	10
Litter layer [cm]	8	8	8	8	1.5	2	1	0.5	0	1	1	3	1.5	7.5	0	1	10	3	3	3
Altitude [m a.s.l.]	800	950	950	1300	1000	1000	1350	1000	1200	1000	800	1300	1200	860	860	600	700	1200	1200	1000
Age of forests [yr]	100	100	100	100	100	100	100	40	50	16	30	100	30	15	15	100	100	60	60	30
Aspect	NE	N	N	N	SW	S	N	NE	S	0	E	0	NE	N	N	W	W	E	E	W
Inclination [°]	30	7	15	30	15	15	35	25	10	0	35	0	10	20	20	30	40	40	30	10
Latitude	28°0 9'	28°0 9'	28°0 9'	28°0 9'	28°0 9'	28°0 9'	28°0 9'	28°0 9'	28°0 9'	28°0 9'	28°0 9'	27°4 3'	27°4 3'	27°4 3'	27°4 3'	28°4 3'	28°4 3'	28°4 3'	28°4 3'	28°4 3'
PDSI [cal/cm²/day]**	476	607	550	417	682	702	369	510	690	648	572	652	607	514	514	587	551	551	587	637

Table 2. Abundances (indiv.) and species richness (spec.) of native and alien arthropods collected with pitfall traps and soil samples.

		Pitfall traps						Soil samples					
Site code		Carabidae/ Staphylinidae		Diplopoda		Isopoda		Chilopoda		Diplopoda		Isopoda	
		natives	aliens	natives	aliens	natives	aliens	natives	aliens	natives	aliens	natives	aliens
L1G	Indiv.	6	0	2	6	0	0	33	8	0	31	0	0
	Spec.	5	0	1	2	0	0	4	2	0	3	0	0
L2G	Indiv.	8	0	5	3	1	1	22	10	2	32	0	0
	spec.	5	0	2	1	1	1	2	4	2	2	0	0
L3G	indiv.	5	0	2	3	0	8	30	5	3	37	0	6
	spec.	2	0	1	2	0	1	4	2	1	2	0	1
L4G	indiv.	42	0	0	2	173	1	61	9	23	4	83	0
	spec.	5	0	0	1	3	1	3	4	2	2	2	0
L5G	indiv.	81	0	0	10	0	0	32	6	6	115	1	0
	spec.	7	0	0	1	0	0	1	2	1	1	1	0
L6G	indiv.	103	0	0	1	13	109	26	6	15	73	2	46
	spec.	5	0	0	1	2	2	2	2	1	1	1	1
M1G	indiv.	47	0	0	1	205	0	43	24	14	3	167	0
	spec.	7	0	0	1	2	0	6	4	2	2	1	0
E1G	indiv.	214	0	0	7	1	3	16	7	35	37	0	6
	spec.	8	0	0	1	1	1	1	2	1	1	0	1
E2G	indiv.	71	0	0	6	9	0	9	3	4	7	1	0
	spec.	9	0	0	1	2	0	3	2	2	1	1	0
E3G	indiv.	48	0	0	0	1	0	41	3	1	36	0	0
	spec.	3	0	0	0	1	0	1	2	1	1	0	0
E4G	indiv.	15	0	0	0	2	4	17	4	4	9	0	0
	spec.	3	0	0	0	2	2	2	3	1	1	0	0
M1H	indiv.	25	4	17	16	67	0	30	17	121	9	25	0
	spec.	5	1	3	2	1	0	1	1	3	2	1	0
M2H	indiv.	57	0	1	42	78	54	67	15	92	97	12	33
	spec.	4	0	1	2	1	1	1	2	2	2	2	1
M3H	indiv.	30	0	0	28	23	1	12	22	0	99	1	0
	spec.	4	0	0	2	1	1	1	2	0	3	1	0
E1H	indiv.	26	0	0	15	9	0	37	15	5	30	0	0
	spec.	4	0	0	2	2	0	1	2	1	2	0	0
L1P	indiv.	0	1	0	9	0	36	5	6	13	29	0	10
	spec.	0	1	0	2	0	2	2	1	1	5	0	2
L2P	indiv.	4	0	0	16	7	95	57	3	13	168	4	135
	spec.	1	0	0	3	2	2	2	1	2	6	2	3
M1P	indiv.	13	16	0	5	0	166	47	6	0	54	55	14
	spec.	3	1	0	2	0	1	2	2	0	4	1	1
M2P	indiv.	9	1	0	7	0	347	72	35	28	105	54	57
	spec.	2	1	0	2	0	1	2	2	2	5	1	1
E1P	indiv.	1	0	0	34	0	855	29	23	3	90	17	129
	spec.	1	0	0	2	0	1	2	2	1	5	1	1
Total	**indiv.**	**805**	**22**	**27**	**211**	**589**	**1680**	**686**	**227**	**382**	**1065**	**422**	**436**
	spec.	**21**	**2**	**7**	**5**	**7**	**3**	**7**	**7**	**8**	**8**	**4**	**3**

Table 3. Results of fitting abundances and species richness of native arthropods and site parameters to the proportion of observed abundances and species richness of aliens using generalised linear models (GLM). Change in deviance (Dev.) was tested using F statistics and the significant (P<0.05) models (minimal adequate models) with function coefficients (Coeff.) are presented.

Abundance proportion of aliens						Species richness proportion of aliens					
Terms included in model	**Coeff.**	**Dev.**	**Df**	**F**	**P**	**Terms included in model**	**Coeff.**	**Dev.**	**Df**	**F**	**P**
(a)					**Carabidae and Staphylinidae, pitfall traps**						**(g)**
Null model	-10.02	133.32	19			Null model	0.10	18.73	19		
Abundance of natives	-0.18	56.14	18	16.06	<0.001	Richness of natives	-0.81	10.75	18	11.23	<0.01
+Altitude	0.01	28.10	17	5.83	<0.05						
(b)					**Chilopoda, soil samples**						**(h)**
Null model	-0.35	96.60	19			Null model	0.62	5.69	19		
Abundance of natives	-0.01	83.44	18	3.47	0.08	Richness of natives	-0.22	3.15	18	14.71	<0.01
+*Laurus* cover	-0.01	65.60	17	4.70	<0.05						
(c)					**Diplopoda, pitfall traps**						**(i)**
Null model	2.20	86.81	17			Null model	13.28	17.10	17		
Abundance of natives	-0.21	33.33	16	43.70	<0.001	Richness of natives	-2.42	4.74	16	69.00	<0.001
+*Erica* cover	0.20	19.65	15	11.18	<0.01	+ Cover of tree layer	-0.11	3.03	15	8.81	<0.01
(d)					**Diplopoda, soil samples**						**(j)**
Null model	2.26	662.94	19			Null model	2.31	16.06	19		
Abundance of natives	-0.03	232.86	18	28.49	<0.001	Richness of natives	-0.87	9.06	18	18.44	<0.001
						+ *Erica* cover	-0.02	6.94	17	5.60	<0.05
(e)					**Isopoda, pitfall traps**						**(k)**
Null model	3.43	2250.63	17			Null model	1.44	20.03	17		
Abundance of natives	-0.06	394.63	16	44.08	<0.001	Richness of natives	-1.10	12.97	16	11.88	<0.01
(f)					**Isopoda, soil samples**						**(l)**
Null model	10.69	755.67	14			Null model	5.32	15.46	14		
Abundance of natives	-0.03	138.20	13	66.66	<0.001	Richness of natives	-1.05	13.12	13	4.27	0.06
+Altitude	-0.01	81.89	12	6.08	<0.05	+ Altitude	-0.004	8.34	12	8.77	<0.05

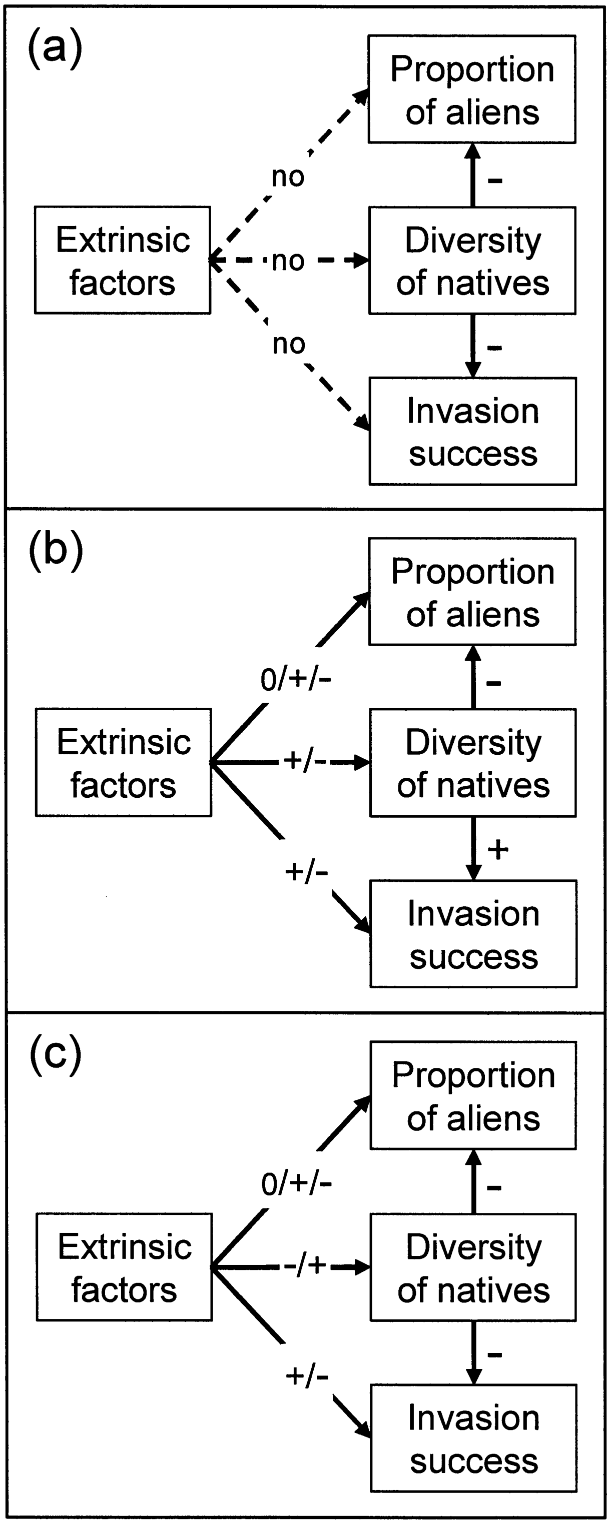

Figure 1. Impacts of extrinsic factors on the diversity of natives and the invasion success of aliens and their relationship to the proportions of aliens. (a) Elton's diversity- resistance hypothesis predicts a negative association between the diversity of natives and the establishment success of aliens and ignores the effects of extrinsic factors. (b) Extrinsic factors might have similar effects on diversity of natives and the invasion success of aliens and therefore create an apparent positive association between them. (c) However, if extrinsic factors (e.g. disturbance) affect the diversity of natives and the invasion success of aliens in an opposite way a negative association is to be expected. In contrast, the proportion of aliens (aliens / (aliens + natives)) should be negative affected by the diversity of natives in all cases (a-c) and should be detectable if a diversity resistance effect really exists in nature. Figure was modified and complemented after Naeem *et al.* (2000).

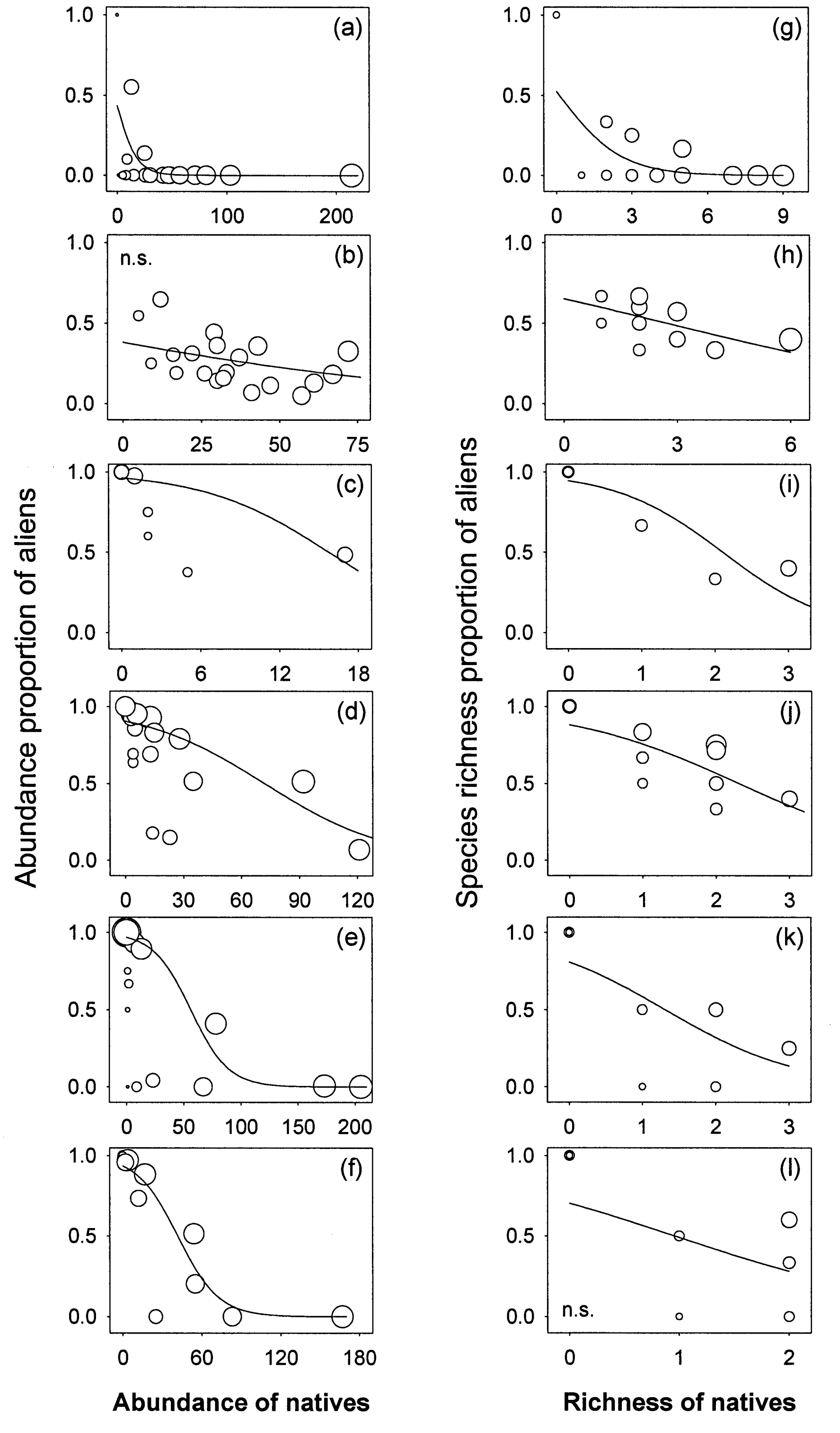

Figure 2. Relations between the proportions of aliens and the observed native arthropods. Lines represent fitted values of GLM including only the abundance (a-f) and species richness (g-l) of natives into model (see also Table 3). Real proportions (aliens / aliens + natives) of samples are included as circles. The different bubble-sizes of circles illustrate the different weights of samples. Carabidae/Staphylinidae - pitfall traps: a, g; Chilopoda - soil samples: b, h; Diplopoda - pitfall traps: c, i, -soil samples: d, j; Isopoda - pitfall traps: e, k, -soil samples: f, l.

13. Abschlussdiskussion und Schlussfolgerungen

Die in dieser Schrift zusammengestellten Manuskripte bekräftigen die besondere Eignung von Arthopoden-Assoziationen als ökologische Indikatoren (sensu McGeoch 1998, Lawton & Gaston 2001) in terrestrischen Lebensräumen. Mit der Bestätigung teilweise bekannter Befunde sowie der Präsentation neuer, indikativ verwertbarer Untersuchungsansätze und Ergebnisse konnte dies belegt werden. Eine effiziente Nutzung des Indikationspotentials von Arthropoden setzt jedoch vielfach die Anwendung fortgeschrittener statistisch-analytischer Verfahren voraus, die für die Interpretation komplexerer Datenstrukturen notwendig sind.

Neben Untersuchungen zu Auswirkungen von Nutzungsumstellungen in der Landwirtschaft auf Arthropoden (*Manuskript III*) und zur Regenerationsdynamik von gestörten Grasland-Ökosystemen (*Manuskripte V und VI*) konnten insbesondere in Kombination mit dem Konzept der funktionellen Gruppen wesentliche Beiträge zum Zusammenhang der Diversitätsmuster von Produzenten und Konsumenten (*Manuskripte IV, V*), zur Komplexität von Interaktionsnetzen in Abhängigkeit von Störungen (*Manuskripte IX, X*), zur klimatischen Sensitivität verschiedener trophischer Ebenen (Manuskript VIII) sowie zur Problematik der Arteninvasionen (*Manuskript XI*) geleistet werden.

Trotz teilweise kontrovers geführter Diskussionen wird Artendiversität als ein wichtiger Grundbaustein nachhaltiger Ökosystem-Entwicklung angesehen (u.a. *ecological resilience hypothesis*: Pimm 1991, *insurance hypothesis*: Walker 1992, Lawton & Brown 1993). Nahezu unbestritten ist dabei, dass sich Änderungen in der Nutzung, Nährstoffanreicherungen oder Umweltstress negativ auf die Diversitäts- und Interaktionsmuster von Organismen in Ökosystemen auswirken können (u.a. Chapin et al. 1997, Vitousek et al. 1997). Untersuchungen zu diesbezüglich sensitiven Bioindikationssystemen fehlen dagegen weitgehend. Dieser Thematik sind die Ergebnisse der *Manuskripte III*, *IV*, *V*, *VIII* und *IX* zuzuordnen. Mit diesen Arbeiten konnten die Kenntnisse zu den kaskadenartigen Abhängigkeiten bzw. den Interaktionsmustern unterschiedlicher trophischer Ebenen wesentlich erweitert werden. Eine schematische Übersicht zu den davon abgeleiteten Schlussfolgerungen zeigt Abbildung 13.1.

Rapide abiotische Änderungen (hier: sich rasch normalisierende Bodenbedingungen nach Schadstoffimmissionen) bewirken drastische Änderungen (hier: Erhöhung) der Artendiversität bei den Produzenten. Die Übertragungsrate dieser Diversitätsänderungen auf die

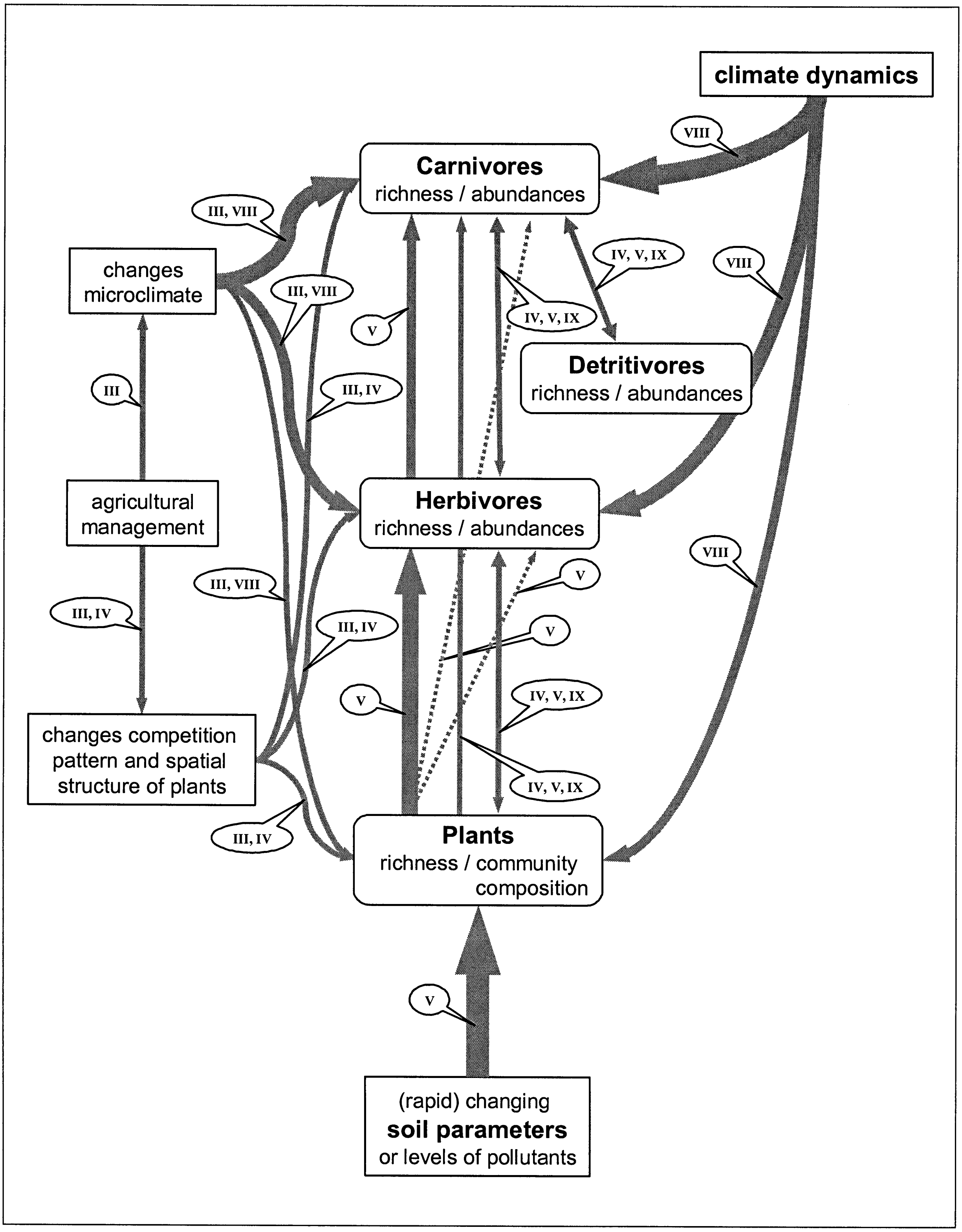

Abb. 13.1: Schematische Darstellung zu den Schlussfolgerungen, die aus Teilen der Ergebnisse der *Manuskripte III*, *IV*, *V*, *VIII* und *IX* gezogen wurden. Die Stärke der Pfeile indiziert die Stärke der ermittelten korrelativen Zusammenhänge und die römischen Zahlen in den Legendensymbolen (🗨) verweisen auf die relevanten Manuskripte.

Konsumenten verringert sich jedoch mit zunehmender trophischer Höhe (*Manuskript V*). Dies erscheint durch eine Vielzahl zusätzlich wirkender Interaktionsmechanismen plausibel. Negative Korrelationen zwischen den Artendiversitäten der Pflanzengemeinschaften und den Abundanzmustern von Arthropoden, wie beispielsweise von (Root 1973) postuliert, wurden nicht gefunden (*Maunsikripte IV* und *V*). Lediglich bei niedriger Pflanzenartenvielfalt konnte eine tendenzielle Abnahme der Abundanzen von Arthropoden mit zunehmender Pflanzenartenvielfalt registriert werden (*Manuskript V*). Hingegen korreliert die Arten-Abundanz-Struktur (*plant community composition*) von Pflanzengemeinschaften signifikant mit den Abundanzmustern von Arthropoden (*Manuskript IV*).

Die von den Assoziationsstrukturen der verschiedenen trophischen Ebenen beeinflussten vertikalen Interaktionen, die neben trophischen auch nicht-trophische Abhängigkeiten beinhalten können, bewirken die Ausbildung von teilweise sehr komplexen Interaktionsnetzen. Deshalb sind einfache kaskadenartige Abhängigkeiten zwischen den trophischen Ebenen an Freilanddaten nur schwer nachzuweisen (*Manuskripte IV, V, IX*). Darüber hinaus wird von signifikanten Korrelationen einiger karnivorer funktioneller Gruppen mit herbivoren als auch detritivoren funktionellen Gruppen abgeleitet, das Karnivore in der Lage sind, sich zumindest teilweise von den trophischen Auswirkungen der Pflanzen-Herbivoren Beziehungen zu entkoppeln (*Manuskripte IV, V, IX*). Der vertikale Vernetzungsgrad (*vertical connectance*) von funktionellen Gruppen unterschiedlicher trophischer Ebenen in Interaktionsnetzen kann als Parameter zur Beschreibung der Komplexität und funktionellen Diversität von Artengemeinschaften und damit zur Indikation von Umwelteffekten auf Lebensgemeinschaften verwendet werden (*Manuskript IX, X*).

Die klimatische Sensibilität von Arten erhöht sich signifikant mit der Höhe der trophischen Ebene wodurch ebenfalls die Interaktionsmuster von Arten bzw. funktionellen Gruppen unterschiedlicher trophischer Ebenen maßgeblich beeinflusst werden (*Manuskript VIII*). Dieser Sachverhalt kann auch indirekt, beispielsweise über landwirtschaftliches Management wirksam werden (*Manuskript III*). Der Entzug pflanzlicher Biomasse durch landwirtschaftliche Bewirtschaftung führt zu (saisonal wechselnden) Veränderungen der Vegetationsstruktur, die wiederum eng mit mikroklimatischen Veränderungen verbunden sind. Die Wirksamkeit solcher bewirtschaftungsabhängiger mikroklimatischer Effekte auf die Populationsdynamik von Arten bzw. die Struktur von funktionellen Gruppen erhöht sich jedoch mit der Höhe der trophischen Ebene (s.o., *Manuskript IX*). Davon werden wiederum Unterschiede in den Indikationsleistungen von Artengruppen verschiedener trophischer Ebenen abgeleitet (*Manuskripte III und VIII*). Landwirtschaftliche Bewirtschaftung beeinflusst außerdem über die Veränderungen der Raumstruktur direkt die Lebensbedingungen für Konsumenten bzw. indirekt die Konkurrenzverhältnisse in Lebensgemeinschaften (besonders bei Pflanzen), wodurch ebenfalls die vertikalen Interaktionsmuster beeinflusst werden (*Manuskript III, IV*).

Die Verwendung funktioneller Gruppen für Produzenten und Konsumenten (hier Arthropoden) ermöglicht die Analyse der spezifischen Interaktionsmuster unterschiedlicher Artengruppen von gleichen als auch von unterschiedlichen trophischen Ebenen. Dies ist eine ausgesprochen nützliche Methode, die Vielfalt von Interaktionen sowie die Funktionsweise von Ökosystemen weiter aufzuklären *(Manuskripte IV, V, VIII, IX, X, XI)*. Durch die Zusammenfassung von einzelnen Arten zu funktionellen Gruppen wird einerseits eine Verminderung des "Datenrauschens" aufgrund von redundanten Arten bewirkt und andererseits die Vergleichbarkeit der Ergebnisse verschiedener Studien, beispielsweise aus unterschiedlichen Regionen, ermöglicht (Bengtsson 1998, Tilman 2001, Rosenfeld 2002). Einige Autoren kritisieren die einfache Zusammenfassung von Arten zu funktionellen oder trophischen Einheiten ohne detaillierte Kenntnis der jeweils enthaltenen Arten mit den Argumenten, dass durch diese Verfahrensweise ein erheblicher Informationsverlust verbunden ist (Paine 1988, Abarca-Arenas & Ulanowicz 2002). Dieser Ansatz wurde in der vorliegenden Schrift lediglich im *Manuskript IV* angewandt. In allen anderen Untersuchungen (*Manuskripte V, VIII, IX, X, XI*) wurden die jeweils zu funktionellen Gruppen zusammengefassten Arten bis auf Artniveau bestimmt und erst dann entsprechend zu funktionellen Gruppen aggregiert, womit ein Großteil artspezifischer Informationen erhalten bleibt. Die Analyse der auf diese Weise entstandenen Arten-Datenmatrizen erforderte jedoch anspruchsvollere, bisher in der Ökologie wenig angewandter statistischer Methoden (z.B. Mantel-Tests; Legendre & Legendre 1998, Scheiner & Gurevitch 2001). Die hier verwendete *a priori*-Klassifikation der Arthropodenarten auf der Grundlage ihrer unterschiedlichen Nahrungserwerbsstrategien innerhalb der verschiedenen trophischen Ebenen kann nur als ein "erster Schritt" hin zu einer, auf detaillierten physiologischen Informationen bzw. *life history*-Kenntnissen basierenden, numerischen Klassifikation verstanden werden, wie dies von verschiedenen Autoren gefordert wird (Simberloff & Dayan 1991, Bengtsson 1998, Blondel 2003).

Hauptsächliche Argumente für die Verwendung von Artengruppen (z.B. funktionellen Gruppen) im Zusammenhang mit Indikationsstudien waren bisher die auf diese Weise berücksichtigte größere taxonomische und funktionelle Vielfalt und die damit im Zusammenhang stehenden größere Vielfalt an Reaktionen auf Umweltveränderungen (u.a. Williams 1996, McGeoch 1998). Anhand eines statistischen Verfahrens zur Abschätzung der notwendigen Stichprobengröße für die Erfassung von Arthropoden im Freiland wurde ein weiteres, formal statistisches Argument abgeleitet. Es konnte gezeigt werden, dass unter der Voraussetzung gleicher Erhebungsintensitäten, bei der Verwendung von Artengruppen (z.B. funktionellen Gruppen) als Bioindikatoren wesentlich präzisere Aussagen als bei der Verwendung von einzelnen Indikatorarten zu erwarten sind. Die ist auf die erheblichen Varianzunterschiede der jeweiligen Zielvariablen zurückzuführen (*Manuskript I*).

Die hier vorgestellten Ergebnisse wurden vorrangig von empirischen Studien abgeleitet die vom Ansatz her als (moderat) holistisch (vgl. Levins & Lewontin 1980) zu klassifizieren sind. An dieser Stelle kann nicht auf die schon seit vielen Jahren anhaltende Holismus-Reduktionismus Debatte in der Ökologie eingegangen werden (u.a. McIntosh 1985, Hagen 1989, Andersen 2001). Es soll lediglich darauf verwiesen werden, dass von kontrollierten, experimentell-reduktionistischen (*bottom-up*) Ansätzen im Idealfall zwar präzise und kausal interpretierbare Ergebnisse ableitbar sind, deren Verwendung im Zusammenhang mit Extrapolationen bzw. Vorhersagen ist jedoch oftmals sehr eingeschränkt (Peters 1991, Inchausti 1994). Empirisch-holistische (*top-down*) Ansätze hingegen liefern meist ungenauere und kaum kausal interpretierbare Ergebnisse, eignen sich in der Regel jedoch besser für Extrapolationen bzw. Vorhersagen in der Ökologie (Peters 1991, Mikkelson 2001). Von diesen Argumenten leitete Peters (1991) den Begriff der *predictive ecology* ab, welcher besagt, dass am Anfang der Untersuchungen von komplexen Systemen (z.B. Artengemeinschaften, Ökosystemen) die Musteranalyse auf der Grundlage empirischer Daten stehen sollte. Darauf aufbauend sollten dann gegebenenfalls erklärende Modelle und deren Untersetzung mit experimentell-reduktionistischen Studien erfolgen. Diese integrative, beide Untersuchungsansätze verbindende Sicht findet in den letzten Jahren zunehmend Berücksichtigung (Weber & Schmid 1995). In diesem Sinn sind auch die hier zusammengestellten Studien als (Muster-)Analysen zu verstehen, die einerseits auf das Indikationspotential von Arthropoden-Assoziationen im Zusammenhang mit Umweltveränderungen aufmerksam machen sowie andererseits Modellableitungen ermöglichen und die Konzipierung weiterführender experimentell-reduktionistischer Ansätze erleichtern. Damit wird der von Eugen P. Odum (1971) seit langem vertretenen Ansicht gefolgt, dass: "Ecology must combine holism with reductionism if applications are to benefit society!".

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14. Zusammenfassung

Anhand von verschiedenen Fallbeispielen im Zusammenhang mit komplexen Umweltveränderungen wird auf das Informationspotenzial aufmerksam gemacht, was die Verwendung von Arthropoden-Assoziationen als ökologische Indikatoren bietet. In 11 Manuskripten werden die Reaktionen von Arthropoden-Assoziationen auf (i) Störungen durch landwirtschaftliche Nutzung oder Schadstoffimmissionen und auf die damit verbundenen Regenerations- und Sukzessionsprozesse analysiert, sowie (ii) deren Sensitivität gegenüber Klimadynamik und Arten-Invasionen untersucht. Außerdem wird (iii) das Konzept der funktionellen Gruppen und dessen Verwendbarkeit im Zusammenhang mit Bioindikation überprüft sowie (iv) ein breites methodisches Spektrum bezüglich der Erhebung und insbesondere der Analyse von komplexen Freilanddaten präsentiert.

(1) Aufgrund von Unterschieden in den Varianzmustern ist im Zusammenhang mit Bioindikationsstudien die Verwendung von Assoziationsparametern gegenüber Populationsparametern begünstigt (*Manuskript I*)**.**

Anhand eines statistischen Verfahrens zur Abschätzung der notwendigen Stichprobengrößen wurde dargestellt, dass signifikante Unterschiede in der Relation der Genauigkeit (level of precision=LOP) einer Parameterschätzung zur dazu erforderlichen Stichprobengröße (required sample size=RSS) zwischen Populations- und Assoziationsparametern existieren. Bei den meisten Arten würde eine hohe Genauigkeit (5-10% Abweichung) in der Parameterschätzung unrealistisch hohe Stichprobenzahlen erfordern.

(2) Es wird ein statistisches Verfahren vorgestellt, welches die Auswahl von zuverlässigen Indikatorarten aus einer Anzahl von potenziell verwendbaren Arten ermöglicht. (*Manuskript I*)**.**

Geeignete Indikatorarten sollten neben der entsprechenden Habitatpräferenz einen niedrigen Variationskoeffizienten (CV) bezüglich der Zielvariablen (z.B. Individuenzahlen) pro Untersuchungseinheit (z.B. Untersuchungsgebiete, - flächen) aufweisen, um eine hohe Genauigkeit (level of precision=LOP) in der Parameterschätzung bei einer möglichst niedrigen Anzahl von Stichproben (required sample size=RSS) zu ermöglichen. Die Analyse von Daten aus landwirtschaftlich unterschiedlich genutzten Flächen ergab, dass aufgrund einer besseren LOP-

RSS-Relation teilweise auch (Lebensraum-)Generalisten als Indikatorarten besser geeignet sein können, als Spezialisten.

(3) Mit dem "Nested-Cross array" wird ein neues Verfahren zur Abschätzung von Populationsdichten von epigäisch-aktiven Arthropoden mittels Bodenfallen beschrieben (*Manuskript II*).

In der vorgestellten Methode wird die Anpassung einer hyperbolischen Funktion an Fangdaten mit der Verwendung von kreuzförmig-angeordneten Bodenfallen, deren Abstände sich vom Zentrum zur Peripherie des Bodenfallenkreuzes verdoppeln (Nested-Cross array), kombiniert.

(4) Im Zusammenhang mit Bioindikationsstudien erweist sich die Evenness als ein sehr aussagekräftiger Assoziationsparameter (*Manuskript III*).

In einer dreijährigen Studie wurden die Auswirkungen veränderter landwirtschaftlicher Nutzungsintensitäten auf die Vegetationsmuster, sowie die Muster von epigäisch aktive Spinnen- und Käfer-Assoziationen untersucht. Während die Artenvielfalt mit abnehmender Bewirtschaftungsintensität lediglich bei den Pflanzen und Spinnen anstieg, nahm der Camargo's Evenness-Wert (E') bei allen drei untersuchten Organismengruppen zu.

(5) Neben den meistens durchgeführten Vegetationsaufnahmen sollten aussagekräftige Monitoring-Programme auch (Kurzzeit-)Untersuchungen zu ausgewählten Arthropoden enthalten, was besonders zu Beginn von Restaurationsprojekten von Bedeutung ist (*Manuskript III*).

Die untersuchten Organismengruppen (Pflanzen, Spinnen, Käfer) wiesen erheblich Unterschiede in den Reaktionszeiten auf veränderte landwirtschaftliche Nutzungen auf. Daraus wurde geschlussfolgert, dass Vegetationsaufnahmen besonders für ein aussagekräftiges Langzeit-Monitoring eingesetzt werden sollten. Hingegen erlauben epigäische Spinnen- und Käfer-Assoziationen aufgrund ihrer empfindlichen Reaktionen gegenüber Änderungen im Mikroklima und der Bodenfeuchte eine effiziente Indikation und Bewertung von Restaurationsmaßnahmen bereits nach kürzerer Zeit (3-5 Jahre).

(6) In Grasland-Ökosystemen zeigen die Abundanz-Muster von Arthropoden keinen generellen Zusammenhang zur Pflanzendiversität (*Manuskripte IV and V*).

Falls die Diversität von Pflanzen einen maßgeblichen Einfluss auf die Abundanz-Muster von Insekten haben sollte, wie es beispielsweise Root (1973) postuliert, müssten derartige Effekte auch in Feldstudien erkennbar sein, besonders dann, wenn Effekte anderer Variablen statistisch kontrolliert werden. In zwei unabhängigen Studien konnte solch ein genereller Zusammenhang nicht gefunden werden. Während in einer Studie keine Effekte ermittelt werden konnten (*Manuskript IV*), war in einer zweiten Studie (Manuskript V) lediglich bei relativ niedriger Pflanzenartenvielfalt (10-35 Arten) eine Tendenz zur Abnahme der Abundanzen von Arthropoden mit zunehmender Pflanzendiversität erkennbar.

(7) Die Arten-Abundanz Struktur von Pflanzengemeinschaften korreliert signifikant mit den Abundanz-Mustern von Arthropoden (*Manuskript IV*).

Einfache Diversitätsmaße in Grasland-Ökosystemen scheinen nur unzureichend die Vegetationseigenschaften zu beschreiben, die für die Abundanz-Muster von Arthropoden relevant sein könnten. Hingegen korreliert die Arten-Abundanz Struktur (durch eine NMDS kondensierte Information der Pflanzenartenzusammensetzung und der jeweiligen Abundanzen) von Grasländern hochsignifikant mit den Abundanzen von Arthropoden.

(8) Die Übertragungsrate der, durch massive abiotische Veränderungen hervorgerufenen Änderungen in der Diversität der Produzenten zu den Konsumenten verringert sich erheblich mit der Höhe der trophischen Ebene *(Manuskript V)*.

Eine rasche Zunahme der Artenvielfalt, der effektiven Diversität und der Evenness der Pflanzen wurde mit abnehmendem pH, als stellvertretenden Schadstoffindikator, ermittelt. Während die Artenvielfalt aller herbivorer funktioneller Gruppen mit zunehmender Artenvielfalt der Pflanzen ebenfalls anstieg, konnte ein ähnliches Muster nur bei einer karnivoren funktionellen Gruppe beobachtet werden.

(9) Relativ hohe Anteile der beobachteten räumlichen und zeitlichen Variabilität von Arthropoden sind durch vertikale Interaktionsmuster zwischen funktionellen Gruppen von Arthropoden erklärbar (*Manuskripte IV, V, IX*).

Die Ergebnisse zahlreicher theoretischer als auch experimenteller Studien belegen die Existenz von intertrophischen Abhängigkeiten, wobei besonders die Beziehungen zwischen herbivoren und karnivoren Konsumenten hervorgehoben werden. Einige karnivore funktionelle

Gruppen sind mit herbivoren als auch detritivoren funktionellen Gruppen signifikant korreliert. Dies deutet darauf hin, dass Karnivore in der Lage sind, sich zumindest teilweise von den trophischen Auswirkungen der Pflanzen-Herbivoren Beziehung zu entkoppeln. Aber auch nicht-trophische Interaktionen sind denkbare Ursachen für die beobachteten Korrelationsmuster.

(10) Die Nutzung funktioneller Gruppen ermöglicht die Analyse der individuellen Interaktionsmuster unterschiedlicher Artengruppen der gleichen als auch unterschiedlicher trophischer Ebenen *(Manuskripte IV, V, IX, X, XI)*.

Die Komplexität und Mannigfaltigkeit von Interaktions-Netzen erklärt, weshalb einfache kaskadenartige Mechanismen zwischen den unterschiedlichen trophischen Ebenen selten nachweisbar sind. Hier wird die Verwendung funktioneller Gruppen für Produzenten und Konsumenten als ein sehr hilfreicher Ansatz angesehen, die Vielfalt der Interaktionen zwischen Pflanzen und Tieren als auch die Funktionsweise von Ökosystemen weiter aufzuklären.

(11) Die Verwendung von Körpergrößen-Klassen ist eine viel versprechende Methode zur ökologischen Indikation auf der Grundlage von Arthropodendaten (*Manuskript VI*).

Räuberische Laufkäfer sind in späteren Sukzessionsstadien signifikant kleiner als in früheren Sukzessionsstadien. Darüber hinaus scheinen die Arten späterer Sukzessionsstadien stärker spezialisiert zu sein. Diese Ergebnisse unterstützen die *efficiency-specialization* Hypothese von Siemann et al. (1999) die besagt, dass im Laufe der Sukzession (oder Regeneration) von Ökosystemen die mittlere Körpergröße von Konsumenten-Assoziationen abnimmt. Die Resultate unterstreichen jedoch teilweise auch die Vorstellungen von Blake et al. (1994) der postuliert, dass mit zunehmender Störungsintensität in Ökosystemen die mittlere Körpergröße von Konsumenten ebenfalls abnimmt, was die sukzessionsbedingten Effekte teilweise überlagern kann.

(12) Im Zusammenhang mit Biomonitoring-Studien ist die Modellierung der Populationsdynamik unter Verwendung von meteorologischen Parametern ein hilfreiches Verfahren, vorhandene Lücken in Langzeitdaten von Arthropoden zu überbrücken (*Manuskript VII*).

Mit Hilfe von multiplen linearen Regressionen und Kreuzvalidierungs-Verfahren wurden statistisch relevante meteorologische Parameter extrahiert und zur Modellierung der Populationsdynmaik von ausgewählten Heuschreckenarten über einen Zeitraum von 20 Jahren verwendet. Die für die untersuchten Arten teilweise unterschiedlichen Kombinationen von meteorologischen Parametern reflektieren dabei weitgehend die unterschiedlichen Phänologien der Arten. Außerdem wird vermutet, dass die Güte der Modellierung mit der Höhe der trophischen Ebene zunimmt (siehe dazu auch nächste These).

(13) Die klimatische Sensibilität von funktionellen Gruppen erhöht sich signifikant mit der Höhe der trophischen Ebene (*Manuskript VIII*).

Um die klimatische Sensibilität von funktionellen Gruppen unterschiedlicher trophischer Ebenen zu untersuchen, wurden Pflanzen- und Arthropodendaten zweier Grasland-Ökosysteme aus einem Zeitraum von 20 Jahren untersucht. Aus den ermittelten Unterschieden wurde geschlussfolgert, dass im Zusammenhang mit globalen klimatischen Veränderungen nicht nur mit einfachen biogeografischen Veränderungen sondern auch mit Destabilisierungen von vorhandenen Artengemeinschaften zu rechnen ist. Diese Erkenntnisse sollten künftig in ökologische Klimamodelle integriert werden.

(14) Der Vernetzungsgrad (*connectance*) von funktionellen Gruppen ist ein aussagekräftiger Parameter zur Beschreibung der Komplexität und funktionellen Diversität von Artengemeinschaften *(Manuskript IX)*.

Die Analysen der Korrelationsmuster zwischen funktionellen Gruppen von Pflanzen und Arthropoden aus einem ungestörten und gestörten Graslandökosystem ergaben (i) einen ungefähr 30%-40% höheren vertikalen Vernetzungsgrad zwischen den untersuchten funktionellen Gruppen und (ii) einen viel höheren prozentualen Anteil signifikanter Korrelationen zwischen den funktionellen Gruppen im ungestörten System sowie (iii), dass im gestörten System einfache biotische Interaktionsmuster dominieren.

(15) Die funktionelle Zuverlässigkeit (*reliability*) von Interaktionsnetzen basierend auf funktionellen Gruppen hängt in natürlichen Systemen von der Netzgröße als auch der Netz-Topologie ab (*Manuskript X*).

Unter Verwendung einer Vielzahl von *Sink-Webs*, die von Interaktionsnetzen zweier Grassland-Ökosysteme abgeleitet wurden, konnte die Beziehung der funktionellen Zuverlässigkeit (*reliability*) zu anderen Netz-Parametern untersucht werden. In der Gegenüberstellung mit klassischen Nahrungsnetzen (*food webs*) wurde deutlich, dass sich die *reliability*-Werte basierend auf funktionellen Gruppen als auch deren Relationen zu anderen Netzparametern kaum unterscheiden.

(16) Das Verhältnis der invasiven Arten zur gesamten Arten-Assoziation ist ein einfaches und robustes Maß zur Indikation von Ökosystemveränderungen, durch die Arteninvasionen begünstigt werden (*Manuskript XI*)**.**
Die separate Analyse der Abundanzen als auch der Artenzahlen unterschiedlicher funktioneller Gruppen epigäisch aktiver Arthropoden aus Lorbeerwäldern zeigte, dass sich in allen Fällen der Anteil invasiver Arten am gesamten Artenbestand negativ zu den Abundanzen bzw. Artenzahlen der autochthonen Arten verhält. Im Zusammenhang mit der Diskussion eines einfachen konzeptionellen Modells wurde außerdem herausgestellt, dass die negativen Effekte der Diversität autochthoner Arten auf den Anteil invasiver Arten, in einigen Fällen auch auf die Wirkung extrinsischer Faktoren zurückgeführt werden können. Dies könnte dann der Fall sein, wenn extrinsische Faktoren die Diversität autochthoner und invasiver Arten in unterschiedlichem Ausmaß oder unterschiedlicher Richtung beeinflussen.

(17) Aus den Ergebnissen der Manuskripte wird die generelle Schlussfolgerung gezogen, dass neben experimentell-reduktionistischen Untersuchungsansätzen empirisch-holistische Studien eine essentielle Grundlage für ein umfassendes Umweltverständnis, auf elementarem als auch aggregiertem Organisationsniveau, darstellen. Mit dieser Schlussfolgerung wird der von Eugen P. Odum (1971) seit langem vertretenen Ansicht gefolgt, dass: **"Ecology must combine holism with reductionism if applications are to benefit society!"**.

15. Summary

“Terrestrial arthropod assemblages as ecological indicators of environmental changes”

The value of information associated with using arthropod assemblages as ecological indicators in the context of complex environmental changes was highlighted by presenting a series of case studies. Based on the work reported in eleven manuscripts, the responses of arthropod assemblages to (i) disturbances caused by agricultural management or industrial pollutions, and the associated regeneration and/or succession processes, and (ii) their sensitivity to climate dynamics and species invasions were analysed. Furthermore, (iii) the appropriateness of using a functional group approach within the context of bioindication was evaluated. Finally, (iv) a broad methodological spectrum of sampling and analysing complex field data of arthropods was presented.

(1) In terms of variance, the use of community parameters should be favoured instead of population parameters for purposes of bioindication (*Manuscript I*)**.**
Testing a procedure for estimating sample size the relation between level of precision (LOP) and required sample size (RSS) showed significant differences between population (e.g. abundances) and community (e.g. diversity, evenness) parameters. For most species, a high precision level (5-10%) would require an unaffordable large sample size.

(2) A statistical procedure is presented which can be used as a tool for the selection of trustworthy indicator species from a pool of potential usable species (*Manuscript I*).
Beside a high degree of habitat preference to allow a LOP as high as possible a good indicator species should have a low coefficient of variation (CV) per target unit (e.g. target sites or plots) for the target parameter (e.g. mean number of individuals). From data sampled in agricultural habitats it was concluded that because of a better LOP-RSS relation habitat generalists may sometimes be more favourable indicator species than habitat specialists.

(3) A new procedure called “Nested-Cross array” for estimating population densities of ground-dwelling arthropods with pitfall trapping is described (*Manuscript II*)**.**
This method couples the fitting of single hyperbolic functions to trap data with the use of a cross shaped trap arrangement (Nested-Cross array); distances between traps double with increasing distance from the central trap.

(4) Evenness appears to be a very dependable community parameter for biological indication studies (*Manuscript III*).

The effects of changing agricultural land use on vegetation, and ground-dwelling spider and beetle assemblages, were investigated comparatively in a three-year study. Whereas species richness increased with decreasing management impact only for plants and spiders, the Camargo's evenness (E') index increased for all three examined assemblages.

(5) Convincing biological monitoring systems with sensitive short-term arthropod monitoring should complement the frequently used vegetation monitoring, especially at the beginning of restoration projects (*Manuscript III*).

The analysed assemblages (plants, spiders, beetles) showed considerable differences in reaction time to changes in land use. Whereas vegetation monitoring appears a more powerful long-term assessment, ground-dwelling spiders and beetles mainly respond to changes in the microclimate and the soil-moisture. The latter two assemblages allow an efficient indication of restoration management after 3-5 years.

(6) In natural grasslands arthropod abundance is not a simple function of plant diversity (*Manuscripts IV and V*).

If plant diversity, as proposed by Root's hypothesis (1973), has an overriding effect on insect abundance, it should be possible to detect the signature of these plant diversity effects also in field studies, especially if confounding variables are adequately controlled for. This was not found in two independent studies. In one study no effects were found (*Manuscript IV*), in the other (*Manuscript V*) consumer abundance tended to decrease with increasing plant diversity only on a low plant species richness range (range of 10 to 35).

(7) Plant community composition significantly correlates with arthropod abundances (*Manuscript IV*).

Whereas simple measures of plant diversity of natural grasslands seems to be less than adequate descriptors of those vegetation characteristics that may be relevant for arthropod abundances, plant community composition (condensed information of species occurrences and abundances using an NMDS-analysis) was highly correlated with arthropod abundances.

(8) The transmission of changes in plant species diversity driven by strong abiotic changes to consumers diminishes massively with increasing trophic level *(Manuscript V)***.**

Using top soil pH as a representative pollution parameter a rapid increase of plant species richness, effective diversity and evenness of plant community was detected with decreasing pH. While the richness of all studied functional groups of herbivores increased with plant species richness, only the richness of one carnivore functional group showed a similar pattern.

(9) A relatively high proportion of arthropods' spatial and temporal variability is explainable by vertical interaction patterns between different functional groups of arthropods (*Manuscripts IV, V, IX*).

The occurrence of intertrophic dependencies was supported by results from both theoretical and experimental studies highlighting, in particular, strong relations between herbivore and carnivore consumers. Some carnivore functional groups are correlated both to herbivores and detritivores suggesting that they may be able to decouple themselves, at least partially, from the plant-herbivore cascading chain. Non-trophic interactions may be further possible explanation for this observed correlation pattern.

(10) The functional group approach allows detection of the very individual interaction patterns of different species groups within and between different trophic levels *(Manuscripts IV, V, IX, X, XI)***.**

The complex and diverse nature of interaction webs explains why the characterisation of simple cascading-up mechanisms between different trophic levels may only rarely be detectable. Using functional group for producers and consumers was proposed as these approaches appear to provide an encouraging step forward to disentangle further the web of interactions between plant and animal diversity, and ecosystem functioning.

(11) Using body size classes is a promising ecological indicator approach for arthropods (*Manuscript VI*)**.**

Carnivore ground beetles are significantly smaller in later than in earlier seral stages; they appear to be more specialized in later seral stages. This supports the efficiency-specialization hypothesis of Siemann et al. (1999) that suggests that during succession (or regeneration) the mean body sizes of consumer assemblages decrease. Furthermore, the results demonstrate also that the hypothesis of Blake et al. (1994), postulating that smaller body sizes were found with increasing level of disturbance, is partly supported and may overlay the effects driven by succession.

(12) Modelling population dynamics of arthropod species using meteorological parameters is a useful tool in bridging gaps of long-term data in the context of biomonitoring studies (*Manuscript VII*).

By means of multiple linear regressions and cross-validation procedures subsets of meteorological parameters were extracted and were used to model the long-term population dynamics of some selected grasshoppers over 20 years. The selected variables for each species revealed different influences of meteorological parameter combinations reflecting the different phenologies. Furthermore it is to be expected that the precision of such modelling procedures will be increase with higher trophic levels (see next point).

(13) The climate sensitivity of functional groups increases significantly with increasing trophic levels (*Manuscript VIII*).

Plant and arthropod data collected over 20 years from two grassland communities were analyzed to determine whether functional group climate sensitivity differed between trophic levels. The observed differential sensitivity would lead, not simply to geographical shifts, but to community destabilization under climate change. This must consequently be incorporated in predictive ecological climate models.

(14) The connectance of functional groups is a powerful measure of complexity and functional diversity of communities *(Manuscript IX)*.

The analyses of correlation pattern between functional groups of plants and arthropods of an undisturbed and a disturbed grassland highlighted (i) an approximately 30% - 40% higher vertical functional group-connectance in the undisturbed than in the disturbed grassland; (ii) a much higher percentage of significant correlations between functional groups in the undisturbed system; and (iii) that disturbed grassland was characterized by more simply structured patterns of biotic interaction.

(15) In nature, the reliability of functional group interaction webs, and also their contribution to mediating the biodiversity-ecosystem relationship, will depend on both web size and topology (*Manuscript X*).

Using the qualities of sink webs derived from interaction webs of two different grasslands, the overall patterns in the relationships between reliability and other web characteristics were considered. Reliabilities for functional group interaction webs are very high, at least as high as those for food webs, and that they show similar relationships to other web characteristics.

(16) The proportion of alien species as compared to the whole assemblage is a simple and robust measure which indicates ecosystem changes promoting species invasions (*Manuscript XI*).

The abundances and species richness of different functional feeding groups of ground dweling laurel forest arthropods were analysed and it was found that the proportion of aliens was negatively related to the natives' abundance or richness in all cases. By developing a simple conceptual model it was shown that the negative effects of natives' diversity may be partially caused by extrinsic factors affecting the diversity of natives, and the invader success in a different extent or direction.

(17) From the results, it was concluded that in addition to experimental (and mostly more reductionistic) studies, also empirical (and mostly more holistic) field studies are essential to understand comprehensively the environment at both an elemental and an aggregate level. These conclusions strongly support Eugen P. Odum's (1971) frequently emphasized viewpoint that: **"Ecology must combine holism with reductionism if applications are to benefit society!"**

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Ich versichere, dass ich nach bestem Wissen die reine Wahrheit gesagt und nichts verschwiegen habe.

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