Effects of experimental small-scale grassland fragmentation on the population dynamics of invertebrates

Inauguraldissertation

zur

Erlangung der Würde eines Doktors der Philosophie

vorgelegt der

Philosophisch - Naturwissenschaftlichen Fakultät

der Universität Basel

von

Brigitte Michèle Braschler

aus Freienbach SZ

Basel, 2005

Genemigt von der Philosophisch-Naturwissenschaftlichen Fakultät auf Antrag von

Prof. Dr. Bruno Baur

PD Dr. Andreas Erhardt

Basel, den 21. Oktober 2003

Prof. Dr. Marcel Tanner

Dekan

Table of contents

Acknowledgements

During my dissertation I had the occasion to work in three beautiful field sites in the Swiss Jura mountains. My thanks go to all those who made this possible.

Numerous people contributed in important ways to this thesis. First and foremost, I would like to thank my supervisor **Bruno Baur** for his enduring support and always valuable advice. In particular, I would like to thank him for the chance to work in his habitat fragmentation project. His expertise greatly improved the papers in this thesis.

I would also like to thank **Samuel Zschokke** for help with everything that consumes electricity (from tiny loggers to desktop computers) and **Samuel Zschokke, Hans-Peter Rusterholz, Peter Stoll**, **Georg Armbruster** and **Andreas Erhardt** for statistical and general advice and valuable comments on early drafts of my manuscripts. **Eric Lüdin** was always ready to discuss statistical problems. His advice greatly improved the statistics presented in this thesis. **Claudine Dolt** and **Hans-Peter Rusterholz** allowed me to use their data on plant species composition and plant productivity in the experimental plots to calculate Landolts indicator scores and examine the relationship between environmental factors and ant density. **Michel Wurtz** helped maintaining the study sites and helped with preparing some photographs for my conference contributions. **Salome Schüpbach, Phillippe Leuenberger**, **Susanna Meyer**, **Nicole Minoretti** and numerous other field assistants helped maintaining the field sites and assisted in data collection. In particular I want to thank all field assistants that were ready to work at rainy Sunday mornings to collect snails. **Gerolf Lampel** collaborated with me on the aphid project and made all aphid determinations. His expertise and advice are highly appreciated. **Ludwika Sygnarski** prepared the aphid specimens for determination. **Samuel Zschokke** was the main author of the article on short-term effects of the experimental fragmentation and **Claudine Dolt**, **Hans-Peter Rusterholz**, **Heinrich Thommen**, **Peter Oggier**, **Eric Lüdin** and **Andreas Erhardt** contributed to the manuscript. **Samuel Zschokke** helped to prepare the manuscript on the relationship between plant productivity and

invertebrate diversity to which **Claudine Dolt**, **Heinrich Thommen** and **Peter Oggier** also contributed data. **Bernhard Seifert**, **Rainer Neumeyer** and **Cesare Baroni Urbani** helped with ant determination. Advice from several anonymous referees improved the manuscripts that form this thesis. Their thorough work behind the scene is greatly appreciated.

I would like to thank the other members of the habitat fragmentation group for discussions during seminars or cake breaks, namely **Samuel Zschokke**, **Claudine Dolt**, **Marcel Goverde**, **Stephan Ledergerber**, **Peter Oggier**, **Heinrich Thommen** and **Andreas Erhardt**. **Evelyn Argast** was always ready to help with administrative problems. The staff of the institute, in particular my roommates provided a very comfortable working climate. I want to thank **Nicole Minoretti**, **Suresh Benjamin**, **Jovanne Mevi-Schütz**, **Ursula Monzeglio**, **Daniel Bloch**, **Katleen Beese**, **Rolf Locher**, **Nenad Bojat, Stefan Müller**, **Alexander Wacker**, **Christoph Jäggi** and all others that worked in the rooms -12 to -14 and 21 to 35 during my time at the NLU.

This thesis was part of the **Swiss Priority Programme Environment** supported by the **Swiss National Science Foundation** (grant 5001-44620 to B. Baur). The **Reisefonds der Universität Basel** awarded me travel grants to enable me to present results from my projects at conferences in Cambridge (UK) and Lund (Sweden).

Last but not least I would like to thank my **family** and **friends** for continued support and for listening to all my tales about the dissertation project. Especially I would like to thank my parents **Doris** and **Hermann Braschler** for their enduring support, including the possibility to borrow their car or other things whenever necessary.

Summary

One of the great questions in ecology is what determines and maintains biodiversity. This question is receiving increased attention as biodiversity is at risk. Species go extinct at such a high rate that some scientists speak of a man-made mass extinction. As biodiversity is related to ecosystem functioning also wide ranging consequences of the current species loss on ecosystem services can be expected.

In addition to habitat loss, habitat fragmentation threatens biodiversity. Small and isolated fragments are expected to host less species than larger and better connected habitat patches. Fragmentation also reduces genetic diversity and disrupts interactions between species. Invertebrates, in particular insects, contribute considerably to species richness of a habitat.

In the present thesis I focus on the effects of an experimental fragmentation on invertebrate diversity in calcareous grasslands. These species-rich, extensively used grasslands have been created by man and are today threatened by changes in agricultural practices and by fragmentation. In a long-term experiment at the University of Basel, fragments of different size (0.5 m^2, 2.25 m^2 and 20.25 m^2) have been isolated and maintained by regularly moving the surrounding vegetation. Corresponding control plots were situated in adjacent continuous grassland. The experimental set-up consisted of 48 fragments and 48 control plots, distributed over three study sites in the northern Swiss Jura mountains. I examined effects of the experimental fragmentation on invertebrate population dynamics 3 to 6 years after the initiation of the fragmentation.

Species richness of grasses increased in fragments while species richness of forbs, ants, aphids, gastropods and grasshoppers were not affected by the fragmentation. Only in butterflies, the most mobile animal group examined, a negative response to the fragmentation was found. The time frame used in the present experiment may have been to short to monitor extinction processes. However, the experimental fragmentation altered the abundance of single species and altered interactions between species. As predicted by theory, many common species were even more abundant in fragments than in control plots. Furthermore, aphids, a group of herbivorous insects, benefited from the fragmentation. However, the increase in aphid

density was not a result from reduced parasitation pressure, but rather a result of a higher degree of ant-tending and an increased plant productivity. The fragmentation also altered competitive interactions among ant species. With increasing density of the dominant ant species *Lasius paralienus* species richness and forager density of the other ant species decreased in fragments but not in control plots. The densities of foragers of the other species at natural and artificial sugar resources were not affected by *L. paralienus* forager density. This could be a result of an increased density of natural sugar resources in fragments and thus decreased competition for them. The fragmentation also affected the spatial distribution and persistence of ant nests. These findings were a result of altered abiotic conditions at the edge of fragments and were more pronounced for the dominant species than for all ant species together.

The experimental fragmentation increased plant productivity. Changes at the base of the food chain could impact higher trophic levels. Therefore, I examined the relationships between productivity (above-ground phytomass) and plant species richness and between productivity and species richness and biomass of consumers (gastropods and grasshoppers) at three spatial scales in two successive years. Only the control plots of the fragmentation experiment were used. The shape of the relationship between productivity and species richness varied between groups and depended on the spatial scale of the investigation.

Deutsche Zusammenfassung

Zu den grossen Fragen der Ökologie gehört, wie Biodiversität entsteht und wie sie erhalten bleibt. Diese Frage gewann in letzter Zeit zusätzlich an Bedeutung, da die Biodiversität heute durch den Menschen in zuvor ungekanntem Ausmass bedroht ist. Weltweit führen vom Menschen verursachte Veränderungen der Lebensräume zum Aussterben vieler Arten. Das Verschwinden von Arten kann auch dazu führen, dass ein Ökosystem nicht mehr alle seine Dienstleistungen im gleichen Masse erbringen kann.

Der heute beobachtete Artenverlust ist teilweise eine direkte Folge der Zerstörung von Lebensräumen, aber auch die Fragmentierung von Lebensräumen trägt zum Artenverlust bei. Es wird davon ausgegangen, dass kleine, stark isolierte Fragmente weniger Arten beherbergen als grosse, gut vernetzte Flächen. Fragmentierung reduziert auch die genetische Vielfalt und stört die Wechselbeziehungen zwischen Arten. Ein grosser Teil der Arten eines Lebensraums gehört zu den Wirbellosen (vor allem Insekten).

In meiner Dissertation untersuche ich den Einfluss einer experimentellen Lebensraumfragmentierung auf Wirbellose in Kalkmagerrasen im Schweizer Jura. Diese halbnatürlichen Rasen sind aussergewöhnlich artenreich. Heutzutage werden Magerrasen durch veränderte landwirtschaftliche Praktiken, sowie Lebensraumfragmentierung bedroht. Im Rahmen eines Langzeit-Experiments der Universität Basel wurden in drei Untersuchungsgebieten Fragmente verschiedener Grösse (0.5 m^2, 2.25 m^2 und 20.25 m^2) durch Mähen der umgebenden Vegetation isoliert. Im benachbarten, zusammenhängenden Rasen wurden Kontrollflächen gewählt. Das ganze Experiment umfasste 48 Fragmente und 48 Kontrollflächen. Ich untersuchte die Einflüsse der Fragmentierung auf die Populationsdynamik von Wirbellosen drei bis sechs Jahre nach dem Start des Experiments.

Obwohl die Schmetterlinge die mobilste der untersuchten Wirbellosengruppen sind, wurde bei ihnen eine Abnahme des Artenreichtums in den Fragmenten beobachtet. Der Artenreichtum der Gräser war in den Fragmenten höher als in den Kontrollflächen. Der Artenreichtum von Kräutern, Ameisen, Blattläusen, Heuschrecken und Schnecken in den Fragmenten unterschied sich nicht von dem in den Kontrollflächen. Die Dauer der Studie war wahrscheinlich zu kurz, um Austerbeereignisse zu beobachten. Trotz der kurzen Zeit seit dem

Beginn des Experiments wurden jedoch bereits grosse Veränderungen in den Häufigkeiten einzelner Arten und in den Wechselbeziehungen zwischen den Arten beobachtet. Viele der häufigen Arten waren in den Fragmenten noch häufiger als in den Kontrollflächen. Auch die Dichte von Blattläusen war in den Fragmenten höher als in den Kontrollflächen. Der Anteil parasitierter Blattläuse unterschied sich nicht zwischen Fragmenten und Kontrollflächen. Die erhöhte Blattlausdichte resultierte wahrscheinlich aus einer intensiveren Wechselwirkung mit Ameisen, sowie aus einer erhöhten pflanzlichen Produktivität in den Fragmenten. Die Lebensraumfragmentierung beeinflusste auch die Wechselbeziehungen zwischen verschiedenen Ameisenarten. Mit zunehmender Dichte der dominanten Ameisenart *Lasius paralienus* nahm die Dichte, sowie der Artenreichtum der anderen Ameisenarten in den Fragmenten ab. In den Kontrollflächen wurde keine solche Beziehung gefunden. Die Lebensraumfragmentierung beeinflusste auch die räumliche Verteilung der Ameisennester, sowie die Zeitspanne während der sie bewohnt waren. Dies war vor allem eine Folge veränderter abiotischer Faktoren an den Rändern der Fragmente. Der Einfluss der Fragmenträndер auf die Verteilung der Ameisennester war besonders stark ausgeprägt, wenn nur die dominante Art berücksichtigt wurde.

Die experimentelle Lebensraumfragmentierung erhöhte die pflanzliche Produktivität und beinflusste die Artenzusammensetzung der Pflanzen. Änderungen an der Basis der Nahrungskette werden weitere Änderungen bei den Konsumenten zur Folge haben. Aus diesem Grund untersuchte ich auch den Zusammenhang zwischen der pflanzlichen Produktivität und dem Artenreichtum der Pflanzen, sowie dem Artenreichtum und der Biomasse von Konsumentengruppen (Heuschrecken und Schnecken). Für diese Analyse wurden nur die Kontrollflächen berücksichtigt. Die Art des Zusammenhangs zwischen Produktivität und Artenreichtum hing von der untersuchten Gruppe, sowie der räumlichen Skala ab.

General introduction

The biodiversity crisis

One of the great questions in ecology is which mechanisms create and maintain biodiversity. This question is receiving increased attention as biodiversity is at risk (Western 1992; Sala et al. 2000; Woodruff 2001). Habitats are destroyed or altered at unprecedented rates and species extinction rates have increased to previously unknown levels. The frequency of species extinctions is now estimated to be at 100-1000 times the background rate (Lawton and May 1995). Population extinction rates are estimated to be at maybe a 100 times higher levels (Hughes et al. 1997). The current situation is referred to by some scientists as a man-made mass extinction (Chapin et al. 2000; Woodruff 2001). In a recent review Purvis and Hector (2000) showed that the current rate of species losses is unsustainable, i. e. exceeds the rate new species are generated.

Even while biodiversity declines, many questions remain unsolved on what determines the patterns of biodiversity naturally. It is thus of crucial importance to identify the mechanisms that maintain biodiversity in undisturbed habitats (Huston 1994). At the same time ecologists world-wide need to examine what the effects of man-made habitat alterations on biodiversity are. Based on such studies, recommendations to policy makers can be developed on how a further decline of biodiversity can be best prevented (Chapin et al. 2000; Woodruff 2001).

Species extinctions are deplorable in themselves. However, as biodiversity has been shown to be related to ecosystem functioning, also wide ranging consequences of the current species loss on ecosystem services can be expected (Hector et al. 2001). Still, the relationship between biodiversity and ecosystem functioning is not yet fully understood. Theory predicts that ecosystem functioning should increase with increasing biodiversity through niche complementarity (Engelhardt and Ritchie 2002). However, with increasing species richness niche overlap of the species increases as well. Thus, adding further species to an already diverse ecosystem will add little to an ecosystem process. In most experimental studies 20-50% of species were sufficient to maintain most biogeochemical ecosystem processes (Purvis

and Hector 2000). However, it has been suggested that the 'redundant' species may render the ecosystem more stable over time, by providing the right species in the right place at the right time under varying conditions (Loreau et al. 2001). Furthermore, a high species richness may make a community more resistant against invasion (Elton 2000).

Other explanations for the often observed increase in ecosystem functioning with increasing biodiversity than niche complementarity have also been proposed (Engelhardt and Ritchie 2002). However, in contrast to the niche complementarity theory, they do not predict that a diverse ecosystem is better than the best monoculture. These theories are partly influenced by sampling effects. At higher diversity the probability is higher that an area includes some species with a high effect on an ecosystem process. Thus, the mean of ecosystem processes increases and the variance decreases as biodiversity increases, while the upper bound of each ecosystem process remains constant. According to this hypothesis it would be enough to retain the most productive species with the strongest effect on ecosystem processes, while other species would be redundant. It is important to note that this theory is based on the assumption that each species' performance is independent of the other species in the mixture. If facilitation occurs among species then an increase in biodiversity would lead to an increase in mean performance (Cardinale et al. 2002; Engelhardt and Ritchie 2002). In contrast, strong interference competition among species would lead to a decrease in overall performance with increasing diversity (Engelhardt and Ritchie 2002).

Habitat fragmentation

The presently observed loss of species is not only a consequence of habitat loss but is also a result of habitat fragmentation (Quinn and Hastings 1987; Saunders et al. 1991). Habitat fragmentation is now considered as a major threat to biodiversity (Saunders et al. 1991; Collinge 2000; Simberloff 2000). Small and isolated fragments are expected to host less species than larger and better connected habitat patches (Andrén 1994). Fragmentation reduces the total area of suitable habitat and creates isolated subpopulations. These small subpopulations are more vulnerable to extinction due to demographic processes or through catastrophic events (Saunders et al. 1991; Rosenzweig 1995). Additionally, many species may have difficulties to recolonise isolated fragments (Kruess and Tscharntke 1994). A low immigration rate may reduce genetic diversity in isolated fragments through increased inbreeding or genetic drift as gene flow between subpopulations is prevented (Lacy and Lindenmayer 1995). Even species with good dispersal abilities may be affected indirectly by

fragmentation if they interact with species that have poor dispersal abilities (Kruess and Tscharntke 1994). The effects of disrupted interactions may vary and be either positive or negative for a species depending on the species involved and the type of interaction concerned. Furthermore, within fragments competitive interactions among species may be affected when the species are differently sensitive to fragmentation-related changes in habitat quality (e.g. edge effects).

Previous research revealed species-specific responses to habitat fragmentation: some species decreased in abundance, others became more abundant, while still others seemed to be unaffected by habitat fragmentation (Kareiva 1984; Kruess and Tscharntke 1994; Davies and Margules 1998). Consequently, further work was dedicated to the identification of traits that allow to predict a species' response to fragmentation (Davies et al. 2000). It has been suggested that species of higher trophic levels should be more vulnerable to fragmentation than groups like herbivores. Predators and parasites often have a small and fluctuating population size and are dependent on prey species that are themselves affected by the fragmentation (Holt 1996). However, even within guilds, different species may respond differently to habitat fragmentation. It has been suggested that strong competitors, abundant species and generalist species may benefit from habitat fragmentation while naturally rare species and specialist species may be lost from fragments (Mac Nally and Brown 2001). Theories on ecosystem functioning based on niche complementarity or facilitation among species would thus predict a decrease in ecosystem functioning in fragments. In contrast, theories assuming that ecosystem processes are mainly driven by the strongest species would expect no effect of habitat fragmentation on ecosystem functioning as long as the fragments are large enough to retain vital populations of 'important' species. However, the 'important' species may depend themselves on many other species, so that a higher diversity is needed to maintain ecosystem functioning than is at first apparent (Hector et al. 2001).

Numerous biodiversity studies have focused on organism groups that are of commercial interest or that are conspicuous (e.g. birds (Schmiegelow et al. 1997; Mason 2001) or butterflies (Hill et al. 2002; Wahlberg et al. 2002; Hawkins and Porter 2003)) or easily sampled (e.g. vascular plants (Waide et al. 1999; Tilman et al. 2001)). Considering the effect of habitat fragmentation on biodiversity, the taxonomic bias is even strongly evident among the relatively well studied vertebrates (Mac Nally and Brown 2001), while experimental studies on the effects of habitat fragmentation on terrestrial invertebrates are rare (Debinski and Holt 2000). However, biodiversity is largely composed of invertebrates, in particular insects. These organisms have an important role in ecosystem functioning. It is widely known

that insect diversity declined over recent decades and that this affected ecosystem functioning (Steffan-Dewenter and Tscharntke 2002; Tscharntke et al. 2002). Yet, little is known about the exact mechanisms by which man-made habitat alterations influence insect diversity. Due to limitations in expertise, time and funding, inventories of plants or small vertebrates have often been used as surrogates of total biodiversity. However, invertebrate diversity is often not directly correlated to those groups and the shape of the relationship may vary depending on the groups involved (Oliver and Beattie 1993). It is thus of great importance to include invertebrates in biodiversity studies and to examine how their diversity correlates with that of frequently examined groups like vascular plants (Oliver and Beattie 1993).

Focus of this thesis

In the present thesis, I focus on the effects of habitat fragmentation on invertebrate diversity in calcareous grasslands. Calcareous grasslands represent a typical example of a threatened, species-rich habitat in central Europe. These semi-natural grasslands harbour large numbers of plant and invertebrate species (Baur et al. 1996; Niemelä and Baur 1998; Balmer and Erhardt 2000; Steffan-Dewenter and Tscharntke 2002). This type of extensively used grassland has been created by man and became a refuge for open habitat species whose original habitats have largely been destroyed (Steffan-Dewenter and Tscharntke 2002). Today these grasslands are threatened by changes in agricultural practices, such as increased fertilisation (Fischer and Stöcklin 1997) or abandonment and reforestation (Zoller and Bischof 1980; Balmer and Erhardt 2000). For example, in the Passwang region 24 km south of Basel, unfertilised grasslands decreased by 78% between 1950 and 1985 (Zoller et al. 1986). In addition to habitat alteration these grasslands are also highly fragmented with remaining patches being often found at remote and steep slopes that are not suitable for intensive agriculture.

Early studies on the effects of habitat fragmentation on biodiversity mostly examined habitat remnants that differed in size, shape, time since isolation and degree of isolation. Recognising the need for replicated and controlled designs, several experiments comprising different habitat types, different focal groups and different spatial scales were conducted in the past two decades (Debinski and Holt 2000). However, few replicated studies on the effects of fragmentation on grassland invertebrates and interactions among different species have been conducted (Debinski and Holt 2000; Steffan-Dewenter and Tscharntke 2002; Tscharntke et al. 2002).

In this thesis I examine effects of experimental small-scale grassland fragmentation on the population dynamics of several groups of invertebrates. In particular, I focus on ants and aphids and the interactions between them. Effects of the experimental fragmentation on other insect groups and on gastropods are also reported in this thesis. Instead of merely reporting fragmentation effects on species richness, I also examine mechanisms by which grassland invertebrates are affected in the fragmentation experiment. Species richness, intuitively easy to understand and often easy to measure, may be a less ideal indicator for assessing effects of fragmentation, as extinctions processes in most organisms take longer than the time covered by a typical ecological study. This may be the case in many small nature reserves where small populations of rare species still exist but may ultimately be doomed. Additionally, extinctions may initially be overlooked when very rare species that are difficult to detect in biodiversity surveys are the first to go extinct (Gonzalez and Chaneton 2002). As money for long-term experimental studies is limited and fast results are needed in order to develop management policies that may prevent further degradation of our threatened ecosystems, ecologists should therefore move to directly examine effects of fragmentation on interactions among species and on ecosystem processes. Behavioural patterns may respond much faster to habitat fragmentation than species richness leading to wide ranging impacts on population dynamics (Kareiva 1987; Goverde et al. 2002). In the present thesis, effects of an experimental fragmentation on the population dynamics of different groups of grassland invertebrates and on interactions between these groups were assessed 3 to 6 years after the initiation of the experimental fragmentation. Thus, I could not only asses short-term responses but also examine the response over time.

The study sites

The fragmentation experiment was carried out in three calcareous grasslands situated in the northern Swiss Jura mountains: in Nenzlingen (13 km south of Basel; 47° 34' N, 7° 35' E), Movelier (26 km south-west of Basel) and Vicques (26 km south-south-west of Basel) (Fig. 1). Originally covered by beech forest, these grasslands have been grazed by cattle for many centuries, leading to the characteristic vegetation of the *Teucrio-Mesobrometum* (Ellenberg 1986).

The study site in Nenzlingen is situated on a south-west-facing slope with an inclination of 19-22° at an altitude of 510 m. A deciduous forest borders the study area in the north-east. Mean annual temperature is around 8.5-9.0 °C (the average July temperature is approximately

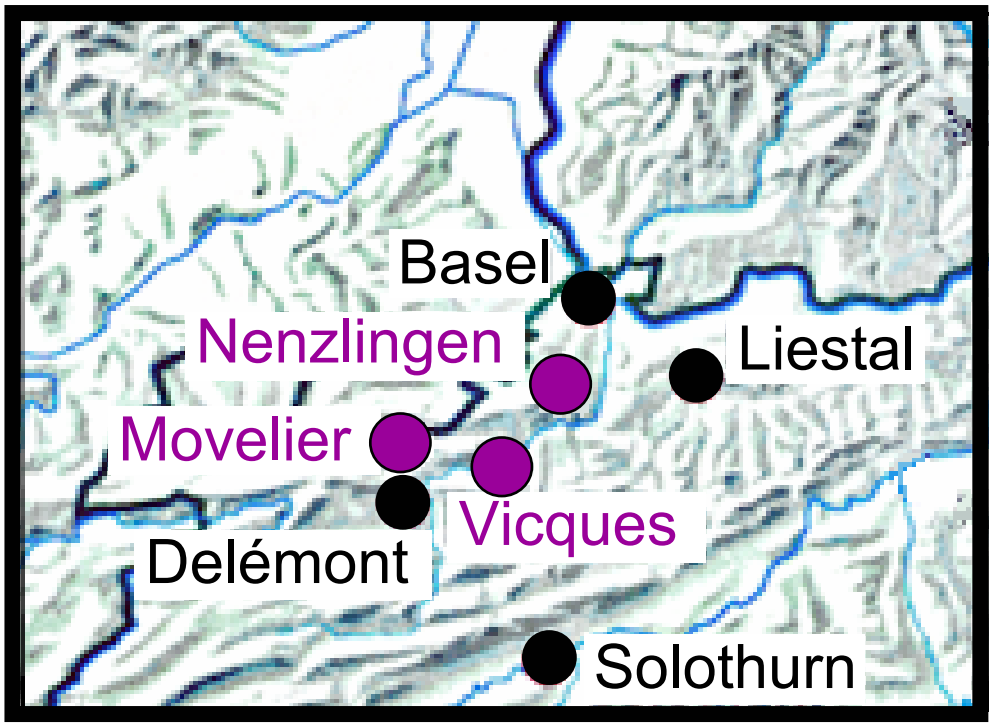


Fig. 1. Location of the three study sites near Nenzlingen (BL), Movelier (JU) and Vicques (JU) in the northern Swiss Jura mountains.

Fig. 2. The study site in Movelier with three experimental blocks. The photograph shows the fragments with the mown isolation area while the control plots are not distinguishable from the surrounding continuous vegetation. The isolation area around fragments was frequently mown. Photograph by M. Wurtz.

17 ˚C) and annual precipitation amounts to 900 mm (Ogermann et al. 1994). Snow covers the area for usually less than one month. Soils are of the rendzina type with an A-horizon varying in depth from 2 to 27 cm (for details on soil properties and profiles see Ogermann et al. (1994)). Until 1993, the site was grazed by cattle from May to September with a high stocking rate. The lower part of the slope was moderately fertilised by cattle dung.

The study site in Movelier is situated on a south-south-east-facing slope (inclination 20-22˚) at an altitude of 770 m (Fig. 2). Half of the site is surrounded by deciduous forest. Snow covers the site for usually more than one month. The humus layer is thicker than in Nenzlingen, contains some clay and is moister than at the other two sites. Until 1993, the site was grazed by cattle and a moderate amount of artificial fertiliser was used.

The study site in Vicques is situated on a south-east-facing slope (inclination 15-27˚) at an altitude of 590 m. There is mixed deciduous forest at the south-west-border of the area. Snow usually covers the area for a few days only. The humus layer is extremely thin and there are several patches of exposed bedrock (this type of habitat is lacking at the other sites). Until 1993, the site was exposed to a low grazing pressure by cattle.

The three grasslands had similar numbers of coexisting plant species in the first year of the experiment (Baur et al. 1996). However, the composition of the plant communities differs among sites with only 53.8% of all species occurring at all three sites (Baur et al. 1996). Diversity indices assessed in the first year of the experiment were similar for the three sites, indicating that similar environmental and ecological factors were influencing these communities (Joshi 1994).

The fragmentation experiment

The experimental fragmentation of the grasslands was created in spring 1993 by mowing the vegetation around the experimental fragments. One experimental unit, called block, contained one large (4.5 x 4.5 m), one medium (1.5 x 1.5 m) and two small (0.5 x 0.5 m) fragments, all of them separated by a 5-m wide strip of mown vegetation, as well as the corresponding control plots, which were mirror-symmetrically arranged and surrounded by undisturbed vegetation (Fig. 3). Within each block, the positions of the different sizes of fragment-control plot pairs as well as the control and fragment halves were randomised. The experimental set-up used in the present study consisted of 12 blocks (five in Nenzlingen, three in Movelier and four in Vicques) with 48 fragments (12 large, 12 medium and 24 small) and 48 corresponding control plots. The distances between blocks within the sites ranged from 25 to 135 m. The

blocks were part of larger study areas (1.5 - 2 ha) that were enclosed by fences to exclude large herbivores. The experimental fragmentation had been maintained since April 1993 by frequently (6-12 times per year) mowing the area between the fragments in the period from March to October. The entire experimental area was mown in late autumn every year to prevent succession (Kienzle 1979). The fragmentation experiment was terminated in October 1999 after seven vegetation periods.

In my thesis I examined effects of the experimental fragmentation on the population dynamics of different invertebrate groups in the years 1996 - 1999 (3 to 6 years after initiation of the fragmentation) allowing for the assessment of short-term and longer-term effects of the fragmentation. As the experiment was run over several years methods were chosen in a way to minimise the impact of the research on the experimental plots (Fig. 4).

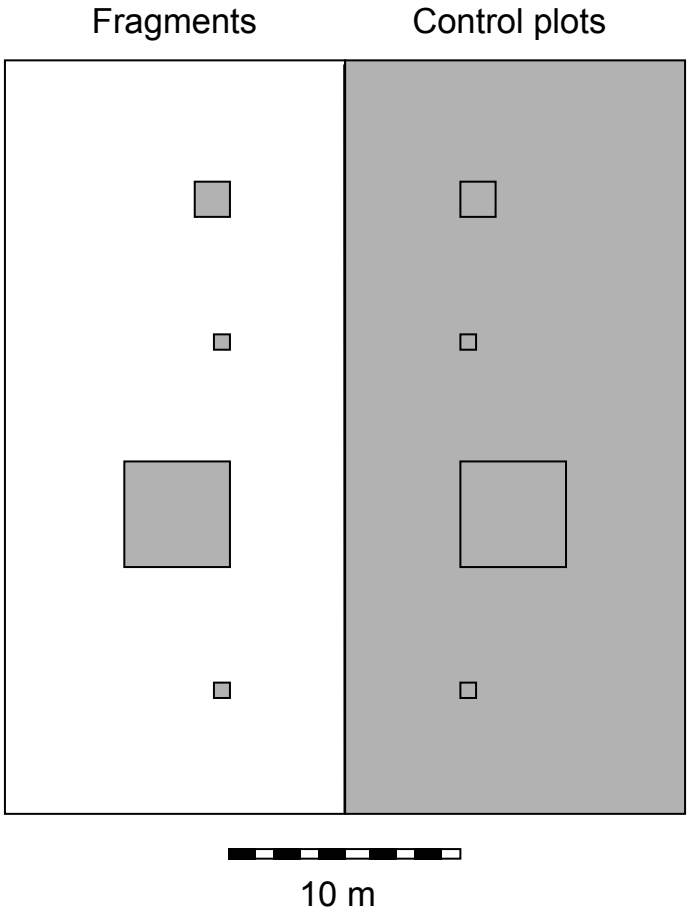


Fig. 3. Diagram of one block of the fragmentation experiment. A block contained two small (0.5 x 0.5 m), one medium (1.5 x 1.5 m) and one large (4.5 x 4.5 m) fragment and corresponding control plots.

Fig 4. Large fragment with a mobile working platform used to minimize trampling in the experimental plots.

Effects of experimental small-scale grassland fragmentation on invertebrate population dynamics

Community disassembly following fragmentation may take time (Gonzalez and Chaneton 2002). Additionally, initial responses may differ from long-term responses. Therefore, it is important to study communities in fragmented ecosystems over time. In **Chapter I** I concentrate on short-term effects of the fragmentation on plants (grasses and forbs) and four groups of invertebrates (ants, butterflies, gastropods and grasshoppers). The species richness and abundance of those groups was assessed in 1996, 3 years after the initiation of the experimental fragmentation. Detailed studies focusing on the response of ants and aphids over time are reported in the **Chapters II-IV**.

Different groups of organisms vary in their reaction to fragmentation (Davies et al. 2000). The invertebrate groups examined vary in traits like mobility and trophic position that may be important in determining their response to the experimental fragmentation. Furthermore, grassland invertebrates with the exception of butterflies have largely been ignored in fragmentation studies despite their great diversity and their large impact on ecosystems (Debinski and Holt 2000; Steffan-Dewenter and Tscharntke 2002). Instead a few indicator groups - often vascular plants - that are easy to sample or for which experts are numerous have been used as an estimate of total biodiversity. However, it is doubtful whether results from studies on vascular plants can be extrapolated to all invertebrate groups (Oliver and Beattie 1993). Therefore, it is important to know to what extend an indicator groups reflects the general picture regarding the effect of environmental change on biodiversity and with which other groups the diversity of the indicator group is correlated. In **Chapter I** the response of plants and invertebrates to the experimental fragmentation is examined simultaneously. In this way, it was possible to test whether general predictions from theory hold for very different taxonomic groups and in which groups the response to the experimental fragmentation is correlated.

I compared species richness, diversity and composition of the different groups and the abundance of single species in fragments with those in corresponding control plots. The abundances of 19 (29%) of the 65 common species examined were affected by the fragmentation. However, the experimental fragmentation affected different taxonomic groups and single species to a different extent. Grass species richness increased in fragments while species richness of forbs was not affected by the experimental fragmentation. Butterflies, the most mobile group among the invertebrates studied, reacted most sensitively: species richness of butterflies was lower in fragments than in control plots. In contrast, species richness of ants, gastropods and grasshoppers was not affected by the fragmentation. Foraging abundances of single butterfly species were lower in fragments than in control plots. Of the few single species of the other groups that were affected by the experimental fragmentation, most had a higher abundance in fragments than in control plots. This is probably so because the type of fragmentation used is beneficial to some plants through a decreased competition intensity along the edge of the fragments, and because some animals may use the fragments as retreats between their foraging bouts into the mown isolation area. Edge effects may also explain the observed increased plant productivity in fragments as compared to control plots. In conclusion, despite the short time frame of this study, some changes in plant and invertebrate abundance

and species richness were found. For many species however, the period of 3 years between the initiation of the experiment and the survey was probably to short to show a detectable reaction.

In **Chapter I** I demonstrated that different groups of insects vary in their responses to habitat fragmentation. In the following **Chapters II - IV** I report more detailed surveys focusing on two groups of insects, namely ants and aphids. In these chapters I do not only report effects of the fragmentation on species richness and the abundance of single species in greater detail but also examine mechanisms that lead to the observed effects.

Chapter II focuses on the effects of the experimental fragmentation on aphid population dynamics. Theory predicts that herbivore abundance increases in fragmented habitats as a consequence of reduced predation and parasitation pressure as species at higher trophic levels like predators and parasitoids are assumed to be especially vulnerable to habitat fragmentation due to their often small population size and their dependence on particular prey species (Holt 1996). Using aphids as model organisms, I tested the hypothesis that herbivore abundance increases in fragmented habitats as a result of reduced parasitoid pressure. However, also other possible mechanisms that may affect aphid population dynamics were investigated. I examined the population dynamics of aphids with respect to host plant abundance and the density of mutualistic ants. The fragments and control plots were examined 1997 - 1999 (4 to 6 years after the initiation of the fragmentation). Only fragments and control plots in Nenzlingen and Vicques were examined.

As predicted by theory, aphid density was higher in fragments than in control plots. This was a combined result of a higher frequency of aphid-infested plants and larger aphid colonies in fragments than in control plots. Furthermore, a larger proportion of aphid colonies was ant-attended in fragments than in control plots, though also not ant-attended colonies were more abundant in fragments than in control plots. Ant-attended aphid colonies were also more frequently visited by ants in fragments than in control plots in one of the 3 years. In contrast to theoretical expectations, parasitoid pressure on aphids was not influenced by the experimental fragmentation. Neither were aphid species richness and diversity affected by the fragmentation.

The observed fragmentation effects on aphid density might be a combined result of several distinct influences including a higher abundance of mutualistic ants, an increased plant productivity and altered abiotic factors in fragments. Other potential influences like reduced predation pressure could not be demonstrated in this study but may also contribute to a higher aphid density in fragments. The effect on aphid density was consistent over 3 years and two sites with slightly different aphid communities. Thus, the present experiment shows that even

small-scale habitat fragmentation can have profound and replicable effects on the abundance of herbivorous insects.

Fragmentation-related effects are of particular importance in species that interact with many other species as changes in their abundance or behaviour will further affect the species with which they interact. Ants species do fulfil this criteria. Ants are mutualists of plant sucking insects and hosts to a great diversity of insect species (Hölldobler and Wilson 1990; Seifert 1996). Ants play an important role as invertebrate predators (Hölldobler and Wilson 1990) and seed distributors (Christian 2001) and are pollinators of some plant species (Schürch et al. 2000). Ants also act as ecosystem engineers (Lawton 2000). Their nest construction behaviour provides free space for plant establishment (Dean et al. 1997) and increases soil drainage (Hölldobler and Wilson 1990) and their foraging behaviour enriches patches with nutrients (Bestelmeyer and Wiens 2003). Some interactions are species-specific (e.g. some *Maculinea* butterfly species rely on a single ant species as host), while other interactions are less specific. Thus, changes in ant species composition, ant density or the spatial distribution of ant nests may affect a large number of other organisms as well. Indeed several studies have found that ant species richness is correlated with that of other invertebrate groups (Oliver and Beattie 1993; Golden and Crist 2000) In the present experiment ant abundance has been shown to affect aphid abundance (**Chapter II**).

In **Chapter III** I examined the effects of the experimental fragmentation on the density, persistence and spatial distribution of nests of 15 ant species. Three years after initiation of the experiment, ant nest density did not differ between fragments and control plots. Six years after initiation of the experiment, however, ant nest density and density of foraging ants were higher in large fragments than in large control plots. Ant nests tended to occur more frequently along the edge of fragments than in the core area. Persistence time of nests of the most abundant species, *Lasius paralienus* Seifert, tended to be shorter in fragments than in control plots. Furthermore, persistence time was longer in nests situated close to the fragment edge than in nests that were situated in the core area.

Effects on nest density, edge effects on the spatial distribution of nests and the relationships between nest density and environmental factors were more pronounced when only nests of *L. paralienus* were considered. Some of the species in the examined grasslands prefer cooler and moister sites for their nests than *L. paralienus*, while the majority prefer dry and warm nest sites. As a consequence, species-specific responses to the changed environmental conditions in the fragments can be expected.

Theory predicts that abundant species like *L. paralienus* should be less affected by fragmentation than naturally rare species (Davies et al. 2000; Mac Nally and Brown 2001; Gibb and Hochuli 2002). Many common species have broad niches and can exist in disturbed habitat or matrix habitat. Consequently, these species are less affected by the isolation following fragmentation than specialist species (Andrén 1994). Assuming that abundant species benefit from habitat fragmentation then their competitive strength may further increase in fragments. As a result the diversity and density of the other species would decline in fragments. In **Chapter IV** I examined the effect of the experimental fragmentation on competitive interactions among ant species. Ant communities are assumed to be structured mainly by intra- and interspecific competition for resources such as food or suitable nest sites and thus are ideal to study effects of fragmentation on competitive interactions.

Ant density and species composition were assessed 3 and 6 years after initiation of the experimental fragmentation. The effect of the dominant ant species on the resource use of the other species was examined at natural sugar resources (aphids and extrafloral nectaries of *Euphorbia cyparissias* plants) and at artificial sugar baits. The most abundant species *L. paralienus* had 66% of all individuals recorded in pitfall traps and 72% of nests in the experimental plots. The proportion of *L. paralienus* foragers at sugar baits was even greater than that in pitfall traps. As most species foraged at baits this indicates that *L. paralienus* is not only numerically but also functionally dominant.

Species richness and forager density in the other species decreased with increasing *L. paralienus* density in fragments but not in control plots. This indicates an increased effect of the density of the dominant *L. paralienus* on the ant species composition in fragments. Overall, forager density of the other species was positively related to their habitat niche overlap with *L. paralienus*. Thus, competitive interactions may have shaped the ant community on a small-scale, while external factors may become more important on a larger scale. The density of foragers of the other species at sugar resources was not affected by *L. paralienus* forager density. The experimental fragmentation resulted in an increase in natural sugar resources of the ants in fragments. This may have reduced the intensity of competition for sugar resources. The present experiment shows that the grassland fragmentation altered the interactions between the dominant *L. paralienus* and the other ant species. As a consequence the ant species composition in fragments may change in the long-term. A changed ant species composition would then further affect the species composition of those organisms that interact with ants.

The relationship between plant productivity and species richness and invertebrate diversity

Declining biodiversity, as predicted as a consequence of increasing habitat fragmentation, represents one of the most dramatic aspects of anthropogenic global change. However, the ecological implications of this change are poorly understood. Changes induced by the loss of biodiversity at the base of an ecosystem (i. e. plants) should impact higher trophic levels (Knops et al. 1999). In order to understand natural patterns of biodiversity ecologists thus need to examine the relationships between different trophic groups.

The relationships among productivity, species richness and consumer biomass are of fundamental importance for understanding determinants of biodiversity. However, the shape of a relationship may depend on spatial scale. Basically, two types of productivity-diversity relationships have been proposed: (1) monotonic, where diversity increases (but may level off) as productivity increases, and (2) unimodal, where diversity increases with productivity at low levels, but eventually decreases at high productivity (Waide et al. 1999; Mittelbach et al. 2001). The decreased diversity at high productivities has often been attributed to increased competitive exclusion under these conditions (Tilman and Pacala 1993; Rosenzweig 1995). However, several alternative explanations for the occurrence of unimodal curves have been proposed (Abrams 1995; Aarssen 2001). Depending on the range of conditions examined, only a part of the unimodal curve may be expressed (e. g. a negative relationship between productivity and diversity in areas with a high to very high productivity).

In **Chapter V** I examined the relationships between productivity (above-ground phytomass) and plant species richness and between productivity and species richness and biomass of gastropods and grasshoppers at three spatial scales in two successive years. For this project, only the control plots of the fragmentation experiment were used. The three spatial scales were 0.5 m^2 (the two small plots of each block combined), 2.75 m^2 (the two small plots and the medium plot combined) and 23 m^2 (all plots of a block combined).

Species richness of forbs had a unimodal relationship with productivity in sampling units of 0.5 m^2 and was negatively correlated with productivity at the other two scales in one year. In the other year, forb species richness tended to decrease with productivity in sampling units of 23 m^2. No similar relationship was found for grasses. Gastropod biomass had a unimodal relationship with productivity at 0.5 m^2 in the first year. Grasshopper species richness was correlated with forb species richness at scales of 2.75 and 23 m^2. This study demonstrates that

patterns detected between productivity and diversity and between productivity and biomass of consumers depend on the spatial scale of the investigation and vary among years.

References

Aarssen LW (2001) On the correlations and causations between productivity and species richness in vegetation: predictions from habitat attributes. Basic Appl Ecology 2:105-114.

Abrams P (1995) Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? Ecology 76:2019-2027.

Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366.

Balmer O, Erhardt A (2000) Consequences of succession on extensively grazed grasslands for european butterfly communities: rethinking conservation practices. Conserv Biol 14:746-757.

Baur B, Joshi J, Schmid B, Hänggi A, Borcard D, Stary J, Pedroli-Christen A, Thommen GH, Luka H, Rusterholz H-P, Oggier P, Ledergerber S, Erhardt A (1996) Variation in species richness of plants and diverse groups of invertebrates in three calcareous grasslands of the Swiss Jura mountains. Rev Suisse Zool 103:801- 833.

Bestelmeyer BT, Wiens JA (2003) Scavenging ant foraging behavior and variation in the scale of nutrient redistribution among semi-arid grasslands. J Arid Environ 53:373-386.

Cardinale BJ, Palmer MA, Collins SL (2002) Species diversity enhances ecosystem functioning through interspecific facilitation. Nature 415:426-429.

Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S (2000) Consequences of changing biodiversity. Nature 405:234-242.

Christian CE (2001) Consequences of a biological invasion reveal the importance of mutualism for plant communities. Nature 413:635-639.

Collinge SK (2000) Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. Ecology 81:2211-2226.

Davies KF, Margules CR (1998) Effects of habitat fragmentation on carabid beetles: experimental evidence. J Anim Ecol 67:460-471.

Davies KF, Margules CR, Lawrence JF (2000) Which traits of species predict population declines in experimental forest fragments? Ecology 81:1450-1461.

Dean WRJ, Milton SJ, Klotz S (1997) The role of ant nest-mounds in maintaining small-scale patchiness in dry grasslands in Central Germany. Biodivers Conserv 6:1293-1307.

Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. Conserv Biol 14:342-355.

Ellenberg H (1986) Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. Eugen Ulmer, Stuttgart, Germany.

Elton CS (2000) The ecology of invasions by animals and plants. Univ Chicago Press, Chicago, Illinois, USA.

Engelhardt KAM, Ritchie ME (2002) The effect of aquatic plant species richness on wetland ecosystem processes. Ecology 83:2911-2924.

Fischer M, Stöcklin J (1997) Local extinctions of plants in remnants of extensively used calcareous grasslands 1950-85. Conserv Biol 11:727-737.

Gibb H, Hochuli DF (2002) Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biol Conserv 106:91-100.

Golden DM, Crist TO (2000) Experimental effects of habitat fragmentation on rove beetles and ants: patch area or edge? Oikos 90:525-538.

Gonzalez A, Chaneton EJ (2002) Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. J Anim Ecol 71:594-602.

Goverde M, Schweizer K, Baur B, Erhardt A (2002) Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands. Biol Conserv 104:293-299.

Hawkins BA, Porter EE (2003) Does herbivore diversity depend on plant diversity? The case of California butterflies. Am Nat 161:40-49.

Hector A, Joshi J, Lawler SP, Spehn EM, Wilby A (2001) Conservation implications of the link between biodiversity and ecosystem functioning. Oecologia 129:624-628.

Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, Asher J, Huntley B (2002) Responses of butterflies to twentieth century climate warming: implications for future ranges. Proc R Soc Lond B 269:2163-2171.

Hölldobler B, Wilson EO (1990) The Ants. Springer-Verlag, Berlin, Germany.

Holt RD (1996) Food webs in space: an island biogeographic perspective. In Polis GA, Winemiller KO (eds) pp. 313-323 Food webs: integration of patterns dynamics. Chapman and Hall, New York, New York, USA.

Hughes JB, Daily GC, Ehrlich PR (1997) Population diversity: its extent and extinction. Science 278:689-692.

Huston MA (1994) Biological diversity: the coexistence of species on changing landscapes. Cambridge Univ Press, Cambridge, UK.

Joshi J (1994) Patterns of plant species diversity in habitat fragments and effects of isolation and fragment size on plant reproductive capacity. Diploma thesis. Univ Basel, Basel, Switzerland.

Kareiva P (1984) Predator-prey dynamics in spatially structured populations: manipulating dispersal in a coccinellid-aphid interaction. In Levin SA, Hallam TG (eds) pp. 368-389 Mathematical Ecology. Springer-Verlag, Berlin, Germany.

Kareiva P (1987) Habitat fragmentation and the stability of predator-prey interactions. Nature 326:388-390.

Kienzle U (1979) Sukzessionen in brachliegenden Magerwiesen des Jura und des Napfgebietes. PHD thesis. Univ Basel, Basel, Switzerland.

Knops J.MH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E, Groth J (1999) Effects of plant species richness on invasion dynamics, desease outbreaks, insect abundances and diversity. Ecol Lett 2:286-293.

Kruess A, Tscharntke T (1994) Habitat fragmentation, species loss, and biological control. Science 264:1581-1584.

Lacy RC, Lindenmayer DB (1995) A simulation study of the impacts of population subdivision on the mountain brushtail possum *Trichosurus caninus* Ogilby (Phalangeridae: Marsupialia), in South-Eastern Australia. II. Loss of genetic variation within and between subpopulations. Biol Conserv 73:131-142.

Lawton JH (2000) Community ecology in a changing world. Ecology Institute, Oldendorf, Germany.

Lawton JH, May RM (1995) Extinction rates. Oxford Univ Press, Oxford, UK.

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804-808.

Mac Nally R, Brown GW (2001) Reptiles and habitat fragmentation in the box-ironbark forests of central Victoria, Australia: predictions, compositional change and faunal nestedness. Oecologia 128:116-125.

Mason CF (2001) Woodland area, species turnover and the conservation of bird assemblages in lowland England. Biodiv Conserv 10:495-510.

Mittelbach GG, Steiner CF, Scheiner SF, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L (2001) What is the observed relationship between species richness and productivity? Ecology 82:2381-2396.

Niemelä J, Baur B (1998) Threatened species in a vanishing habitat: plants and invertebrates in calcareous grasslands in the Swiss Jura mountains. Biodiv Conserv 7:1407-1416.

Ogermann P, Spycher B, Schaub D, Sollberger R (1994) Die Landschaftsstruktur im Raum Nenzlingen - geoökologisch gesehen. Regio Basiliensis 35:91-100.

Oliver I, Beattie AJ (1993) A Possible Method for the Rapid Assessment of Biodiversity. Conserv Biol 7:562-568.

Purvis A, Hector A (2000) Getting the measure of biodiversity. Nature 405:212-219.

Quinn JF, Hastings A (1987) Extinction in subdivided habitats. Conserv Biol 1:198-208.

Rosenzweig ML (1995) Species diversity in space and time. Cambridge Univ Press, Cambridge, UK.

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Biodiversity - global biodiversity scenarios for the year 2100. Science 287:1770-1774.

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5:18-32.

Schmiegelow, FKA, Machtans CS, Hannon SJ (1997) Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78:1914-1932.

Schürch S, Pfunder M, Roy BA (2000) Effects of ants on the reproductive success of *Euphorbia cyparissias* and associated pathogenic rust fungi. Oikos 88:6-12.

Seifert B (1996) Ameisen beobachten, bestimmen. Naturbuch Verlag, Augsburg, Germany.

Simberloff D (2000) What do we really know about habitat fragmentation. Tex J Sci 52 (Suppl.):5-22.

Steffan-Dewenter I, Tscharntke T (2002) Insect communities and biotic interactions on fragmented calcareous grasslands - a mini review. Biol Conserv 104:275-284.

Tilman D, Pacala S (1993) The maintenance of species richness in plant communities. Pages 13-25 *in* Ricklefs RE, Schluter D (eds) Species diversity in ecological communities: historical and geographical perspectives. Univ Chicago Press, Chicago, Illinois, USA.

Tilman D, Reich PB, Knops J, Wedin D, Mielke T, Lehman C (2001) Diversity and productivity in a long-term grassland experiment. Science 294:843-845.

Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002) Characteristics of insect populations on habitat fragments: a mini review. Ecol Res 17:229-239.

Wahlberg, N, Klemetti T, Selonen V, Hanski I (2002) Metapopulation structure and movements in five species of checkerspot butterflies. Oecologia 130:33-43.

Waide, RB, Willig MR, Steiner CF, Mittelbach GG, Gough L, Dodson SI, Juday GP, Parmenter R (1999) The relationship between productivity and species richness. Ann Rev Ecol Syst 30:257-300.

Western D (1992) The biodiversity crisis - a challenge for biology. Oikos 63:29-38.

Woodruff DS (2001) Declines of biomes and biotas and the future of evolution. Proc Nat Acad Sci USA 98:5471.

Zoller H, Bischof N (1980) Stufen der Kulturintensität und ihr Einfluß auf Artenzahl und Artengefüge der Vegetation. Phytocoenologia 7:33-51.

Zoller H, Wagner C, Frey V (1986) Nutzungsbedingte Veränderungen in Mesobromion-Halbtrockenrasen in der Region Basel - Vergleich 1950-1980. Abh Westf Mus Naturkundemus 48:93-107.

Chapter I

Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation

S. Zschokke, C. Dolt, H.-P. Rusterholz, B. Braschler, P. Oggier, G. H. Thommen, E. Lüdin, A. Erhardt, B. Baur

Oecologia 125: 559-572

S. Zschokke, C. Dolt, H.-P. Rusterholz, B. Braschler, P. Oggier, G. H. Thommen, A. Erhardt, B. Baur

Department of Integrative Biology, Section of Conservation Biology (NLU), University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland

E. Lüdin

F. Hoffmann-La Roche et Cie AG, Abt. PDBS, Grenzacherstrasse, CH-4002 Basel, Switzerland

Abstract

The fragmentation of natural habitats is generally considered to be a major threat to biodiversity. We investigated short-term responses of vascular plants (grasses and forbs) and four groups of invertebrates (ants, butterflies, grasshoppers and gastropods) to experimental fragmentation of calcareous grassland in the north-western Jura mountains, Switzerland. Three years after the initiation of the fragmentation – which was created and maintained by mowing the area between the fragments – we compared species richness, diversity and composition of the different groups and the abundance of single species in fragments of different size (area: 20.25 m^2, 2.25 m^2 and 0.25 m^2) with those in corresponding control plots. The abundances of 19 (29 %) of the 65 common species examined were affected by the fragmentation. However, the experimental fragmentation affected different taxonomic groups and single species to a different extent. Butterflies, the most mobile animals among the invertebrates studied, reacted most sensitively: species richness and foraging abundances of single butterfly species were lower in fragments than in control plots. Of the few other taxonomic groups or single species that were affected by the experimental fragmentation, most had a higher species richness or abundance in fragments than in control plots. This is probably so because the type of fragmentation used is beneficial to some plants via decreased competition intensity along the fragments edges, and because some animals may use fragments as retreats between foraging bouts into the mown isolation area.

Key Words

biodiversity, calcareous grassland, habitat fragmentation, species richness

Introduction

Due to human pressures, many terrestrial habitats are being rapidly changed, destroyed and fragmented, species are becoming extinct and gene pools are reduced – and all this at an increasing and historically unprecedented rate. Habitat fragmentation is generally considered to be one of the major threats to biodiversity (Quinn and Hastings 1987; Bolger et al. 1991; Harrison 1991; Saunders et al. 1991; Seitz and Loeschcke 1991; Margules and Milkovits 1994; Diffendorfer et al. 1995b). Fragmentation reduces the total area of original habitat, creates isolated subpopulations, thus disrupting individual behaviour (e.g. Davies and Margules 1998),

the exchange of genes between populations (e.g. Lacy and Lindenmayer 1995; Gaines et al. 1997), species interactions (e.g. Kruess and Tscharntke 1994; Arango-Velez and Kattan 1997; Lei and Hanski 1997) and ecological processes (e.g. Robinson et al. 1992). Thus, habitat fragmentation can influence an entire suite of processes, ranging from individual behaviour through population dynamics to ecosystem fluxes.

The response of plant and animal species to habitat fragmentation depends on their dispersal behaviour, their demography, their competitiveness, and on the size of the fragments (Kareiva 1987; Saunders et al. 1991; Tilman 1994). Furthermore, habitat fragmentation occurs on many different spatial scales (Simberloff 1988; Lord and Norton 1990; Kareiva and Wennergren 1995), and ranges from small breaks in an otherwise homogeneous habitat to widely scattered fragments in a surrounding area (Wiens 1989). For each species, the relevant spatial scale is different (Forman and Godron 1986; Wiens 1994).

Up to now, few studies have simultaneously examined effects of habitat fragmentation on different taxonomic groups (Robinson et al. 1992). However, only multispecies approaches covering different groups of organisms allow an assessment of species interactions at higher trophic levels. For example, changing plant diversity due to fragmentation may also influence parasite and predator foraging efficiency and the interactions between herbivores and their predators (e.g. Strong et al. 1984; Golden and Crist 1999). Furthermore, most earlier studies of habitat fragmentation have focused on conspicuous animals like large mammals (Bowers et al. 1996; Peacock and Smith 1997), birds (Schmiegelow et al. 1997) and butterflies (Cappuccino and Martin 1997; Sutcliffe et al. 1997), or plants (Holt et al. 1995). Experimental studies on the influence of small-scale fragmentation on less conspicuous animal species are scarce.

The unfertilised calcareous grassland in the north-western Jura mountains in Switzerland harbours a variety of invertebrates and vascular plants (Zoller 1954; Baur et al. 1996). This sensitive habitat type has diminished dramatically during recent decades due to changes in agricultural practices, such as increased fertilisation (Fischer and Stöcklin 1997) or abandonment and reforestation (Zoller and Bischof 1980; Küchli et al. 1999). For example, in the Passwang region 24 km south of Basel, unfertilised grasslands have decreased by 78% between 1950 and 1985 (Zoller et al. 1986). The rapid habitat change and fragmentation of the grasslands have resulted in significant losses of specialist plant species (Fischer and Stöcklin 1997) and the same may be true for invertebrates as well (Baur et al. 1996).

The aim of the present study was to examine effects of habitat fragmentation under experimental, controlled conditions. Large-scale fragmentation, such as occurs on the landscape level is hardly amenable to experimental investigations. However, findings obtained

in a controlled small-scale experiment may to some degree give important insights into the effects of fragmentation at the landscape level.

We investigated the short-term responses of vascular plants (grasses and forbs) and four groups of invertebrates (ants, butterflies, grasshoppers and gastropods) to small-scale experimental grassland fragmentation. In particular, we compared species richness, diversity and composition, and the abundance of single species between fragments of various sizes and corresponding control plots 3 years after the initiation of the fragmentation experiment. We also examined how microclimate and productivity (above-ground biomass) were influenced by fragmentation, and whether productivity was correlated with species richness in plants and four invertebrate groups in the fragments and control plots.

Material and methods

Study sites

The fragmentation experiment was carried out in three calcareous grasslands situated in the region of Basel (47˚ 34' N, 7˚ 35' E) in the north-western Swiss Jura mountains: in Nenzlingen (13 km S of Basel), Movelier (26 km SW of Basel) and Vicques (26 km SSW of Basel). Originally covered by beech forest, these grasslands have been grazed by cattle for many centuries, leading to the characteristic vegetation of the *Teucrio-Mesobrometum* (Zoller 1947; Schläpfer et al. 1998).

The study site in Nenzlingen is situated on a south-west-facing slope with an inclination of 19-22˚ at an altitude of 510 m. A deciduous forest borders the study area to the north-east. Mean annual temperature is around 8.5-9.0 ˚C (the average July temperature is approximately 17 ˚C) and annual precipitation amounts to 900 mm (Ogermann et al. 1994). Snow covers the area for usually less than 1 month. Soils are of the rendzina type with an A-horizon varying in depth from 2 to 27 cm (for details on soil properties and profiles see Ogermann et al. 1994). Until 1993, the site was grazed by cattle from May to September with a high stocking rate. The lower part of the slope was moderately fertilised by cattle dung.

The study site in Movelier is situated on a south-south-east-facing slope (inclination 20-22˚) at an altitude of 770 m. Half of the site is surrounded by deciduous forest. Snow covers the site for usually more than 1 month. The humus layer is thicker than in Nenzlingen, contains some clay and is moister than at the other two sites. Until 1993, the site was grazed by cattle and a moderate amount of artificial fertiliser was used.

The study site in Vicques is situated on a south-east-facing slope (inclination 15-27˚) at an altitude of 590 m. Snow usually covers the area for a few days only. The humus layer is

extremely thin and there are several patches of exposed bedrock (this type of habitat is absent at the other sites). There is mixed deciduous forest at the south-west border of the area. Until 1993, the site was exposed to a low grazing pressure by cattle.

Fragmentation experiment

The experimental fragmentation of the grasslands was created in spring 1993 by mowing the vegetation around the experimental fragments. One experimental unit ("block"), contains one large (4.5 x 4.5 m), one medium (1.5 x 1.5 m) and two small (0.5 x 0.5 m) fragments, all of them separated by a 5-m-wide strip of mown vegetation, as well as the corresponding control plots, which are mirror-symmetrically arranged and surrounded by undisturbed vegetation (Fig. 1). Within each block, the positions of the different sizes of fragment-control plot pairs as well as the control and fragment halves were randomised. The experimental set-up consists of 12 blocks with 48 fragments (24 small, 12 medium and 12 large) and 48 corresponding control plots distributed over the three study sites. Five blocks are situated at Nenzlingen, three blocks at Movelier and four blocks at Vicques. The distances between blocks within the sites range from 25 to 135 m. The distance between sites ranges from 9 to 19 km. At each site, the blocks are part of a larger study area (1.5 - 2 ha) enclosed by a fence to exclude large herbivores. The experimental fragmentation has been maintained since April 1993 by frequently (6-12 times per year) mowing the area between the fragments in the period from March to October. The entire experimental area is mown in late autumn every year to prevent succession (Kienzle 1979).

Field methods

Abundance data on vascular plants, ants, butterflies, grasshoppers and gastropods were collected between March and October 1996 in all fragments and control plots of every block. We used exclusively non-destructive methods, i.e. no plants or animals were removed.

To estimate the abundance of the various plant species, the number of grass and graminoid culms and the number of rooting shoots and rosettes of herbaceous plants were counted in each plot. A grid (0.5 m x 0.5 m) laid over the plots facilitated the counting. Woody plants were regularly removed and are therefore not considered. Each plot was examined three times: in May/June, June/July and August/September. Nomenclature of the vascular plants follows Binz and Heitz (1990). The term "grasses" includes all true grasses (Poaceae) as well as sedges (*Carex* spp.) and rushes (Juncaceae).

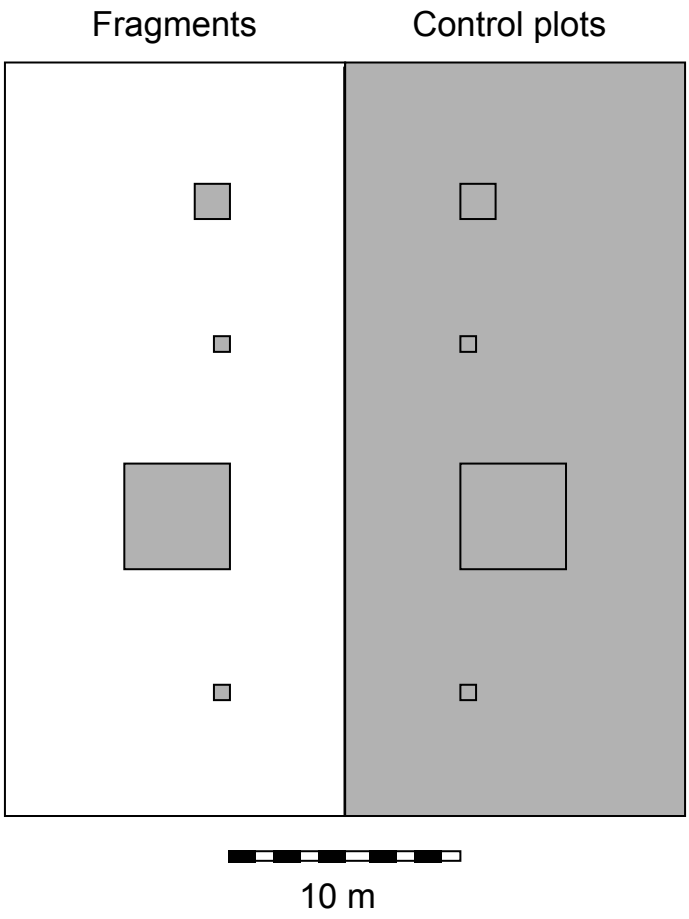


Fig. 1. Diagram of one block of the fragmentation experiment. A block contains two small (0.5 x 0.5 m), one medium (1.5 x 1.5 m) and one large (4.5 x 4.5 m) fragment and corresponding control plots. The isolation area between the fragments (shown in white) is frequently mown.

Nest counts were used as a measure for ant abundance. Nests were detected by carefully searching the whole area of the plots and by setting baits (sugar solution offered in small plastic caps) and following the attracted ants back to their nests. The plots were searched on consecutive days until no further nests were detected. Behavioural clues like fighting helped to distinguish between colonies (nests) of the same species. Ant surveys were made between 12 March and 18 April in Nenzlingen, between 22 April and 17 May in Vicques and between 20 May and 12 June in Movelier. Consequently, seasonal differences in ant activity cannot be excluded during the period of mapping; however, fragments and their corresponding controls were mapped on the same or on succeeding days. Nomenclature of ants follows Seifert (1996).

Butterfly diversity and abundance were recorded at intervals of 10-14 days during the peak flight period between 3 June and 16 August 1996. In each block, butterflies were observed during 13 periods of 30 minutes. Both the number of butterflies and the species were recorded. Observations were conducted only between 10 a.m. and 4.30 p.m. and under the following weather conditions: cloudiness <30%, air temperature >18 ˚C and wind speed ≤ 2 m/sec. Within sites, observation periods were randomised with respect to time of day to avoid any bias due to time-dependent butterfly activity. Nomenclature of butterflies follows Koch (1991) and Lepidopterologen-Arbeitsgruppe (1987).

A direct census method was used to record the relative abundance of the different grasshopper species (including bush crickets). The entire vegetation of the plots was carefully searched for grasshoppers. Plants were slightly moved with a bamboo rod for easier detection of the insects. The number of individuals observed was recorded for each species. Monitoring was repeated three times in all blocks between July and early September 1996. Nomenclature of grasshoppers follows Bellmann (1993).

Wet sheets of cardboard placed in the grassland vegetation attract gastropods (Boag 1981; Oggier et al. 1998). We used this technique to assess the relative abundance of gastropod species. In the evening of a rainy day, sheets of cardboard (measuring 10 x 10 cm) were placed at a distance of 50 cm in the vegetation of the plots (1 cardboard sheet in small plots, 9 in medium plots and 81 in large plots). In the morning of the following day (between 6 and 8 a.m.) the cardboard sheets were checked for adhering gastropods. Specimens were identified in the field and the number of individuals were recorded for each species. Animals were released at the same spot where they were found. Field work was done in autumn when gastropods are most active in dry grasslands (in Nenzlingen on 24-25 September, in Movelier on 6-7 October and in Vicques on 1-2 October 1996). Nomenclature of gastropods follows Kerney et al. (1983).

The above-ground plant biomass was used as a measure of productivity. When the whole study site was mown in late autumn, the plant biomass was clipped at a height of 5 cm above ground level (to preserve the rosettes of several plant species) in all 12 blocks between 6 and 15 October 1996. In the small plots, the entire vegetation was collected. In the other plots, subsamples covering 0.25 m^2 (5 subsamples in medium sized plots and 20 subsamples in large plots) were randomly chosen and the plants harvested. A total of 648 samples were harvested, oven-dried and weighed to the nearest 0.1 gram.

The effect of fragmentation on the ground air temperature was measured using Tinytalk temperature loggers (Gemini Data Loggers, Chichester, UK). Loggers were placed along six transects across the edge of large fragments in Vicques. In each transect, nine loggers were placed at distances of 0, 5, 10, 15 and 25 cm on both sides of the edge of the fragment, i.e. into the vegetation of the fragment and onto the mown area. Temperature was recorded every 10 minutes for 12 d from 31 August to 12 September 1995, a period with no rain and little cloud cover. Loggers placed in the mown area measure temperatures which are close to the surface temperature of the ground (S. Zschokke, unpubl. observations). For comparison, measurements of air temperature were obtained from a recording thermometer in a standard shaded box, 2 m above the ground, situated 30 m away from the fragments.

Data analysis

Two different methods were used to examine possible effects of the grassland fragmentation on species richness, species diversity and productivity. First, species richness (square-root transformed), species diversity (Shannon diversity index) and productivity (dry weight of above-ground biomass, log-transformed) were compared between fragments and control plots using a four-way ANOVA (Table 1). Statistical analyses were performed using the program package SAS 6.08 (SAS Institute 1990). Second, fragments and control plots were compared for each plot size separately using paired *t*-tests. Because of the great variation in the field, we set $\alpha = 0.10$ for all statistical tests. Bonferroni-corrected significance levels for the ANOVAS were set at 0.10 / 7 = 0.0143. Similarly, Bonferroni-corrected significance levels for the *t*-tests were set at 0.10 / 21 = 0.0048. All *P*-values presented are uncorrected.

To determine the effect of fragmentation on the species composition, we calculated the similarity of species composition (log-transformed abundance data) among all large and among all medium plots (fragments and control plots) using the percentage similarity or Renkonen index (Renkonen 1938; Krebs 1999). The percentage similarity is defined as the sum of the shared importance values (percentage within a sample) of each species found in both samples. We compared the percentage similarities between fragments and control plots of the same block with the similarities among all plots with the same treatment and with the similarities among all plots with different treatments, excluding the plots of the same block. Bonferroni corrected significance level was set at 0.10 / 6 = 0.0167.

The effect of fragmentation on the abundance of the 65 common species distributed over all groups of organisms (i.e. species present in at least 10 of the 12 blocks) was assessed using a sign test. The differences were classified either as "strong" (equivalent to a $P < 0.01$, sign

test), "moderate" (equivalent to $P < 0.05$, sign test) or "no difference". This analysis is descriptive, and therefore no Bonferroni correction was applied. Consequently, differences found in species abundance cannot be considered as a proof of a real difference. A list of all species found in this study is given in the Appendix.

The relationships between productivity and species richness and species abundance of the common invertebrates were examined using a two-way ANCOVA with site and fragmentation as factors and productivity (log-transformed) as covariate. For this analysis, only large plots were used, because many species were too rare in medium and small plots. Bonferroni corrected significance levels were set at 0.10 / 7 = 0.0143 for the relationships with species richness and at 0.10 / 22 = 0.0046 for the relationships with species abundance.

Air temperatures were analysed in two ways. First, to evaluate edge effects, the average temperatures and the average minima and average maxima along the transects were compared between neighbouring loggers using unpaired *t*-tests. Second, to assess the microclimatic differences between fragments and the surrounding mown area, data from loggers inside the fragments were pooled and compared with those from loggers in the mown area using unpaired *t*-tests.

Table 1. ANOVA model (Type III) used to analyse the effects of fragmentation on species richness, species diversity and productivity. The interaction Fragmentation * Plot size was omitted when $P > 0.20$.

Source of variation		*df*	*F*	Remark
Site	S	2	MS S / MS B(S)	
Fragmentation	F	1	MS F / MS F*B(S)	
Block(Site)	B(S)	9	MS B(S) / MS F*B(S)	random factor
Plot size	P	2	MS (P) / MS Residual	
Fragmentation * Block(Site)[a]	F*B(S)	11	MS (F*B(S)) / MS Residual	random factor
Fragmentation * Plot size	F*P	2	MS (F*P) / MS Residual	

[a] this term also includes the interaction fragmentation * site

Results

Species richness and diversity

Species richness differed between fragments and control plots in two taxonomic groups. Considering all plot sizes, more grass species and fewer butterfly species were found in fragments compared to the corresponding control plots. Fragments and control plots did not

differ in species richness of forbs, ants, grasshoppers and gastropods (four-way ANOVAs, fragmentation effect, in all cases $P>0.18$).

Considering plots of the same size, small fragments contained more grass species ($t = 3.26$, $n = 24$, $P = 0.004$) than small control plots. In all plot sizes, fragments contained fewer butterfly species than the corresponding control plots (small: $t = 3.47$, $n = 24$, $P = 0.002$; medium: $t = 4.47$, $n = 12$, $P = < 0.001$; large: $t = 4.20$, $n = 12$, $P = 0.002$). In the other taxonomic groups, fragments did not differ in species richness from the corresponding control plots (paired t-test, in all cases $P > 0.11$). Plot size per se significantly affected species richness in all taxonomic groups (Table 2, Fig. 2).

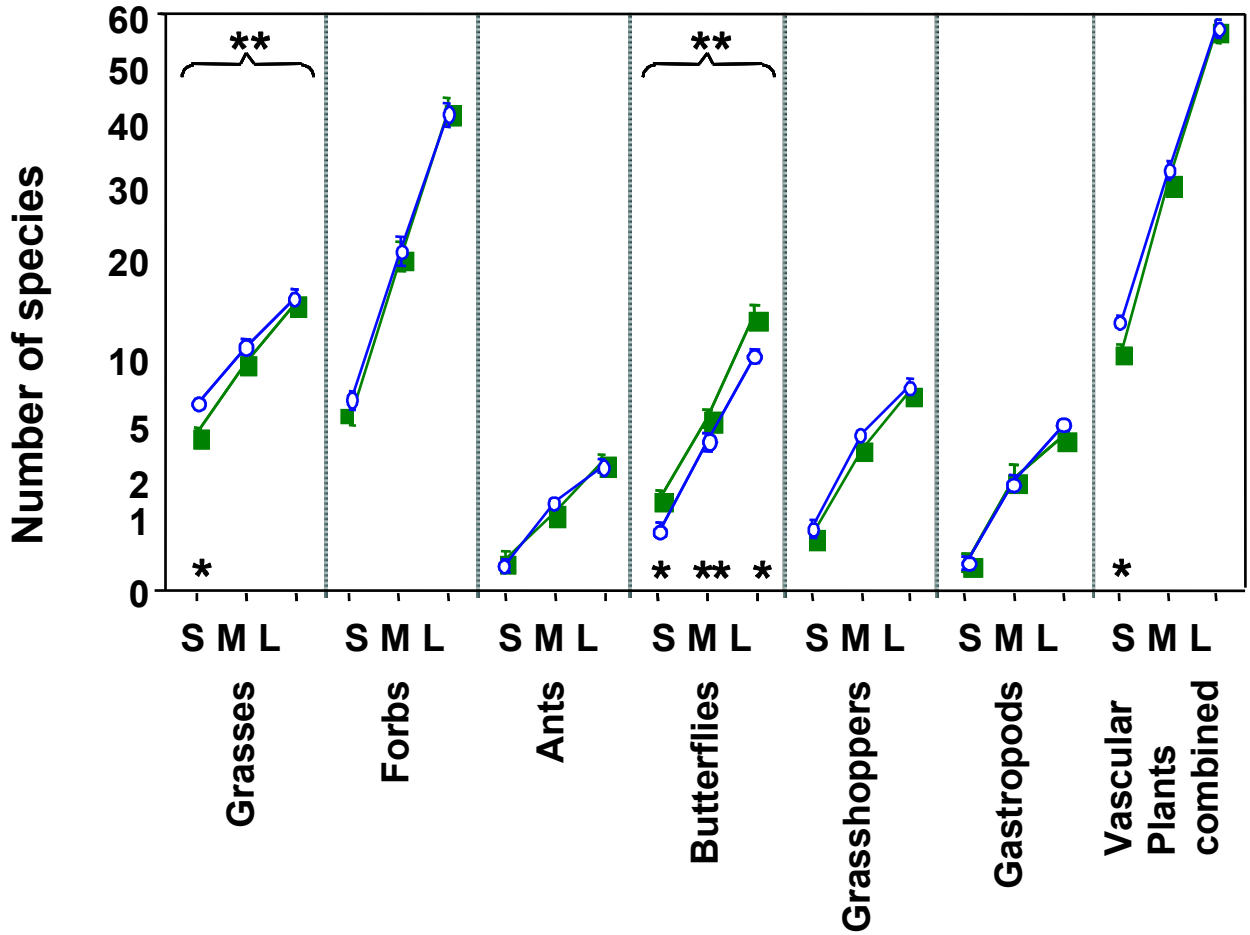


Fig. 2. Species richness (mean ± 1 SE, $\log_{10}(x+1)$ scale) in grasses, forbs and four groups of invertebrates in small (S, $n = 24$), medium (M, $n = 12$) and large (L, $n = 12$) fragments (○) and the corresponding control plots (■). Asterisks indicate differences between fragments and control plots. Those in the upper line refer to the overall difference (ANOVA), those in the lower line to plot size specific differences (paired t-test). * is equivalent to $P < 0.10$, ** $P < 0.01$ (Bonferroni corrected).

Table 2. Summary of analyses of variance testing the effects of different sites (S), experimental fragmentation (F), block (B) and plot size (P) on species richness (square-root transformed) in all taxonomic groups. For details of the model see Table 1. Bonferroni corrected significance levels were set at 0.10 / 7 = 0.0143.

		Grasses		Forbs		Ants		Butterflies		Grasshoppers		Gastropods		Vascular plants combined	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
S	2	14.02	0.002	10.75	0.004	9.12	0.007	4.55	0.043	2.24	0.162	5.01	0.035	3.09	0.095
F	1	9.13	0.009	2.02	0.183	0.26	0.622	34.23	<0.001	2.07	0.178	0.03	0.874	4.24	0.060
B(S)	9	1.47	0.268	4.45	0.012	1.63	0.221	3.48	0.028	3.67	0.023	0.63	0.753	2.84	0.053
P	2	174.46	<0.001	811.73	<0.001	81.22	<0.001	275.33	<0.001	176.43	<0.001	126.48	<0.001	921.95	<0.001
F*B(S)	11	0.85	0.595	1.05	0.417	0.54	0.866	0.73	0.709	0.86	0.585	1.45	0.169	1.35	0.219
F*P	2	1.72	0.188											2.32	0.106

Table 3. Summary of analyses of variance testing the effects of different sites (S), experimental fragmentation (F), block (B) and plot size (P) on species diversity (Shannon index) in all taxonomic groups. For details of the model see Table 1. Bonferroni corrected significance levels were set at 0.10 / 7 = 0.0143.

		Grasses		Forbs		Ants		Butterflies		Grasshoppers		Gastropods		Vascular plants combined	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
S	2	2.75	0.117	7.66	0.011	0.83	0.467	0.90	0.440	0.50	0.621	3.73	0.066	12.38	0.003
F	1	2.17	0.169	0.30	0.598	0.01	0.921	7.21	0.018	1.10	0.317	0.99	0.341	5.20	0.044
B(S)	9	1.04	0.469	1.80	0.177	2.27	0.100	3.26	0.034	5.21	0.006	0.70	0.699	3.28	0.034
P	2	13.81	<0.001	239.39	<0.001	51.18	<0.001	258.83	<0.001	177.49	<0.001	120.78	<0.001	94.87	<0.001
F*B(S)	11	0.84	0.598	1.93	0.049	0.95	0.501	1.05	0.418	0.70	0.732	1.56	0.130	0.73	0.708
F*P	2							2.23	0.115						

We found no significant differences in species diversity between fragments and control plots (Table 3, Fig. 3). Considering plots of the same size, the diversity of butterflies was lower in small fragments than in the corresponding control plots ($t = 3.51$, $n = 24$, $P = 0.002$). In the other taxonomic groups, diversity did not differ significantly between fragments and control plots (paired t-test, in all cases $P > 0.02$). Plot size per se significantly affected species diversity (Table 3, Fig. 3).

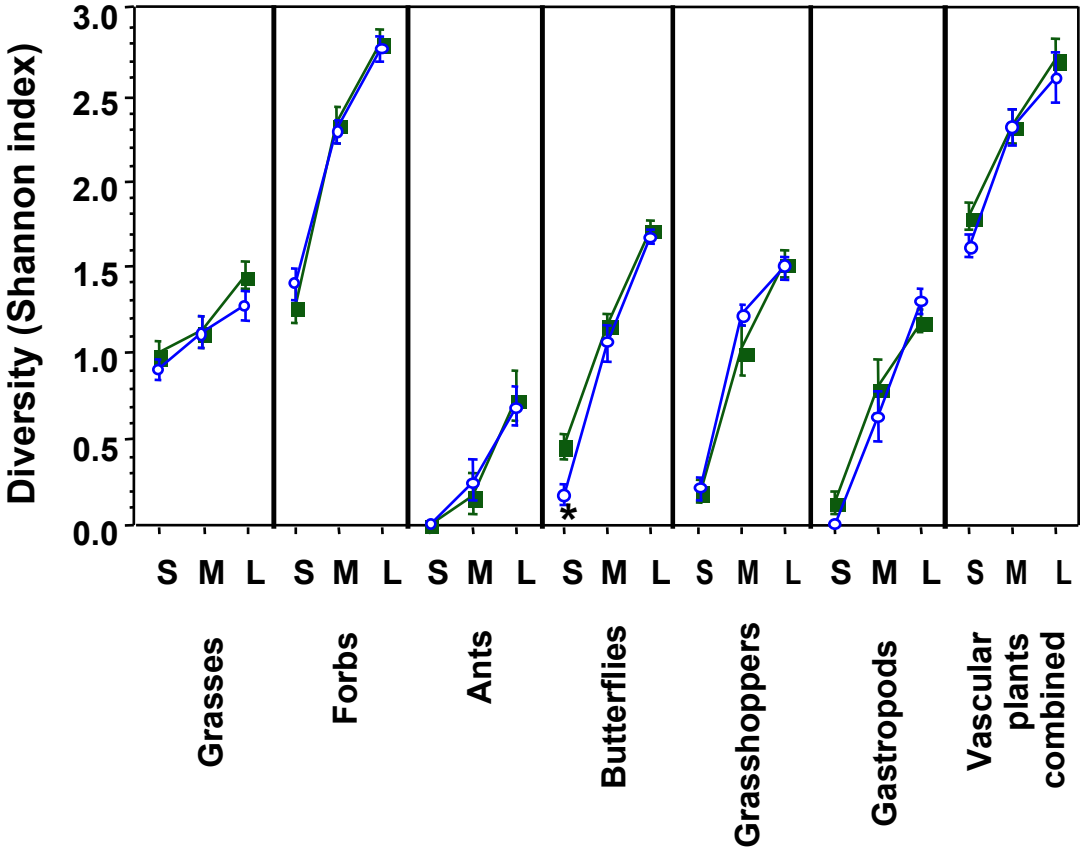


Fig. 3. Species diversity (mean ± 1 SE) in grasses, forbs and four groups of invertebrates in small (S, n = 24), medium (M, n = 12) and large (L, n = 12) fragments (○) and in the corresponding control plots (■). Asterisks indicate differences between fragments and control plots. Those in the upper line refer to the overall difference (ANOVA), those in the lower line to plot size specific differences (paired t-test). * is equivalent to $P < 0.10$, ** $P < 0.01$ (Bonferroni corrected).

Species composition

In general, species composition was more influenced by location of the block than by the experimental fragmentation. In all taxonomic groups, except in ants, the similarity in species

composition was higher between large fragments and corresponding control plots than among all large plots with identical treatment (pairwise comparisons among all large fragments and among all large control plots; Figure 4, $t \geq 3.66$, $df = 22$, $P < 0.0014$ in all cases). This means that the heterogeneity in species composition within and between the study sites was stronger than the fragmentation effect. The average similarity of all pairs of large plots with identical treatments was higher than the average similarity of all pairs of large plots with different treatments (excluding those within the same block) for the butterflies ($t = 2.96$, $df = 22$, $P = 0.007$), indicating that the fragmentation had some influence on the species composition only in this group, even though this effect was much smaller than that of the geographic location. For medium plots, the results were similar (data not shown). For small plots, no comparisons were made (not enough data).

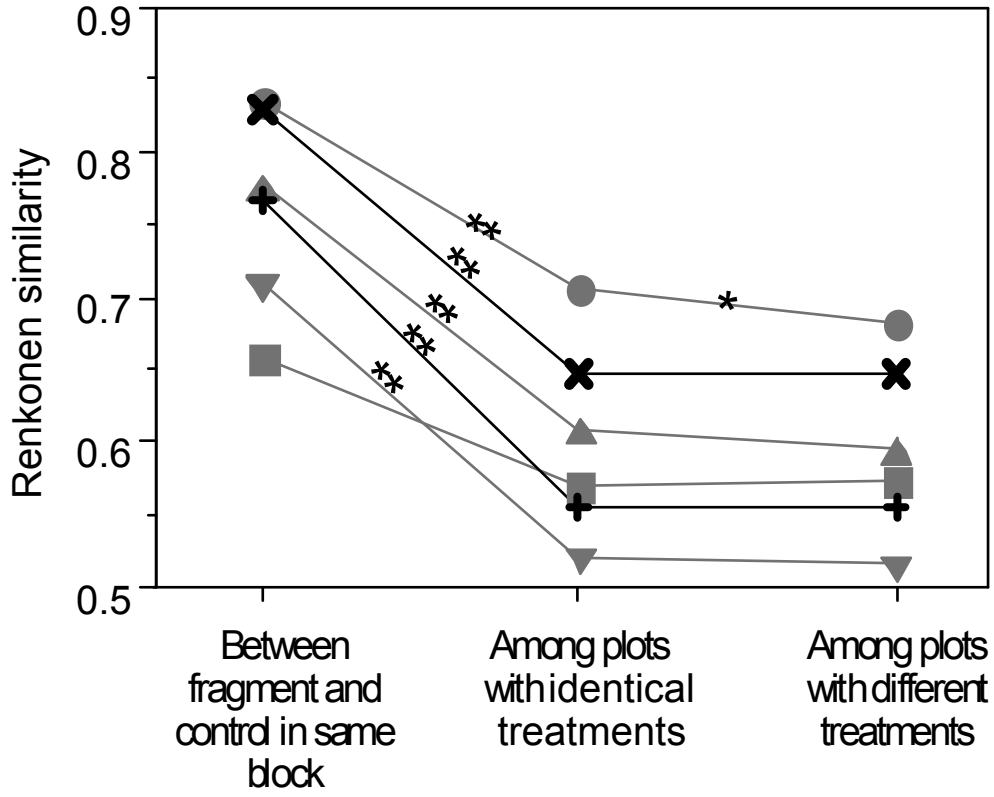


Fig. 4. Comparison of percentage similarities between different large plots for grasses (✖), forbs (✚), ants (■), butterflies (●), grasshoppers (▲) and gastropods (▼). * is equivalent to $P < 0.10$, ** $P < 0.01$ (Bonferroni corrected).

Table 4. List of all common species (present in at least 10 of the 12 blocks) which showed a difference in abundance between fragments and control plots. An asterisk (*) indicates species on the Red List for Switzerland (Landolt 1991; Duelli 1994).

Taxonomic Group	Species	Small plots [a]	Medium plots [a]	Large plots [a]	Overall trend [a]
Grasses	*Bromus erectus*	++	+		++
	Dactylis glomerata	++			+
	Danthonia decumbens	+			
	Luzula campestris			–	
	Phleum pratense				+
Forbs	*Ranunculus bulbosus*	++		+	++
	Sanguisorba minor		+	++	++
Butterflies	*Coenonympha pamphilus*			–	
	Cynthia cardui				–
	Macroglossum stellatarum			––	––
	Maniola jurtina	––	––	––	––
	Melanargia galathea	––	––	––	––
	Ochlodes venatus			––	––
	Polyommatus icarus				–
	Thymelicus sylvestris			––	
	Zygaena filipendulae			––	––
Grasshoppers	*Chorthippus biguttulus*				+
	*Platycleis albopunctata**		++	+	++
	Stenobothrus lineatus			–	–

[a] +/+ + Higher abundance in fragments (moderate/strong); –/– – lower abundance in fragments (moderate/strong)

Species which did not differ in abundance between fragments and control plots:

Grasses: *Agrostis tenuis*, *Brachypodium pinnatum*, *Briza media*, *Carex caryophyllea*, *C. flacca*, *Cynosurus cristatus*, *Festuca ovina*, *F. pratensis*, *Koeleria pyramidata**, *Poa pratensis*

Forbs: *Achillea millefolium*, *Agrimonia eupatoria*, *Betonica officinalis*, *Centaurea jacea*, *Cirsium acaule*, *Daucus carota*, *Helianthemum nummularium*, *Hieracium pilosella*, *Hypericum perforatum*, *Lathyrus pratensis*, *Linum cartharticum**, *Lotus corniculatus*, *Medicago lupulina*, *Plantago lanceolata*, *P. media*, *Potentilla erecta*, *Prunella grandiflora*, *P. vulgaris*, *Teucrium chamaedris*, *Trifolium medium*, *T. montanum**, *T. orcholeucon**, *T. pratense*, *T. repens*, *Veronica officinalis*, *Vicia hirsuta*

Ants: *Lasius paralienus*, *Myrmica sabuleti*

Grasshoppers: *Chorthippus parallelus*, *Metrioptera bicolor**, *Omocestus rufipes**

Gastropods: *Cochlicopa lubrica*, *Deroceras reticulatum*, *Limax* spp., *Trichia plebeia*, *Vertigo pygmaea*

Abundances and densities of single species

Our results suggest that the abundances of 19 (29%) of the 65 common species examined were influenced by habitat fragmentation (Table 4, Fig. 5). Butterflies were most affected: all nine species considered in this analysis foraged less frequently in fragments than in control plots. The two most abundant species, *Melanargia galathea* and *Maniola jurtina*, showed a decrease in foraging activity of 65% and 81% respectively in the small plots. Of the six grasshopper species, three (50%) were affected by the fragmentation: two of them showed a higher density in fragments than in control plots, whereas one species showed a lower density in the fragments. Of the 15 grass species 5 (33%) were also affected by the experimental fragmentation. One of them had a lower density in fragments than in control plots, whereas four had a higher density in the fragments. The density of *Bromus erectus* was 159% higher in small fragments compared with control plots. Of the 28 common forbs, however, only 2 (7%) were affected. Both occurred at a much higher density in the fragments (*Ranunculus bulbosus*, small fragments: + 236%; *Sanguisorba minor*, small fragments: + 184%).

Plant productivity

The productivity measured as above-ground biomass was significantly higher in fragments of all three sizes than in corresponding control plots (Tables 5, 6). Small fragments had on average 80.8% (pairwise comparison) more biomass than the corresponding control plots. In the medium and large plots, the difference was smaller (30.2% and 22.4% respectively), but still highly significant.

Productivity was negatively correlated with species richness of forbs and with that of vascular plants (Table 7, Fig. 6). There was no relationship between productivity and species richness in any other group (grasses: $P = 0.25$, ants: $P = 0.51$, butterflies: $P = 0.45$, grasshoppers: $P = 0.18$, gastropods: $P = 0.82$). Furthermore, there were no significant relationships between productivity and the abundance of any invertebrate species ($P > 0.02$).

Air temperature on ground surface

Along the transect across the edge of a large fragment, the average ground air temperature did not differ significantly within distances of 5-10 cm (Fig. 7). When temperature data measured in the mown area were pooled and compared with those measured in the fragment vegetation, the average temperature in the mown area (15.6 ˚C, SD = 0.3) was slightly (0.7 ˚C) higher than that in the fragment vegetation (14.9 ˚C, SD = 0.3; $t = 7.13$, $n = 22$, $P < 0.001$). However, average daily maximum ground air temperatures differed strongly between the fragment and the surrounding mown area with a sharp change at the edge of the fragment (Fig. 7). Overall,

the average daily maximum temperature was lower inside the fragments (pooled data: 26.2 ˚C, SD = 2.6) than in the mown area (36.5 ˚C, SD = 1.9; $t = 14.92$, $n = 22$, $P < 0.001$). Similarly, the average daily minimum temperatures changed abruptly at the edge of the fragment (Fig. 7). The daily minimum temperature in the fragment (pooled data: 10.5 ˚C, SD = 0.6) was higher than the corresponding value in the mown area (8.5 ˚C, SD = 0.5; $t = 12.48$, $n = 22$, $P < 0.001$). The minimum temperatures measured on the ground surface were lower than the minimum air temperatures recorded under standard conditions, whereas the maximum temperatures on the ground surface were higher than those measured under standard conditions, indicating the large temperature variations on the ground surface.

Table 5. Summary of ANOVAs testing the effects of different sites (S), experimental fragmentation (F), block (B) and plot size (P) on above-ground biomass (g/m^2, log-transformed).

Source of variation	*df*	MS	*F*	*P*
S	2	0.714	3.98	0.058
F	1	2.130	30.51	<0.001
B(S)	9	0.179	2.54	0.074
P	2	0.103	1.67	0.196
F*B(S)	11	0.071	1.15	0.336
F*P	2	0.257	4.20	0.019

Table 6. Above-ground biomass (mean ± SE, in g/m^2 dry weight) in small, medium and large fragments and the corresponding control plots. *t*-values were calculated using a paired *t*-test on log-transformed data.

Plot size	Control plot	Fragment	*n*	*t*	*P*
Small	227.4 ± 15.7	379.0 ± 25.9	24	5.89	<0.001
Medium	261.8 ± 18.7	336.4 ± 29.4	12	3.74	0.003
Large	234.6 ± 13.3	284.7 ± 17.5	12	5.89	<0.001

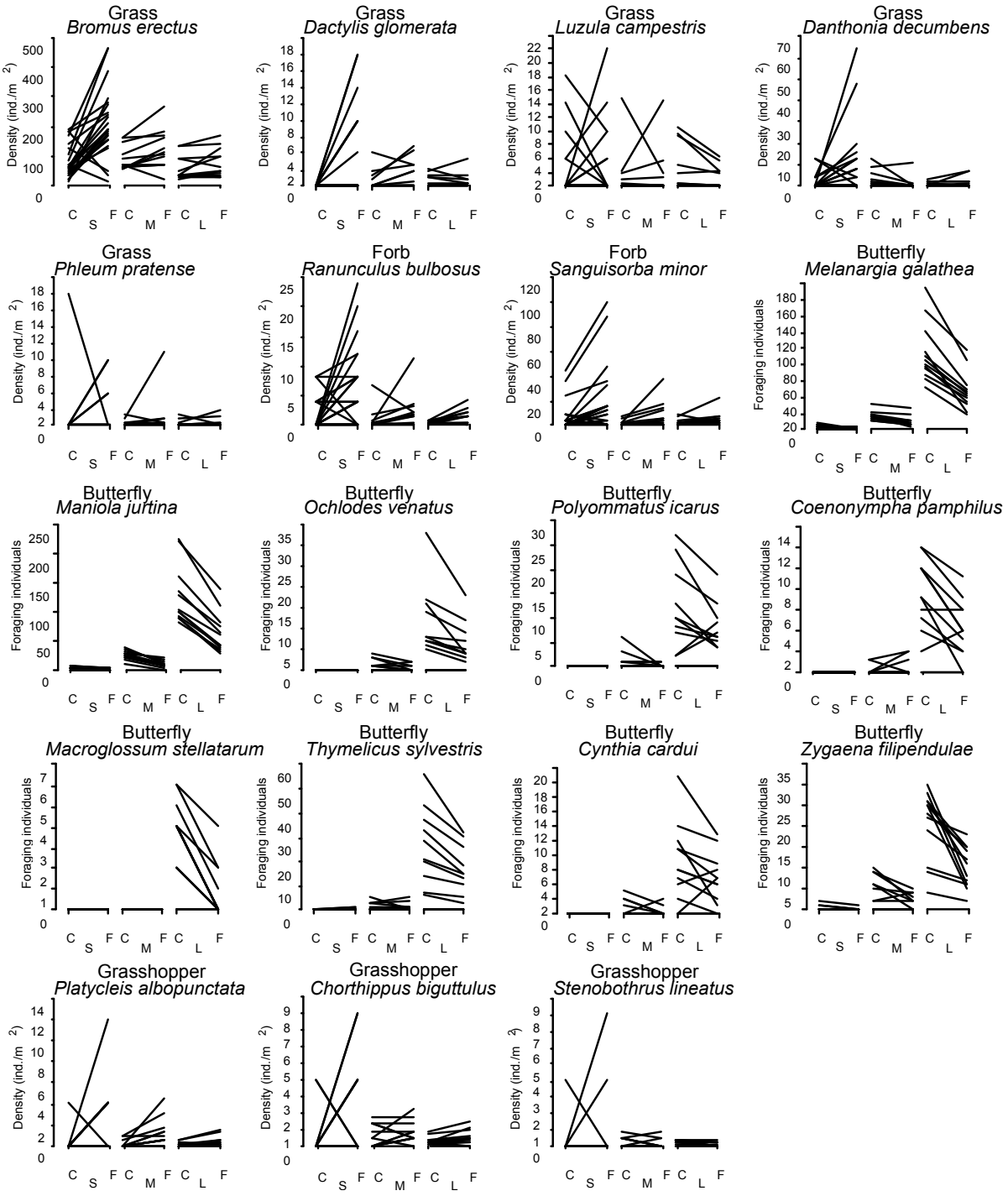


Fig. 5. Pairwise comparison of the density of all common species (present in at least 10 of the 12 blocks) which showed a difference in abundance between fragments (F: small [S], medium [M] and large [L]) and corresponding control plots (C). Lines connect fragments with the corresponding control plots in the same block. In butterflies the total number of foraging individuals observed over a period of 6.5 hours is shown.

Table 7. Results of a two-way ANCOVA examining the relationship between productivity (R, measured as above-ground dry biomass, log-transformed) and species richness of forbs and of vascular plants combined (square-root transformed). The factors site (S) and fragmentation (F) were considered. Bonferroni corrected significance levels were set at 0.10 / 7 = 0.0143.

Source of variation		Forbs			Vascular plants combined		
	df	MS	*F*	*P*	MS	*F*	*P*
S	2	1.70	10.06	0.001	1.36	9.10	0.002
F	1	0.37	2.21	0.153	2.83	3.17	0.091
R	2	1.22	7.28	0.014	0.40	8.03	0.011

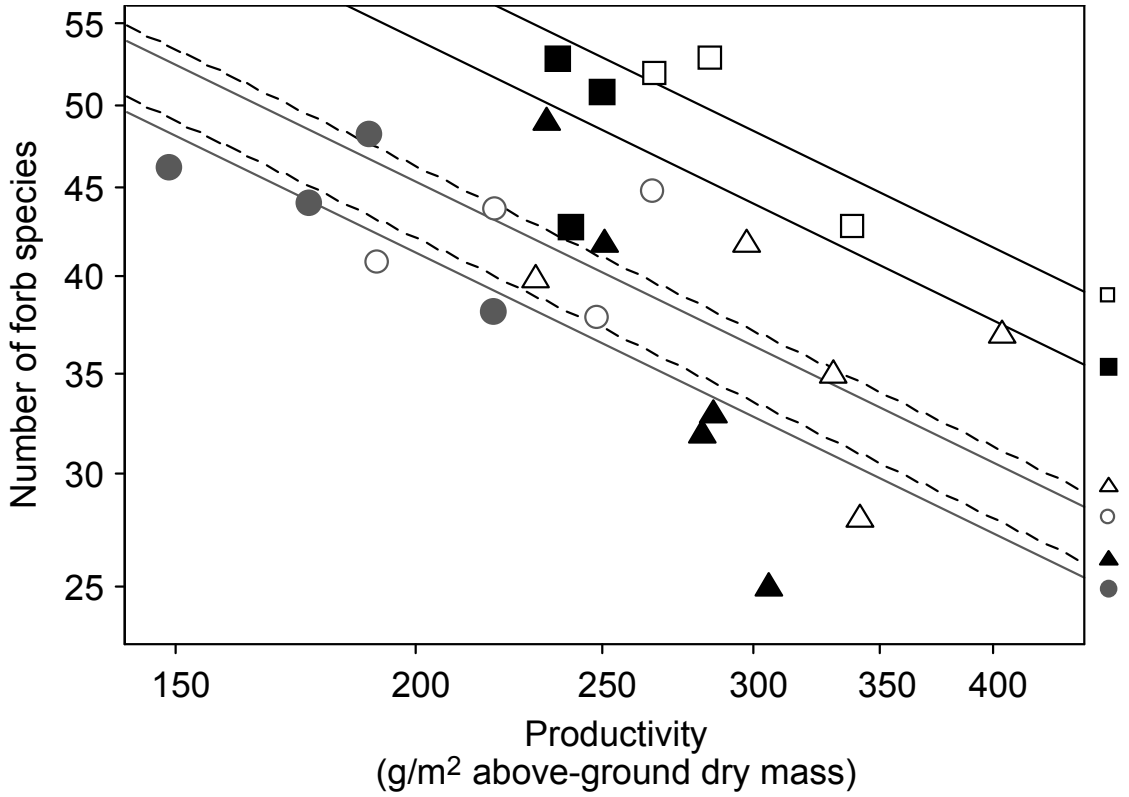


Fig. 6. Relationship between forb species richness (square-root transformed) and productivity (log-transformed) in large patches. Empty symbols refer to fragments, filled symbols denote control plots. Triangles refer to patches in Nenzlingen, squares to patches in Movelier and dots to those in Vicques. The lines shown are the regression lines based on the two-way ANCOVA (Table 7). The small symbol at the right hand side indicates to which group each line belongs.

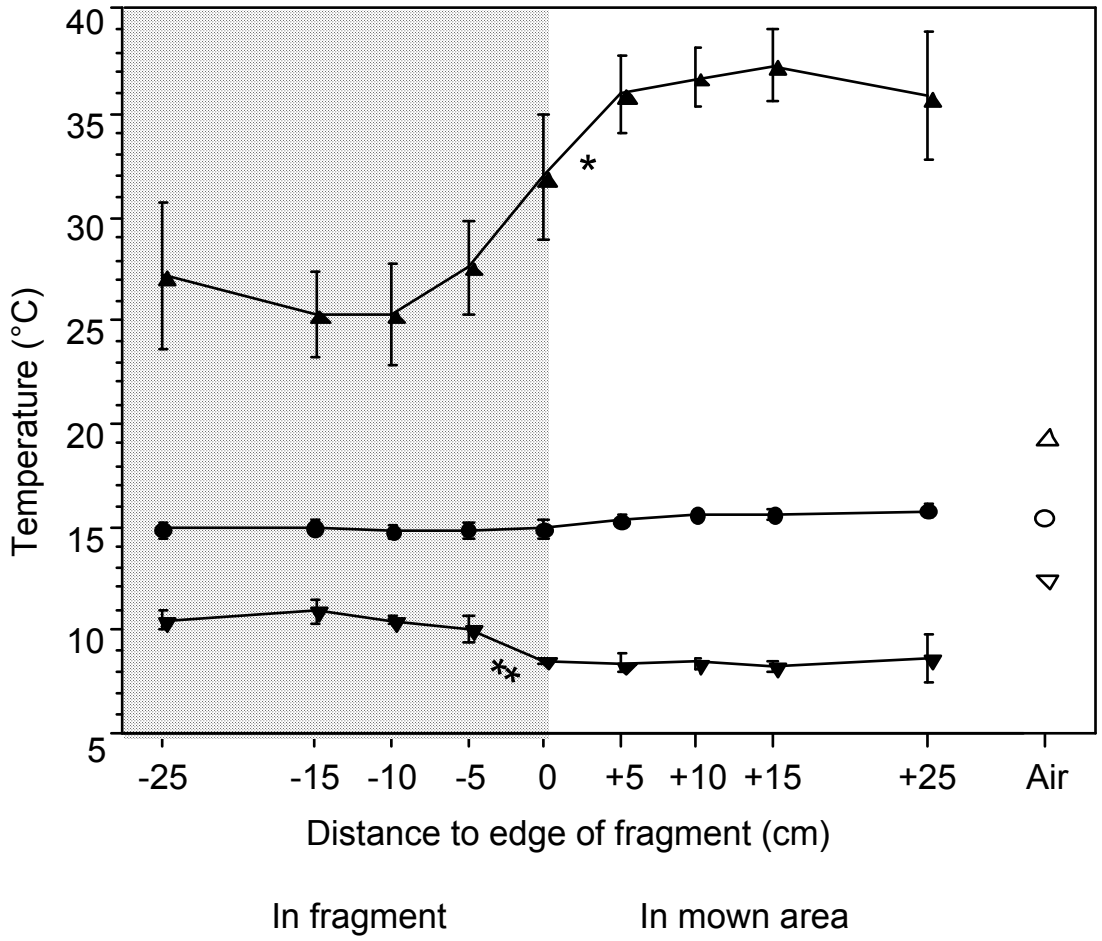


Fig. 7. Ground air temperature (black symbols, mean ± 1 SD) along six transects across the edge of large fragments and air temperature (open symbols) measured 2 m above ground in a standard shaded box. ▲ indicates average daily maximum temperature, ● average temperature and ▼ average daily minimum temperature. * indicates $P < 0.05$, ** $P < 0.01$ (*t*-test)

Discussion

This study shows that the experimental fragmentation over three years affected different species and groups to a different extent. Butterflies, the most mobile group examined, reacted most sensitively: both species richness and foraging abundance of single species were lower in fragments than in corresponding control plots. Most of the other groups or species that were influenced by the fragmentation had a higher species richness or abundance in the fragments. This can be explained by a so-called "retreat effect". For several animal species, the mown area surrounding the fragments is no longer the preferred habitat, but it may still function as foraging area. Thus the animals spend most of their life in a fragment, but leave it to forage.

Ambush predators like the sand lizard *Lacerta agilis* and workers of various ant species are examples (G.H. Thommen, unpubl. data; B. Braschler unpubl. data). As a consequence, the species richness and abundance in the fragments will increase in these species. Reactions to habitat fragmentation were in most cases species-specific, as found in other studies (Margules and Milkovits 1994; Diffendorfer et al. 1995a; Davies and Margules 1998).

Habitat patches are parts of a landscape mosaic and the presence of plant species may depend on the initial composition of the plant community, history of the patch, patch size, type of neighbouring habitat, isolation, and other factors (Andrén 1996). The calcareous grasslands at the three study sites had similar numbers of coexisting plant species (Baur et al. 1996). However, the composition of the plant communities differs among sites with only 53.8% of all species occurring at all three sites (Baur et al. 1996). Diversity indices assessed in the first year of the experiment (1993) were also similar for the three sites, indicating that similar environmental and ecological factors were influencing these communities (Joshi 1994, J. Joshi personal communication).

Three years after the initiation of the experiment, we recorded more grass species in fragments, especially in the small ones, than in the corresponding control plots. No such differences were found in forbs. This suggests that fragmentation influenced plant communities at the level of the smallest plots within a period of 3 years. The abundance of 5 of the 15 common grasses differed between fragments and control plots. This difference was most pronounced in *Bromus erectus* which seems to benefit from the conditions in the fragments, most probably because of a reduced competition for light. Another factor that could positively influence *B. erectus* is the change of grassland management from grazing to mowing at the beginning of the experiment. Tufts of *B. erectus* grow better on mown than on grazed grasslands (Zoller 1954; Schläpfer et al. 1998). *Dactylis glomerata* also occurred in higher densities in fragments than in control plots. However, in contrast to *B. erectus*, the density of *D. glomerata* decreased in the control plots since the beginning of the experiment in 1993 (Joshi 1994, J. Joshi personal communication).

Only two forb species, *Sanguisorba minor* and *Ranunculus bulbosus*, both typical species of calcareous grasslands, differed in abundance between fragments and control plots. Both occurred in higher densities in fragments than in control plots. Compared with the densities at the beginning of the experiment, the densities of *S. minor* increased in the fragments, whereas the density of *R. bulbosus* decreased in the control plots. The increase of the density of *S. minor* in the fragments can be explained by better light conditions in the fragments in combination with the ability of *S. minor* to overcome summer droughts with its

long tap-root (Grime et al. 1988). In contrast, *R. bulbosus* prefers grasslands where shading is prevented by heavy grazing (Grime et al. 1988), a situation no longer present in the control plots.

In ants and gastropods, we neither detected any difference in species richness and diversity nor in the abundance of single species between fragments and control plots. A few ant species (e.g. *Lasius paralienus* and *Solenopsis fugax*) seemed to benefit from mowing, but most ant species are too rare in the study sites (of three species only a single nest was found) to allow statistical analysis. In gastropods, between-site differences in species composition were more pronounced than the effects of habitat fragmentation. A more detailed study using mark-release-recapture techniques showed that habitat fragmentation affected plot occupancy, extinction and colonisation rates and population sizes in land snails (Oggier 1999). Three of six snail species were found less frequently in fragments than in control plots, whereas three other species were not affected by the experimental fragmentation.

A total of 19 butterfly species were recorded foraging in the fragments and 29 species in the control plots. This indicates that even small-scale fragmentation reduces butterfly species richness. The decline in species richness in the fragments was rather unexpected, since butterflies are the most mobile species investigated in the present study. Of the 29 species 14 were rare, with less than 20 individuals recorded during the entire observation period. Individuals of these rare species were patchily distributed in the investigation area, but preferred to forage in the continuous grassland (control plots). Since species richness of butterflies is mainly determined by rare species, the observed decline in species richness in the fragments concerns particularly rare species. Thus, fragmentation had a particularly adverse effect on rare butterfly species.

Several studies have shown that the abundance and distribution of larval host plants and nectar source plants determine the abundance and distribution of butterfly species (Murphy et al. 1983; Lörtscher et al. 1995). In our study, however, the composition and abundance of larval food plants and nectar plants did not differ between fragments and control plots and we recorded an increase in flower offer (forbs had more flowers per individual) in the fragments (H.–P. Rusterholz, unpubl. data). Consequently, we expected to observe more butterflies in the fragments. The smaller number of foraging butterflies in the fragments was probably caused by behavioural inhibition of the butterflies crossing the mown isolation areas or by reduced attractiveness of the fragments as a result of their small size compared with the control area. Even though butterflies have the physical ability to disperse over long distances, their reduced flower visitation rate in spite of an increased flower offer in the fragments shows that an

unsuitable matrix surrounding the fragments can become an effective barrier for the movement of butterflies as well as of other animals (Mader 1984).

Separate analyses of the nine common butterfly species showed a reduced foraging abundance in the fragments. Moreover, different butterfly species differed in the observed response to fragmentation. In the statistical analysis, the most abundant species *Maniola jurtina* and *Melanargia galathea* showed the strongest reaction, whereas the less abundant species *Cynthia cardui* and *Coenonympha pamphilus* exhibited the weakest responses to the experimental fragmentation (Table 4). However, this difference may well be the result of a sample size artefact. The among-species difference in response to fragmentation is partly due to differences in foraging abundance (cf. Fig. 5). Detailed field observations revealed that butterflies exhibit different foraging behaviours in the fragments and the control plots (H.–P. Rusterholz, unpubl. data). Our results parallel findings in the skipper butterfly *Hesperia comma*, which showed an increasing probability for re-colonisation of suitable habitat (and a declining probability for extinction) with increasing patch size (Thomas and Jones 1993). Furthermore, the observed response of butterflies to small-scale fragmentation may well be an example of the foraging patterns of other animals that need larger areas for foraging, such as migrating birds. Thus, fragmentation and reduction of foraging grounds will generally affect and reduce foraging in animals and hence reduce their fitness and population size, which in turn might lead to inbreeding and the accompanying deleterious effects as was recently observed in Glanville fritillary butterflies (*Melitaea cinxia*; Saccheri et al. 1998). Island size and the degree of plant specialisation affected also pollination success in hummingbird pollinated plants. Pollination in a generalised plant (*Justicia secunda*, Acanthaceae) was not affected by island size, whereas in the specialised *Mandevilla hirsuta* (Apocynaceae) pollination and hence fruit set were significantly reduced in a small compared with a large island (Linhart and Feinsinger 1980). Jennerston (1988) also found a reduced pollinator activity and hence reduced seed sets in fragmented, small populations of *Dianthus deltoides* in Sweden.

A significant effect of fragmentation was also found in the bushcricket *Platycleis albopunctata*, the most efficient flyer among the orthopterans studied. In contrast to butterflies, however, *P. albopunctata* occurred more frequently in the fragments. Since *P. albopunctata* had a somewhat higher abundance in plots with low productivity, we can conclude that it does not prefer fragments because of their higher productivity. We rather suggest that this species uses the fragments as retreats and forages in the mown isolation area. *P. albopunctata* is a thermophilic species that prefers dry habitats with a mosaic of varying plant densities and

heights (e.g. Harz 1957). This type of diverse habitat is better represented in fragments surrounded by mown area than in the more homogeneous control area. A similar, but less pronounced influence of fragmentation was observed in the grasshopper *Chorthippus biguttulus* in 1994-1996. This very common species occupies a much wider niche (temperature, air humidity and vegetation structure) and was also found in relatively high densities in the mown area between the fragments.

Habitat fragmentation affects the ecology of plants in many ways. For example, rain forest fragments in central Amazonia were found to experience a dramatic loss of above-ground tree biomass that was not offset by recruitment of new trees (Laurance et al. 1997). In our experiment, fragments had an increased above-ground biomass which was most likely the result of an edge effect. In large and medium fragments, the above-ground biomass was on average 6% higher in samples collected at the edge than in samples from the centre of the fragments (C. Dolt, unpubl. data). Plants at the edge may experience less competition for light and nutrients. It is also possible that interactions among plants are altered at the fragment edge due to differences in microclimatic conditions. The observed negative correlation between productivity and species richness of forbs can be explained by competitive interactions between grasses and forbs. High productivity was associated with a high density of grasses which displaced many forbs.

The average air temperatures differed only slightly between fragments and the surrounding mown area. However, temperature fluctuations were more pronounced in the mown area than in the fragments. We found no differences among the temperatures measured inside the fragment or among those measured inside the mown area. This indicates that the temperature change at the edge of the fragment occurred within less than 5 cm from the fragment edge. Inside the fragments, temperature was mainly influenced by the vegetation cover.

To summarise, taxonomic groups and single species which benefited from the conditions in the mown isolation area (e.g. some plants and grasshoppers) were more abundant in the fragments, whereas species for which the isolation area was disadvantageous (e.g. butterflies) occurred less frequently in fragments. Within groups of organisms, reactions to experimental habitat fragmentation were species-specific. For many species, the period of 3 years between the initiation of the experiment and the present study was probably too short to show a detectable reaction.

The extremely low abundance of rare species does not allow any statistical analysis of a single rare species. However, since rare species are the main determinant of species richness,

we may conclude that the experimental fragmentation had an adverse effect on rare invertebrates, especially butterflies.

In conclusion, despite the short time frame of the present study, we did find some changes in plant and invertebrate abundance and species richness. The study also revealed pronounced edge effects which could cause the increase in plant productivity in the fragments. Interestingly, the most mobile organisms investigated in our study, the butterflies, showed the strongest negative effect to small-scale habitat fragmentation. This shows (1) that butterflies are sensitive indicators of habitat change, and (2) that they may serve as model organisms for potential reactions of other species (e.g. birds) to large-scale habitat fragmentation.

Acknowledgements

We are grateful to Christoph Seibert, Stephan Ledergerber, Salome Schüpbach, Michel Wurtz and numerous students for field assistance and to Bernhard Seifert and Cesare Baroni Urbani for help with species determinations of ants. We thank Paul Jordan for statistical advice, and Ann Rypstra, Christoph Jäggi, Ian Sanders and two anonymous reviewers for helpful comments on the manuscript. This work is part of the Swiss Priority Programme Environment supported by the Swiss National Science Foundation (grants 5001-44620 to B. Baur and 5001-46622/1 to A. Erhardt).

References

Andrén H (1996) Population responses to habitat fragmentation: statistical power and the random sample hypothesis. Oikos 76:235-242

Arango-Velez N, Kattan GH (1997) Effects of forest fragmentation on experimental nest predation in Andean cloud forest. Biol Conserv 81:137-143

Baur B, Joshi J, Schmid B, Hänggi A, Borcard D, Stary J, Pedroli-Christen A, Thommen GH, Luka H, Rusterholz H-P, Oggier P, Ledergerber S, Erhardt A (1996) Variation in species richness of plants and diverse groups of invertebrates in three calcareous grasslands of the Swiss Jura mountains. Rev Suisse Zool 103:801-833

Bellmann H (1993) Heuschrecken beobachten – bestimmen. Naturbuch Verlag, Augsburg

Binz A, Heitz C (1990) Schul- und Exkursionsflora für die Schweiz, mit Berücksichtigung der Grenzgebiete: Bestimmungsbuch für die wildwachsenden Gefässpflanzen. Schwabe, Basel

Boag DA (1981) Overcoming sampling bias in studies of terrestrial gastropods. Can J Zool 60:1289-1292

Bolger DT, Alberts AC, Soulé ME (1991) Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. Am Nat 137:155-166

Bowers MA, Matter SF, Dooley Jr. JL, Dauten JL, Simkins JA (1996) Controlled experiments of habitat fragmentation: a simple computer simulation and a test using small mammals. Oecologia 108:182-191

Cappuccino N, Martin MA (1997) The birch tube-maker *Acrobasis betulella* in a fragmented habitat: The importance of patch isolation and edges. Oecologia 110:69-76

Davies KF, Margules CR (1998) Effects of habitat fragmentation on carabid beetles: Experimental evidence. J Anim Ecol 67:460-471

Diffendorfer JE, Gaines MS, Holt RD (1995a) Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). Ecology 76:827-839

Diffendorfer JE, Slade NA, Gaines MS, Holt RD (eds) (1995b) Population dynamics of small mammals in fragmented and continuous old-field habitat. Univ Minnesota Press, St. Paul, Minneapolis

Duelli P (1994) Rote Listen der gefährdeten Tierarten in der Schweiz. Bundesamt für Umwelt, Wald und Landschaft, Bern

Fischer M, Stöcklin J (1997) Local extinctions of plants in remnants of extensively used calcareous grasslands 1950-85. Conserv Biol 11:727-737

Forman RTT, Godron M (1986) Landscape Ecology. John Wiley, New York

Gaines MS, Diffendorfer JE, Tamarin RH, Whittam TS (1997) The effects of habitat fragmentation on the genetic structure of small mammal populations. J Hered 88:294-304

Golden DM, Crist TO (1999) Experimental effects of habitat fragmentation on old-field canopy insects: community, guild and species responses. Oecologia 118:371-380

Grime JP, Hodgson JG, Hunt R (1988) Comparative Plant Ecology. Unwin Hyman, London

Harrison S (1991) Local extinction in a metapopulation context: an empirical evaluation. Biol J Linn Soc 42:73-88

Harz K (1957) Die Geradflügler Mitteleuropas. VEB G. Fischer Verlag, Jena

Holt RD, Robinson GR, Gaines S (1995) Vegetation dynamics in an experimentally fragmented landscape. Ecology 76:1610-1624

Jennersten O (1988) Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. Conserv Biol 2:359-366

Joshi J (1994) Patterns of plant species diversity in habitat fragments and effects of isolation and fragment size on plant reproductive capacity. Diploma thesis, Univ Basel

Kareiva P (1987) Habitat fragmentation and the stability of predator-prey interactions. Nature 326:388-390

Kareiva P, Wennergren U (1995) Connecting landscape patterns to ecosystem and population processes. Nature 373:299-302

Kerney MP, Cameron RAD, Jungbluth JH (1983) Die Landschnecken Nord- und Mitteleuropas. Parey, Berlin

Kienzle U (1979) Sukzessionen in brachliegenden Magerwiesen des Jura und des Napfgebietes. PhD thesis, Univ Basel

Koch M (1991) Wir bestimmen Schmetterlinge. J. Neumann, Leipzig

Krebs CJ (1999) Ecological Methodology. Benjamin/Cummings, Menlo Park

Kruess A, Tscharntke T (1994) Habitat fragmentation, species loss, and biological control. Science 264:1581-1584

Küchli C, Bolliger M, Rüsch W (1999) Schweizer Wald wird älter, vielfältiger und vorratsreicher. Umweltschutz 1999:10-16

Lacy RC, Lindenmayer DB (1995) A simulation study of the impacts of population subdivision on the mountain brushtail possum *Trichosurus caninus* Ogilby (Phalangeridae: Marsupialia), in South-eastern Australia: II. Loss of genetic variation within and between subpopulations. Biol Conserv 73:131-142

Landolt E (1991) Rote Liste. Gefährdung der Farn- und Blütenpflanzen in der Schweiz. Bundesamt für Umwelt, Wald und Landschaft, Bern

Laurance WF, Laurance SG, Ferreira LV, Rankin-de Merona JM, Gascon C, Lovejoy TE (1997) Biomass collapse in Amazonian forest fragments. Science 278:1117-1118

Lei G-C, Hanski I (1997) Metapopulation structure of *Cotesia melitaearum*, a specialist parasitoid of the butterfly *Melitaea cinxia*. Oikos 78:91-100

Lepidopterologen-Arbeitsgruppe (1987) Tagfalter und ihre Lebensräume. Schweizerischer Bund für Naturschutz, Basel

Linhart YB, Feinsinger P (1980) Plant-hummingbird interactions: effects of island size and degree of specialization on pollination. J Ecol 68:745-760

Lord JM, Norton DA (1990) Scale and the spatial concept of fragmentation. Conserv Biol 4:197-202

Lörtscher M, Erhardt A, Zettel J (1995) Microdistribution of butterflies in a mosaic-like habitat: The role of nectar sources. Ecography 18:15-26

Mader HJ (1984) Animal habitat isolation by roads and agricultural fields. Biol Conserv 21:81-96

Margules CR, Milkovits GA (1994) Contrasting effects of habitat fragmentation on the scorpion *Cercophonius squama* and an amphipod. Ecology 75:2033-2042

Murphy DD, Launer AE, Ehrlich PR (1983) The role of adult feeding in egg production and population dynamics of the checkerspot butterfly, *Euphydryas editha*. Oecologia 56:257-263

Ogermann P, Spycher B, Schaub D, Sollberger R (1994) Die Landschaftsstruktur im Raum Nenzlingen - geoökologisch gesehen. Regio Basiliensis 35:91-100

Oggier P (1999) Effects of habitat fragmentation on the population dynamics of land snail species. PhD thesis, Univ Basel

Oggier P, Zschokke S, Baur B (1998) A comparison of three methods for assessing the gastropod community in dry grasslands. Pedobiologia 42:348-357

Peacock MM, Smith AT (1997) The effect of habitat fragmentation on dispersal patterns, mating behavior, and genetic variation in a pika (*Ochotona princeps*) metapopulation. Oecologia 112:524-533

Quinn JF, Hastings A (1987) Extinction in subdivided habitats. Conserv Biol 1:198-208

Renkonen O (1938) Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. Ann Zool Soc Bot Fenn Vanamo 6:1-231

Robinson GR, Holt RD, Gaines MS, Hamburg SP, Johnson ML, Fitch HS, Martinko EA (1992) Diverse and contrasting effects of habitat fragmentation. Science 257:524-526

Saccheri I, Kuussaari M, Kankare M, Vikman P, Fortelius W, Hanski I (1998) Inbreeding and extinction in a butterfly metapopulation. Nature 392:491-492

SAS Institute (1990) SAS/STAT user's guide: version 6. SAS Institute, Cary,

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5:18-32

Schläpfer M, Zoller H, Körner C (1998) Influences of mowing and grazing on plant species composition in calcareous grassland. Bot Helv 108:57-67

Schmiegelow FKA, Machtans CS, Hannon SJ (1997) Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78:1914-1932

Seifert B (1996) Ameisen beobachten, bestimmen. Naturbuch Verlag, Augsburg

Seitz A, Loeschcke V (1991) Species Conservation: A Population-Biological Approach. Birkhäuser Verlag, Berlin

Simberloff D (1988) The contribution of population and community biology to conservation science. Annu Rev Ecol Syst 19:473-511

Strong DR, Simberloff D, Abele LG, Thistle AB (eds) (1984) Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton

Sutcliffe OL, Thomas CD, Peggie D (1997) Area-dependent migration by ringlet butterflies generates a mixture of patchy population and metapopulation attributes. Oecologia 109:229-234

Thomas CD, Jones TM (1993) Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges: Lessons for conservation in a fragmented landscape. J Anim Ecol 62:472-481

Tilman D (1994) Competition and biodiversity in spatially structured habitats. Ecology 75:2-16

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385-397

Wiens JA (1994) Habitat fragmentation: island versus landscape perspectives on bird conservation. Ibis (Suppl) 137:97-104

Zoller H (1947) Studien an *Bromus erectus* - Trockenrasengesellschaften in der Nordwestschweiz, speziell im Blauengebiet. Ber Geobot Inst ETH 1946:51-81

Zoller H (1954) Die Typen der *Bromus erectus*-Wiesen des Schweizer Juras. Hans Huber, Bern

Zoller H, Bischof N (1980) Stufen der Kulturintensität und ihr Einfluß auf Artenzahl und Artengefüge der Vegetation. Phytocoenologia 7:33-51

Zoller H, Wagner C, Frey V (1986) Nutzungsbedingte Veränderungen in Mesobromion-Halbtrockenrasen in der Region Basel – Vergleich 1950-1980. Abh Westf Mus Naturk 48:93-107

Appendix

Species list
Each line contains the species name (with authority). Asterisks (*) indicate species on the Red Lists of Switzerland (Landolt 1991; Duelli 1994). The number of blocks (out of 12) in which each species was found and the sites (N Nenzlingen, M Movelier, V Vicques) are also indicated.

Grasses

•*Agrostis stolonifera* L. 1 M

•*A. tenuis* Sibth. 12 N,M,V

•*Anthoxanthum odoratum* L. 7 N,M,V

•*Avenula pubescens* Dumortier 5 N

•*Brachypodium pinnatum* P. B. 12 N,M,V

•*Briza media* L. 12 N,M,V

•*Bromus erectus* Hudson 12 N,M,V

•*Carex caryophyllea* La Tourrette 12 N,M,V

•*C. flacca* Schreber 12 N,M,V

•*C. pilulifera* L. 1 M

•*Cynosurus cristatus* L. 12 N,M,V

•*Dactylis glomerata* L. 12 N,M,V

•*Danthonia decumbens* DC. 12 N,M,V

•*Festuca ovina* L. 12 N,M,V

•*F. pratensis* Hudson 10 N,M,V

•*F. rubra* L. 5 N,M

•*Holcus lanatus* L. 5 N

•*Koeleria pyramidata* P. B. * 10 N,M,V

•*Lolium perenne* L. 9 N,M,V

•*Luzula campestris* DC. 11 N,M,V

•*Phleum pratense* L. 11 N,M,V

•*Poa compressa* L. 7 N,M,V

•*P. pratensis* L. 12 N,M,V

•*P. trivialis* L. 6 N,M,V

Forbs

•*Achillea millefolium* L. 10 N,M,V

•*Acinos arvensis* Dandy 2 V

•*Agrimonia eupatoria* L. 12 N,M,V

•*Ajuga reptans* L. 1 N

•*Alchemilla* agg. L. * 1 M

•*Allium oleraceum* L. 2 M,V

•*Anacamptis pyramidalis* Rich. * 3 M

•*Anemone nemorosa* L. 1 N

•*Anthericum ramosum* L. 1 M

•*Anthyllis vulneraria* L. 3 N,V

•*Asperula cynanchic*a L. * 6 M,V

•*Aster amellus* L. 1 M

•*Bellis perennis* L. 4 N

•*Betonica officinalis* L. 12 N,M,V

•*Campanula glomerata* L. * 3 M

•*C. rotundifolia* L. 5 N,M,V

•*Cardamine hirsuta* L. 1 N

•*Carlina acaulis* L. 3 M

•*C. vulgaris* L. * 1 V

•*Centaurea jacea* L. 11 N,M,V

•*Centaurium erythraea* Rafn * 4 N,V

•*Cerastium fontanum* Baumg. 7 N,M

•*Chamaespartium sagittale* P. Gibbs 7 N,M,V

•*Cirsium acaule* Scop. 12 N,M,V

•*Colchicum autumnale* L. 2 N, M

•*Convolvulus arvensis* L. 1 V

•*Crepis biennis* L. 3 N, M

•*C. taraxacifolia* Thuill. 2 M

•*Daucus carota* L. 11 N, MY

•*Euphorbia cyparissias* L. 9 N,V

•*E. verrucosa* L. * 1 M

•*Galium album* Miller 4 N,M,V

•*G. pumilum* Murray 1 M

•*G. verum* L. 9 N,M,V

•*Genista tinctoria* L. * 1 V

•*Gentiana cruciata* L. * 1 V

•*G. verna* L. * 1 M

•*Gentianella ciliata* Borkh. * 1 M

•*G. germanica* Börner * 2 M

•*Geranium dissectum* L. 1 N

•*Gymnadenia conopsea* R. Br. 3 M

•*Helianthemum nummularium* Miller 11 N,M,V

•*Hieracium pilosella* L. 12 N,M,V

•*Hippocrepis comosa* L. 6 N,V

•*Hypericum perforatum* L. 12 N,M,V

•*Hypochoeris radicata* L. 7 N,M,V

•*Knautia arvensis* Duby 9 N,M,V

•*Lathyrus pratensis* L. 10 N,M,V

•*Leontodon hispidus* L. 7 N,M,V

•*Leucanthemum vulgare* Lam 8 N,M,V

•*Linum catharticum* L. * 12 N,M,V

•*Lotus corniculatus* L. 12 N,M,V

•*Medicago lupulina* L. 10 N,M,V

•*Ononis repens* L. 9 N,M,V

•*Orchis militaris* L. * 1 M

•*O. morio* L. * 1 M

•*O. ustulata* L. 3 N,M

•*Origanum vulgare* L. 5 N,M,V

•*Pimpinella saxifraga* L. 6 N,V

•*Plantago lanceolata* L. 12 N,M,V

•*P. major* L. 2 N, M

•*P. media* L. 12 N,M,V

•*Platanthera chlorantha* Rchb. * 1 M

•*Polygala amarella* Crantz 4 N,M,V

•*P. comosa* Schkuhr * 6 N,M,V

•*Potentilla erecta* Räuschel 11 N,M,V

•*P. neumanniana* Rchb. 8 N,M,V

•*P. reptans* L. 1 N

•*P. sterilis* Garcke 8 N,M,V

•*Primula veris* Hudson 9 N,M,V

•*Prunella grandiflora* Scholler 11 N,M,V

•*P. vulgaris* L. 12 N,M,V

•*Ranunculus acris* L. 1 N

•*R. bulbosus* L. 12 N,M,V

•*R. repens* L. 2 N,V

•*Rumex acetosa* L. 4 N

•*Salvia pratensis* L. * 8 N,V

•*Sanguisorba minor* Scop. 12 N,M,V

•*Scabiosa columbaria* L. * 8 N,M,V

•*Sedum sexangulare* Grimm 5 N,V

•*Senecio erucifolius* L. 9 N,M,V

•*Silaum silaus* Sch. et Th. * 2 M

•*Spiranthes spiralis* Chevallier * 1 M

•*Succisa pratensis* Moench 4 N,M

•*Taraxacum officinale* Weber 1 N

•*Tetragonolobus maritimus* Roth * 3 M

•*Teucrium chamaedrys* L. 10 N,M,V

•*T. montanum* L. 1 M

•*Thlaspi perfoliatum* L. 1 M

•*Thymus serpyllum* L. 9 N,M,V

•*Trifolium campestre* Schreber 8 N,V

•*T. medium* L. 11 N,M,V

•*T. montanum* L. * 11 N,M,V

•*T. ochroleucon* Hudson * 11 N,M,V

•*T. pratense* L. 12 N,M,V

•*T. repens* L. 11 N,M,V

•*Veronica arvensis* L. 5 N, M

•*V. chamaedrys* L. 7 N,V

•*V. officinalis* L. 12 N,M,V

•*V. prostrata* L. * 3 N

•*V. serpyllifolia* L. 8 N,M,V

•*V. teucrium* L. * 1 V

•*Vicia cracca* L. 1 M

•*V. hirsuta* S. F. Gray 11 N,M,V

•*V. sativa* L. 6 N,V

•*Viola hirta* L. 2 V

Ants

•*Formica cunicularia* Latreille 1798 3 N,M,V

•*F. rufibarbis* Fabricius 1793 3 N,M,V

•*Lasius flavus* (Fabricius 1781) 6 N,M

•*L. paralienus* Seifert 1992 12 N,M,V

•*Myrmecina graminicola* (Latreille 1802) 1 N,

•*Myrmica sabuleti* Meinert 1860 10 N,M,V

•*M. scabrinodis* Nylander 1846 1 M

•*M. schencki* Emery 1894 2 N,M

•*M. specioides* Bondroit 1918 * 1 V

•*Solenopsis fugax* (Latreille 1798) 3 N,M

•*Tapinoma ambiguum* Emery 1925 2 V

•*T. erraticum* (Latreille 1798) 6 N,M

•*Tetramorium caespitum* (L. 1758) 4 N,M,V

Butterflies

•*Aphantopus hyperantus* (L. 1758) 1 N

•*Argynnis paphia* (L. 1758) * 4 M,V

•*Aricia agestis* (Denis & Schiffermüller 1775) 1 V

•*Brintesia circe* (Fabricius 1775) * 7 N,M,V

•*Clossiana dia* (L. 1767) * 3 M

•*Coenonympha pamphilus* (L. 1758) 11 N,M,V

•*Cupido minimus* (Fuesslin 1775) * 4 N,M,V

•*Cynthia cardui* (L. 1758) 11 N,M,V

•*Erebia aethiops* (Esper 1777) * 1 M

•*Gonepteryx rhamni* (L. 1758) 1 N

•*Hesperia comma* (L. 1758) 6 N,M,V

•*Inachis io* (L. 1758) 3 M,V

•*Lasiommata megera* (L. 1767) * 4 N,M,V

•*Lycaena tityrus* (Poda 1761) * 1 M

•*Lysandra coridon* (Poda 1761) * 8 N,M,V

•*Macroglossum stellatarum* (L. 1758) 11 N,M,V

•*Maniola jurtina* (L. 1758) 12 N,M,V

•*Melanargia galathea* (L. 1758) 12 N,M,V

•*Mellicta parthenoides* (Keferstein 1851) * 2 M

•*Ochlodes venatus* (Bremer & Grey 1803) 10 N,M,V

•*Papilio machaon* (L. 1758) 1 M

•*Pieris brassicae* (L. 1758) 6 N,M,V

•*P. rapae* (L. 1758) 9 N,M,V

•*Plebicula dorylas* (Denis & Schiffermüller 1775) * 1 M

•*Polyommatus icarus* (Rottemburg 1775) 10 N,M,V

•*Pyronia tithonus* (L. 1771) * 1 M

•*Spialia sertorius* (Hofmannsegg 1804) 6 N,M,V

•*Thymelicus sylvestris* (Poda 1761) 10 N,M,V

•*Zygaena filipendulae* (L. 1758) 12 N,M,V

Grasshoppers

•*Chorthippus biguttulus* (L. 1758) 12 N,M,V

•*C. parallelus* (Zetterstedt 1821) 12 N,M,V

•*Chrysochraon brachyptera* (Ocskay 1826) 7 N,M

•*Decticus verrucivorus* (L. 1758) * 6 M,V

•*Gomphocerus rufus* (L. 1758) 8 N,M,V

•*Gryllus campestris* L. 1758 * 2 N

•*Metrioptera bicolor* (Philippi 1830) * 12 N,M,V

•*M. brachyptera* (L. 1761) * 1 M

•*M. roeselii* (Hagenbach 1822) 5 N,M

•*Omocestus rufipes* (Zetterstedt 1821) * 10 N,M,V

•*Pholidoptera griseoaptera* (De Geer 1773) 6 N,M

•*Platycleis albopunctata* (Goeze 1778) * 11 N,M,V

•*Stenobothrus lineatus* (Panzer 1796) 11 N,M,V

•*Tettigonia cantans* (Fuessly 1775) 1 M

•*T. viridissima* L. 1758 5 N,M,V

Gastropods

•*Arion lusitanicus* Mabile 1868 2 N

•*Cochlicopa lubrica* (O.F. Müller 1774) 11 N,M,V

•*Cochlodina laminata* (Clessin 1882) 1 N

•*Deroceras reticulatum* (O.F. Müller 1774) 11 N,M,V

•*Helicella itala* (L. 1758) 5 N,M,V

•*Limax* spp. 10 N,M,V

•*Punctum pygmaeum* (Draparnaud 1801) 5 M,V

•*Pupilla muscorum* (L. 1758) 5 N,V

•*Succinea oblonga* (Draparnaud 1801 1 M

•*Trichia plebeia* (Draparnaud 1805) 12 N,M,V

•*Vertigo pygmaea* (Draparnaud 1801) 12 N,M,V

•*Vitrina pellucida* (O.F. Müller 1774) 4 M,V

Chapter II

Experimental small-scale grassland fragmentation alters aphid population dynamics

B. Braschler, G. Lampel, B. Baur

Oikos 100: 581-591

B. Braschler, B. Baur

Department of Integrative Biology, Section of Conservation Biology (NLU), University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland

G. Lampel

Zoological Institute, University of Fribourg, Pérolles, CH-1700 Fribourg, Switzerland

Abstract

Theory predicts that at higher trophic levels species are especially vulnerable to habitat fragmentation due to small population size and dependence on particular prey species. Using aphids as model organism, we tested the hypothesis that herbivore abundance increases in fragmented habitats as a result of reduced predator and parasitoid densities. In a 3 year-study, we examined the population dynamics of aphids with respect to host plant abundance and ant nest density in experimentally fragmented calcareous grasslands at two sites in the northern Jura mountains. Fragments of different size (area: 20.25 m^2, 2.25 m^2 and 0.25 m^2) were isolated by a 5-m wide strip of frequently mown vegetation and corresponding control plots were situated in the adjacent undisturbed grassland. Aphid density was higher in fragments than in control plots. This was a combined result of a higher frequency of aphid-infested plants and larger aphid colonies in fragments than in control plots. Furthermore, a larger proportion of aphid colonies was ant-attended in fragments than in control plots. Aphid colonies were also more frequently visited by ants in fragments than in control plots in one of the 3 years. Parasitoid pressure on aphids was not influenced by the experimental fragmentation. Neither were aphid species richness and diversity affected by the fragmentation. Our study shows that even small-scale habitat fragmentation can have profound effects on the abundance of herbivorous insects. The effect on aphid density was consistent over 3 years and two sites with slightly different aphid communities.

Introduction

Habitat fragmentation is considered as a major threat to biodiversity (Saunders et al. 1991, Collinge 2000, Simberloff 2000). Fragmentation reduces the area suitable to the organisms and creates isolated subpopulations by disrupting the exchange of individuals and preventing gene flow (Lacy and Lindenmayer 1995). Fragmentation also influences interactions among species (Kruess and Tscharntke 1994, Groppe et al. 2001, Goverde et al. 2002) and ecological processes (Robinson et al. 1992).

Habitat fragmentation affects different species and different trophic groups to a different extent (Davies and Margules 1998, Debinski and Holt 2000, Zschokke et al. 2000). Theory predicts that at higher trophic levels species are especially vulnerable to fragmentation due to their small population size and dependence on particular prey species which itself may be affected by fragmentation (Holt 1996). There is some experimental evidence supporting this

hypothesis. Aphids reached higher population densities in experimentally fragmented patches of goldenrod than in continuous habitat as a result of the predator's (ladybird beetles) delay to colonise the fragments (Kareiva 1984, 1987). Herbivorous insects occurred at increased densities in experimental patches of red clover as some of their predators and parasitoids failed to colonise the patches (Kruess and Tscharntke 1994).

We examined the effect of experimental small-scale habitat fragmentation on the population dynamics of aphids in two calcareous grasslands. In contrast to other studies on the dynamics of one or a few herbivore species in patches of a single host plant we investigated a naturally diverse host plant-herbivore-predator system in a controlled field experiment.

Aphids are particularly useful model organisms because many species show high rates of population growth through parthenogenetic reproduction. Outbreaks may occur in the absence of predators and under favourable climatic conditions. Habitat fragmentation may affect aphid populations either directly or via their host plants, predators or mutualists. Firstly, migrating foundresses of aphid colonies may be differently attracted by small vegetation patches (fragments) and continuous habitat. The number of aphid colonies may increase in fragments when colonising females prefer small habitat patches. However, the contrary may occur when foundresses prefer continuous habitat. Secondly, fragmentation may affect the distribution and abundance of host plants (Robinson and Quinn 1988, Holt et al. 1995). As many aphid species depend on one or a few host species, the distribution of host plants will influence aphid species composition in fragments. Thirdly, plants growing along the edges of fragments are exposed to altered microclimatic conditions (Laurance and Yensen 1991). In addition, plants at the edges of fragments may benefit from reduced competition for light and nutrients. These factors may increase host plant quality which in turn enhances aphid population growth (Breton and Addicott 1992, Kindlmann and Dixon 1992, Stadler 1995). Indeed, several studies revealed positive effects of habitat edges on the dynamics of insect species (Roland and Kaupp 1995, Cappuccino and Martin 1997). Fourthly, many aphid species interact with ants. In our long-term experiment fragmentation affected the density and species composition of ants (B. Braschler, unpubl. data). Fragmentation also influenced other food resources of ants. Thus, ant-tending intensity should increase and ant predation on attended aphids decrease when alternative sugar resources like extrafloral nectaries (Offenberg 2000, 2001, Sakata and Hashimoto 2000) or other homopteran colonies are in short supply (Cushman and Addicott 1989). Changes in ant species composition due to fragmentation could influence aphid populations as different ant species attended aphids in different ways (Addicott 1978, 1979). Changes in ant attendance may further affect parasitoid pressure on aphids (Völkl 1992). In

general, ant-attended aphids benefit from an increased ant density. Finally, some predators and parasitoids may be absent in fragments and thus release herbivores from top-down control and potentially allow outbreaks (Kruess and Tscharntke 1994, 2000).

In the present paper we tested these hypotheses using data on aphid density and species composition, host plant abundance, interactions among aphids and attending ants and parasitoid pressure collected over 3 years in a controlled field experiment.

Material and methods

Study sites

The fragmentation experiment was carried out in two calcareous grasslands situated in the northern Swiss Jura mountains: in Nenzlingen (13 km S of Basel; 47˚ 34' N, 7˚ 35' E) and Vicques (26 km SSW of Basel). Originally covered by beech forest, these grasslands have been grazed by cattle for many centuries, leading to the characteristic vegetation of the *Teucrio-Mesobrometum* (Zoller 1947, Ellenberg 1986). A description of the sites is given in Zschokke et al. (2000).

Fragmentation experiment

The experimental fragmentation of the grasslands was created in spring 1993 by mowing the vegetation around the experimental fragments. One experimental unit, called block, contained one large (4.5 x 4.5 m), one medium (1.5 x 1.5 m) and two small (0.5 x 0.5 m) fragments, all of them separated by a 5-m wide strip of mown vegetation, as well as the corresponding control plots, which were mirror-symmetrically arranged and surrounded by undisturbed vegetation (Fig. 1). Within each block, the positions of the different sizes of fragment-control plot pairs as well as the control and fragment halves were randomised. The experimental set-up used in the present study consisted of 9 blocks (five in Nenzlingen and four in Vicques) with 36 fragments (9 large, 9 medium and 18 small) and 36 corresponding control plots. The distances between blocks within the sites ranged from 25 to 135 m. The blocks were part of larger study areas (1.5 - 2 ha) that were enclosed by fences to exclude large herbivores. The experimental fragmentation had been maintained since April 1993 by frequently (6-12 times per year) mowing the area between the fragments in the period from March to October. The entire experimental area was mown in late autumn every year to prevent succession (Kienzle 1979).

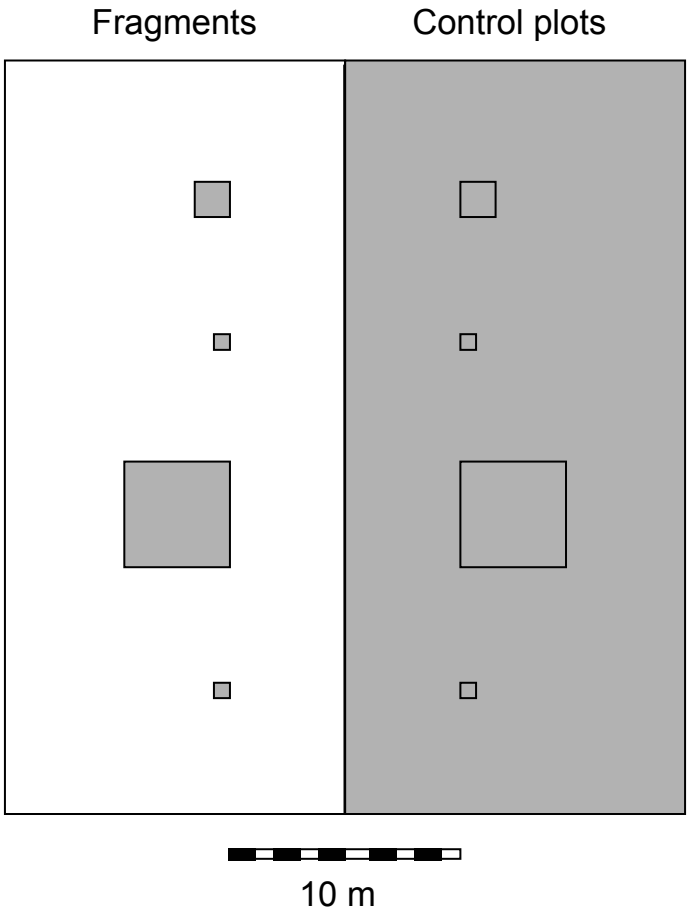


Fig. 1. Diagram of one block of the fragmentation experiment. A block contained two small (0.5 x 0.5 m), one medium (1.5 x 1.5 m) and one large (4.5 x 4.5 m) fragment and corresponding control plots. The isolation area between the fragments (shown in white) was frequently mown.

Fragmentation experiment

The experimental fragmentation of the grasslands was created in spring 1993 by mowing the vegetation around the experimental fragments. One experimental unit, called block, contained one large (4.5 x 4.5 m), one medium (1.5 x 1.5 m) and two small (0.5 x 0.5 m) fragments, all of them separated by a 5-m wide strip of mown vegetation, as well as the corresponding control plots, which were mirror-symmetrically arranged and surrounded by undisturbed vegetation (Fig. 1). Within each block, the positions of the different sizes of fragment-control plot pairs as well as the control and fragment halves were randomised. The experimental set-up used in the present study consisted of 9 blocks (five in Nenzlingen and four in Vicques) with 36 fragments (9 large, 9 medium and 18 small) and 36 corresponding control plots. The distances between blocks within the sites ranged from 25 to 135 m. The blocks were part of larger study areas (1.5 - 2 ha) that were enclosed by fences to exclude large herbivores. The

experimental fragmentation had been maintained since April 1993 by frequently (6-12 times per year) mowing the area between the fragments in the period from March to October. The entire experimental area was mown in late autumn every year to prevent succession (Kienzle 1979).

Field methods

Above-ground aphid density was assessed in the years 1997-1999 by recording the number of aphids on infested plants growing in fragments and control plots. Aphid density was calculated as number of aphids per 0.25 m^2. Aphid colony size was defined as number of aphids of the same species occurring on a single plant. Most colonies were small enough to count all individuals. In large colonies (> 100 individuals) the area covered by aphids on a plant was determined and a subsample from a defined area was collected using a paintbrush. The number of individuals counted in the subsample was then extrapolated to the entire area occupied by the colony. The number of aphid mummies was also recorded as a measure of parasitoid pressure.

The species of aphid-infested plants were determined. The density of infested plants was calculated as number of infested plants per 0.25 m^2. To assess infestation rates, we recorded the numbers of both infested and non-infested plants in the three species most frequently infested by aphids and in another nine frequently infested species in 1999. The plant species were chosen according to the following four criteria: presence in both study sites, infestation with aphids in 1997 or 1998, easy to determine when not flowering, only one species per genus. Nomenclature of the plants follows Binz and Heitz (1990).

In 1997, aphid density was assessed in 32 fragments and 32 control plots (five blocks in Nenzlingen and three blocks in Vicques). In small patches (fragments and control plots) we determined aphid number on each host plant. In medium-sized patches we assessed aphid number in five subplots measuring 50 x 50 cm. One of these subplots was located in the centre of the patch and four at the edge. In large patches, aphid number was determined in twelve subplots: four in the centre and eight at the edge.

In 1998 and 1999, aphid density was assessed in 36 fragments and 36 control plots (five blocks in Nenzlingen and four blocks in Vicques). In small patches the aphids were recorded on each infested plant. In medium-sized patches we recorded aphids in three subplots (one in the centre and two at the edge). In large patches, aphid density was assessed in 27 subplots,

which corresponded to one third of the entire area. Sixteen subplots were randomly chosen from the centre area and eleven at the edge.

Aphid density was recorded between 2 and 29 July 1997, 18 and 30 May 1998 and 1 and 24 July 1999. The order of field work followed the stage of the vegetation period: plots in Nenzlingen were studied before those in Vicques. The order in which fragments and control plots of the same block were studied was randomised.

The present study was part of a larger project to examine effects of grassland fragmentation on plants and different groups of invertebrates over several years. For this reason we used non-destructive sampling methods whenever possible. In 1998, however, up to 17 aphids (most frequently one to six individuals) were collected from each colony and preserved in 70% alcohol for later species identification. Whenever possible the majority of individuals of a colony was left on the plants to minimise the impact of sampling. On some plants only one or very few aphids were found. Some aphids dropped from the plant before sampling. Species identification was not always possible when only nymphs or alatae (winged aphids) were present. Thus, some colonies were not considered in a few analyses.

The aphids were mounted for species identification. This was done by first removing all embryos and then embedding the aphids into a mixture of polyvinylalcohol and lactophenol following the method of Heinze (1952). All aphids collected were identified by one of us (GL). Nomenclature of the aphids follows Remaudière and Remaudière (1997).

Ant-tending intensity was assessed as the number of ants that tended aphids when the colony was surveyed for the first time. Visitation rate was estimated as number of ants tending a colony within 2 min.. Colonies not visited during 2 min. were classified as not visited. In the case of a misclassification this procedure makes our interpretations more conservative.

The density of ant nests was recorded in large experimental plots between 29 July and 10 September 1999 to examine whether differences in ant-tending intensity were a result of differential ant density. Nests were identified by carefully searching the plots for visual signs and following the workers from baits (plastic caps 2.9 cm in diameter filled with sucrose solution) back to their nests. Fragments and control plots of the same block were examined on the same day to avoid any confounding influence of the season. Similarly, foraging activity of ants (number of ants recorded in 2 min. on a bait, 1 h after it was offered) was recorded in large experimental plots in 1999. In each patch we placed 181 baits (sucrose solution baits as above). Ant species were identified on site, but in some cases a few specimens were removed for later identification in the lab using a binocular microscope. Nomenclature of the ants follows Bolton (1995).

Statistical analyses

A repeated measurement ANOVA (type III) was used to examine the effects of fragmentation, study site (Nenzlingen or Vicques), block (nested in site, random factor) and patch size (large, medium, small) on aphid density over all years. Due to missing data in four fragments and four control plots in 1997, only a reduced data set could be used for this analysis. An ANOVA (type III) was used to evaluate the data from each year separately. Using the same ANOVA model, fragmentation effects on colony size and density of aphid-infested plants were evaluated. To examine whether aphid density differed between the edge zone (a 50-cm wide strip along the edge) and the interior (core area) of fragments and control plots, an ANOVA with the additional factor 'edge' was used. Possible edge effects were only analysed in medium-sized and large plots (small plots consisted exclusively of edge zone). Unpaired t-tests were used to examine fragmentation effects on the densities of the two most abundant aphid species. As variances were unequal between groups approximate degrees of freedom were calculated following Satterthwaite (1946). Aphid densities of single species were calculated on the basis of plots occupied by the particular species (Appendix A).

Differences in infestation rate between fragments and control plots were examined in 12 plant species using Fisher's exact tests. As aphid species composition differed between study sites, data from each site were analysed separately. Similarly, the effect of fragmentation on the frequency of ant-attended aphid colonies and on parasitoid pressure were analysed using Fisher's exact tests. To eliminate confounding factors such as different weather conditions, paired t-tests were used to examine differences in ant nest density and forager activity between large fragments and corresponding control plots. Ant-tending intensity depended on aphid colony size. Differences in ant-tending intensity between fragments and control plots were examined by comparing the residuals of the logarithmic regression of ant-tending intensity = 0.53 - 0.094 x log(mean aphid colony size) using Mann-Whitney U-tests (data did not fit normal distributions).

Unpaired t-tests were used to analyse differences in aphid diversity (Shannon-Wiener diversity index) between large fragments and control plots. Statistical analyses were performed using SAS 6.08 (SAS Institute 1990) for linear models and StatView 5.0 (SAS Institute 1998) for Fisher's exact tests and correlations. Data on aphid colony size and ant density were log-transformed, those on aphid density and density of infested plants log(y+1). In the text and figures mean values are presented with 95% confidence intervals (note that backtransformed values have asymmetric error bars (Sokal and Rohlf 1995)).

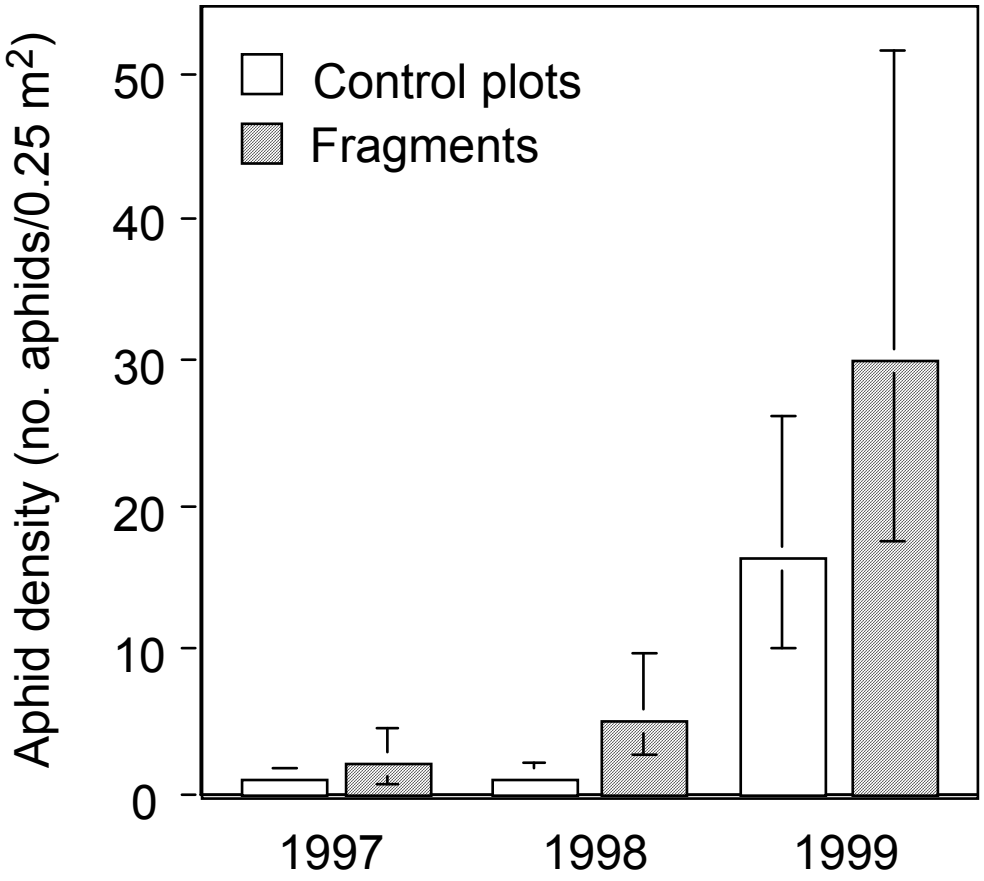


Fig. 2. Among-year variation in aphid density (number of individuals per 0.25 m^2, mean ± 95% confidence interval) in fragments and control plots. 32 fragments and 32 control plots were examined in 1997. In 1998 and 1999, 36 fragments and 36 control plots were examined. For statistical tests see Table 1.

Results

Effect on aphid density

The experimental fragmentation affected the number of aphids (Fig. 2; Table 1). Aphid density was higher in fragments than in control plots (repeated measurement ANOVA, $F_{1,44} = 12.71$, $p = 0.0009$). However, aphid density varied also among years (Fig. 2; repeated measurement ANOVA, $F_{2,88} = 60.43$, $p < 0.0001$) and between study sites ($F_{1,44} = 7.15$, $p = 0.0105$). Aphid density was higher in Nenzlingen than in Vicques in 1999. Aphid density was also affected by patch size ($F_{2,44} = 3.80$, $p = 0.0300$). However, this effect was differently pronounced in different years (Fig. 3; Table 1). Furthermore, there was a significant interaction between

Table 1. Summary of ANOVAs (type III) testing the effects of experimental fragmentation (T), study sites (S), block (B, nested in S) and patch size (P) on density of aphids. B(S) and the interaction T*B(S) were entered as random factors. In 1997 only 8 out of 9 blocks were examined.

	1997				1998				1999			
Source	df	MS	*F*	*p*	df	MS	*F*	*p*	df	MS	*F*	*p*
T	1	3.7712	3.1279	0.1105	1	25.6100	29.2567	0.0001	1	11.6695	6.0954	0.0334
S	1	9.8291	4.3564	0.0819	1	6.8154	3.4462	0.1058	1	7.0968	6.4919	0.0382
B(S)	6	2.2562	1.9279	0.2064	7	1.9777	2.5837	0.1035	7	1.0932	0.5725	0.7617
P	2	7.7633	5.2199	0.0092	2	8.4070	4.5091	0.0158	2	1.9174	0.9787	0.3829
T*B(S)	7	1.1744	0.7896	0.5998	8	0.7655	0.4106	0.9092	8	1.9095	0.9746	0.4665
T*P	2	0.4504	0.3029	0.7402	2	3.4066	1.8271	0.1715	2	7.5181	3.8374	0.0282
Error	44	1.4873			50	1.8645			50	1.9592		

experimental fragmentation and patch size in 1999 (Table 1). No consistent edge effects on aphid density were found. In 1998, we determined all aphid species. Considering the density of single species, contrasting results were found for the two most abundant species. *Acyrthosiphon malvae poterii* Prior et Stroyan was more abundant in fragments than in control plots (aphids/0.25 m^2: fragments: 0.27 (0.06, 0.53); control plots: 0.02 (0.00, 0.04); $t = 2.48$, df = 35.7, $p = 0.0181$), while no difference in the density of *Aphis stachydis* Mordvilko between fragments and control plots was found (aphids/0.25 m^2: fragments: 0.18 (0.02, 0.36); control plots: 0.22 (-0.06, 0.57); $t = 0.22$, df = 55.9, $p = 0.83$). Species other than *A. malvae* contributing to the overall higher aphid density in fragments were: *Aphis craccivora* Koch, *Aphis euphorbiae* Kaltenbach, *Aphis helianthemi* Ferrari, *Myzus langei* (Börner) and *Aphis* sp. on *Origanum vulgare* L.. These species were abundant in some fragments, but no individuals were found in control plots (Appendix A). Furthermore, *Macrosiphum rosae* (Linnaeus) mainly occurred in fragments. Some species represented by a few individuals were recorded either in fragments or in control plots (Appendix A).

The higher aphid density in fragments was mainly a result of a larger number of plants infested by aphids in fragments than in control plots (Fig. 4). Fragments contained a larger number of infested plants in all years, although in 1999 there was only a tendency (ANOVA, 1997: $F_{1,9.24} = 6.80$, $p = 0.0278$; 1998: $F_{1,10.11} = 11.82$, $p = 0.0063$; 1999: $F_{1,9.66} = 3.46$, $p = 0.0935$). A larger number of infested plants could result from a higher density of potential host plants or a higher rate of infestation. To distinguish between these two explanations, the infestation rate was measured in twelve plant species which were frequently infested by aphids in 1999. Considering data from both study sites separately, this would result in 24 different fragment-control plot comparisons. However, no individuals of the plant species *Lathyrus pratensis* L. were found in Vicques, reducing the total number of comparisons to 23. In five out of 23 fragment-control plot comparisons, potential host plants showed a higher infestation rate in fragments than in control plots, in a further comparison there was a tendency (Table 2). No plant species was significantly more often infested by aphids in control plots than in fragments after sequential Bonferroni correction. This indicates an enhanced infestation risk for some plants in fragments. Most plant species showed no difference in abundance between fragments and control plots. In only two comparisons a plant species was more abundant in fragments than in control plots (*Agrimonia eupatoria* L. and *Knautia arvensis* Duby, both in Vicques) and in another two comparisons a plant species was more abundant in control plots than fragments (*Betonica officinalis* L. in Vicques and *Salvia pratensis* L. in Nenzlingen) after

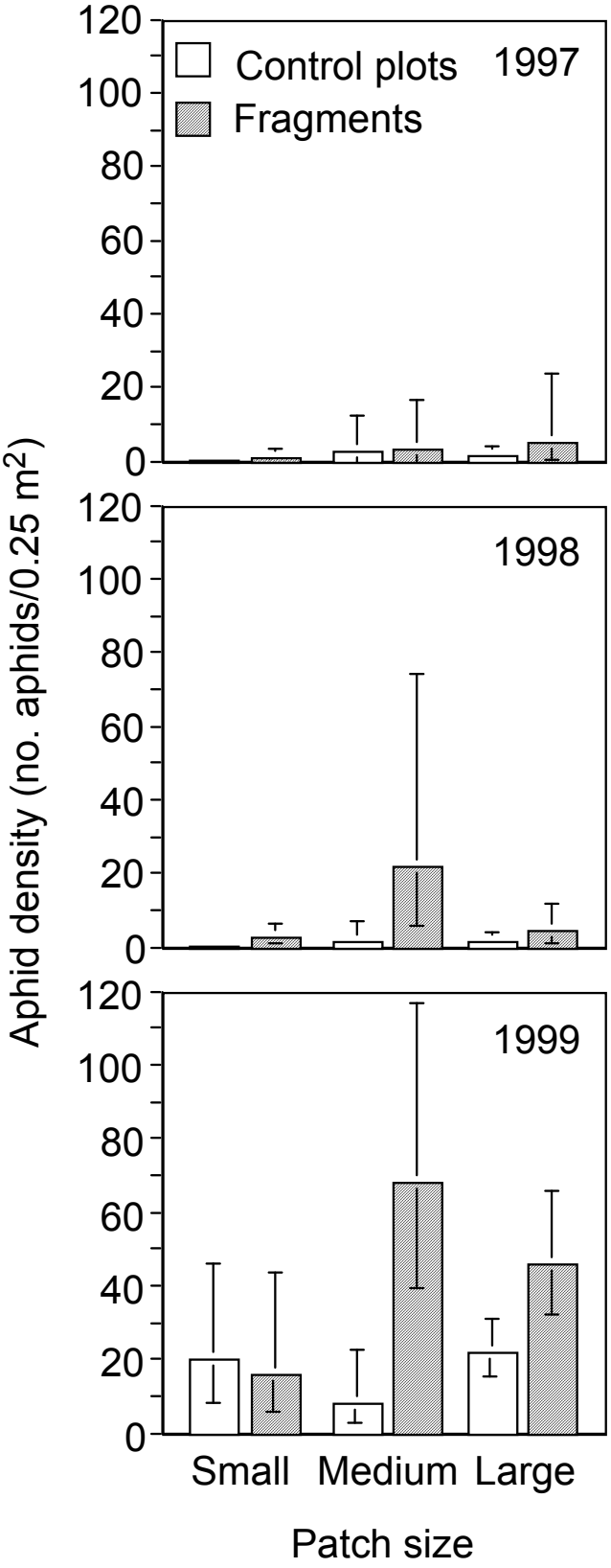


Fig. 3. Effect of patch size on the density of aphids (number of individuals per 0.25 m^2, mean ± 95% confidence interval) in 1997 - 1999. In 1997, we examined 16 small, 8 medium and 8 large fragments and control plots each. In 1998 and 1999, the sample size was 18 for small, 9 for medium and 9 for large fragments and control plots each. For statistical tests see Table 1.

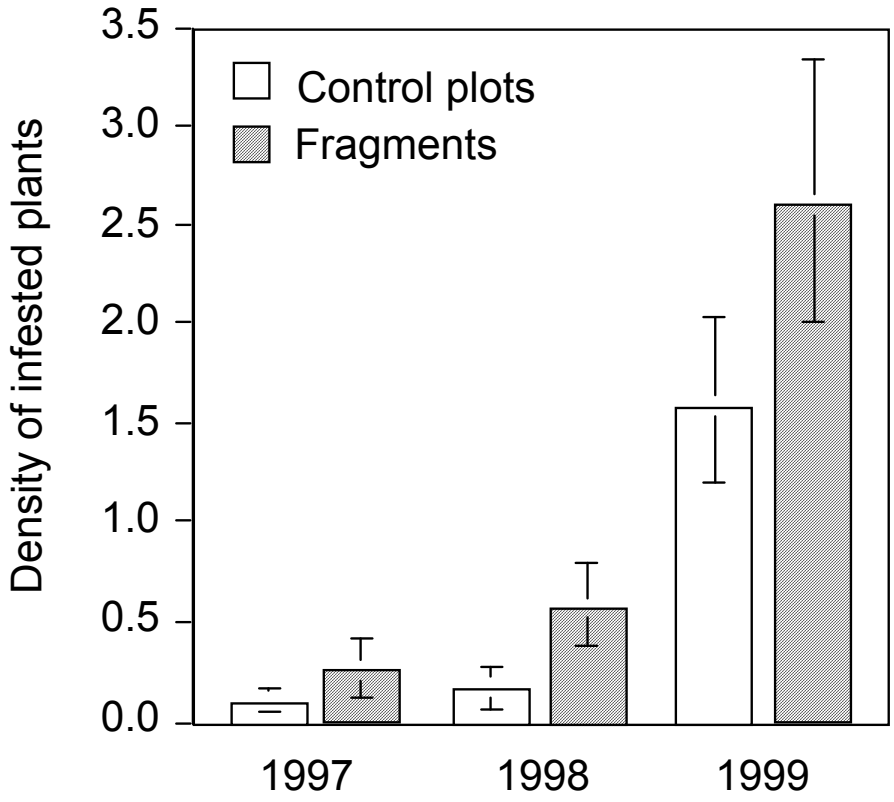


Fig. 4. Effect of habitat fragmentation on the density of plants infested by aphids (number of infested plants per 0.25 m^2, mean ± 95% confidence interval) in 1997 - 1999. 32 fragments and 32 control plots were examined in 1997. In 1998 and 1999, 36 fragments and 36 control plots were examined.

sequential Bonferroni correction. However, in only one of these cases (*K. arvensis* in Vicques) the infestation rate differed between fragments and control plots. This indicates that the higher infestation rates of some plant species in fragments were not a result of differences in abundance.

Aphid colonies in fragments were larger than those in control plots in 1999 (mean number of individuals: fragments: 15.91 (10.69, 23.67), control plots: 10.12 (7.29, 14.04); ANOVA, $F_{1,9.55} = 6.63$, $p = 0.0287$), while in the other 2 years no significant difference was found (1997: $F_{1,13.50} = 1.31$, $p = 0.27$; 1998: $F_{1,16.77} = 0.01$, $p = 0.93$). Considering all years, large aphid colonies (≥ 100 individuals) occurred more frequently in fragments (5.6% of colonies) than in control plots (1.9%; Fisher's exact test: $p = 0.0006$). The majority of species were represented by only one or a few individuals. This prevented any comparisons between fragments and control plots. In the two most abundant species, *Aphis stachydis* with ant-attendance and *Acyrtosiphon malvae poterii* without ant-attendance, no difference in colony

size between fragments and control plots was found (mean number of individuals: *A. stachydis*: 7.89 (3.18, 19.61) vs. 10.94 (2.46, 48.62), $t = 0.48$, df = 13, $p = 0.64$; *A. malvae*: 1.57 (1.14, 2.15) vs. 1.78 (0.95, 3.34), $t = 0.46$, df = 18, $p = 0.65$).

Aphid species diversity

A total of 24 aphid species were recorded on 19 different plant species in 1998 (Appendix A). Most aphid species were rare; in 14 species only a single individual or a single colony were found. The species composition differed between the two study sites. Six of the 24 species (25%) were found at both sites. Considering the diversity of plant species infested by aphids, further 13 plant species were infested by aphids in 1997 and 1999 (Appendix B).

Considering large plots, experimental habitat fragmentation did not affect aphid species richness (fragments: 4.11 (2.81, 5.41), control plots: 3.11 (1.70, 4.52), $t = 1.20$, df = 16, $p = 0.25$) and diversity (Shannon-Wiener index, fragments: 1.09 (0.90, 1.27), control plots: 0.92 (0.42, 1.41), $t = 0.74$, df = 16, $p = 0.47$).

Effects on aphid-ant interactions

The densities of ant nests and foragers were assessed in large fragments and the corresponding control plots in 1999. Fragments had a higher density of ant nests than control plots (number of nests per 0.25 m^2: fragments: 0.23 (0.20, 0.26), control plots: 0.17 (0.13, 0.22); paired $t = 2.62$, df = 8, $p = 0.0306$). Forager density (number of ants counted per bait in 2 min) was larger in fragments than in control plots (1.46 (0.99, 2.12) vs. 0.61 (0.33, 1.12); paired $t = 3.73$, df = 8, $p = 0.0058$).

Most aphid species recorded were ant-attended. Exceptions were some rare species and *Acyrthosiphon malvae poterii* of which numerous colonies occurred at both study sites (species without ant-attendance accounted for 35% of colonies and 6% of individual aphids in 1998). The majority of ants that attended aphids belonged to *Lasius paralienus* Seifert. *L. paralienus* was also the most abundant ant species in the study sites (60 - 80% of ant nests recorded in the experimental plots and 97% of the aphid-attending ants). Other aphid-attending ants were in order of decreasing abundance: *Myrmica sabuleti* Meinert, *Myrmica scabrinodis* Nylander, *Myrmica schencki* Emery, *Lasius flavus* (Fabricius), *Formica pratensis* Retzius, *Formica rufibarbis* Fabricius, *Formica cunicularia* Latreille and *Lasius niger* (Linnaeus). Considering data from 1997-1999, a larger proportion of the aphid colonies in fragments were attended by ants than in control plots (fragments: 41.4%, control plots: 32.4%; Fisher's exact test, $p = 0.0009$). Ant-attended aphid colonies were larger than aphid colonies not visited by

ants (mean number of individuals: 28.9 (23.7, 35.2) vs. 4.7 (3.9, 5.7); $t = 12.90$, df = 211, $p = 0.0001$). The larger proportion of ant-attended colonies may contribute to the higher aphid density in fragments than in control plots, though both ant-attended and unattended colonies were more numerous in fragments than in control plots (Fisher's exact test, $p < 0.0001$ in both cases). Considering data collected in large plots in 1999, aphid density tended to be correlated with ant nest density in fragments ($r = 0.60$, $n = 9$, $p = 0.0893$), but not in control plots ($r = -0.46$, $n = 9$, $p = 0.22$). In contrast, aphid density was not correlated with ant forager density in large experimental plots in 1999 (fragments: $r = 0.34$, $n = 9$, $p = 0.39$, control plots: $r = -0.12$, $n = 9$, $p = 0.77$). In 1998, attended colonies were more intensively visited by ants in fragments than in control plots (Mann-Whitney U-test, $p = 0.0477$). In 1997 and 1999, there was no difference in frequency of visiting ants between fragments and control plots (1997: $p = 0.96$; 1999: $p = 0.59$).

Parasitoid pressure

As a measure of parasitoid pressure we counted the number of aphid mummies. Mummified aphids were found both in fragments and control plots in 1997 and 1999. In 1998, no mummified aphids were found either in fragments or in control plots. The proportion of aphid colonies with mummies was higher in 1997 (23.8%) than in 1999 (4.1%; Fisher's exact test, $p < 0.0001$). A total of 730 mummies were found in 1997 and 391 in 1999. Thus, the number of mummies was twice as large in 1997 than in 1999, even though the total number of recorded aphids was smaller in 1997 than in 1999 (3174 vs. 22773 individuals). However, the experimental habitat fragmentation neither affected the proportion of aphid colonies that were parasitised (considering data from 1997 and 1999, Fisher's exact test, $p > 0.99$) nor the number of mummies (ANCOVAs with fragmentation as fixed factor and mean aphid colony size as covariate; 1997: $F_{1,3} = 2.83$, $p = 0.19$; 1999: $F_{1,13} = 0.86$, $p = 0.37$).

Discussion

The present study shows that the experimental habitat fragmentation caused an increased aphid density in fragments over 3 years at two sites with different aphid and plant species compositions. Thus, the fragmentation effect was temporarily and spatially replicated. The weather conditions may vary between sites and among years. However, the fragmentation

Table 2. Number of aphid-infested and aphid-free individuals in 12 plant species in fragments and control plots in Nenzlingen (N) and Vicques (V) in 1999. *Lathyrus pratensis* was not recorded in Vicques. * indicates a higher infestation rate in fragments than in control plots, $p < 0.05$ after sequential Bonferroni correction, $^{+}$ indicates a trend for a difference ($p < 0.1$).

Plant species	Study site	Fragments		Control plots		Fisher's exact test
		Number of plants		Number of plants		
		with aphids	without aphids	with aphids	without aphids	*p*
Agrimonia eupatoria L.	N	1	20	4	20	0.35
	V	12	59	2	27	0.34
Betonica officinalis L.	N	86	39	36	52	< 0.0001 *
	V	80	100	116	139	0.85
Centaurea jacea L.	N	0	2	0	6	> 0.99
	V	4	37	9	43	0.37
Helianthemum nummularium Miller	N	3	10	2	15	0.63
	V	0	18	0	30	> 0.99
Hypericum perforatum L.	N	8	8	9	16	0.52
	V	20	25	15	19	> 0.99
Knautia arvensis Duby	N	49	22	27	46	0.0001 *
	V	13	75	0	45	0.0045 $^{+}$
Lathyrus pratensis L.	N	22	3	11	0	0.54
Lotus corniculatus L.	N	25	33	13	20	0.83
	V	15	73	0	110	< 0.0001 *
Plantago media L.	N	4	11	3	13	0.69
	V	3	40	12	36	0.0249
Salvia pratensis L.	N	2	14	7	134	0.23
	V	0	7	0	17	> 0.99
Sanguisorba minor Scop.	N	188	267	93	292	< 0.0001 *
	V	31	294	18	285	0.10
Scabiosa columbaria L.	N	7	3	1	17	0.0007 *
	V	0	0	0	4	> 0.99

effect was consistent despite variation in environmental conditions which influence local aphid density.

The experimental fragmentation resulted in a larger number of aphid colonies and a higher infestation rate of some host plants, but also in a trend towards larger colonies in fragments. Large aphid colonies can seriously harm their host plant (Dixon 1985). In our field experiment, most colonies were relatively small. However, sampling later in the year would have revealed larger colony sizes as some aphid species reach their peak colony size later in the season. The fragmentation seemed to promote aphid colony growth. Large aphid colonies were found more frequently in fragments than in control plots. Furthermore, mean aphid colony size was larger in fragments than in control plots in one year.

In most of the plant species examined only a minority of individuals were infested by aphids. However, more plants may have become infested later in the season. Alatae (= winged aphids) production can be caused by crowding (Robert 1987). Indeed, a larger proportion of colonies with alatae occurred in fragments than in control plots (B. Braschler, unpubl. data). Thus, there were more alatae in fragments to colonise new plants. Furthermore, it has been shown that apterous (= unwinged) aphids may be able to colonise neighbouring plants, though the frequency with which apterae migrate to other plants differs among species (Edson 1985, Cappuccino 1987). In some species the apterae's tendency to migrate increases with crowding (Robert 1987). Combined, the higher proportion of alatae and the larger colony size in fragments may indicate a relatively high risk of future infestation for potential host plants that were not colonised at the sampling date.

In 1999, the final year of the aphid survey, no significant fragmentation effect on species richness and species composition of plants was found (H.-P. Rusterholz, unpubl. data). In the plant species examined the infestation rate was not related to the relative abundance in the plots. Plant quality can promote population growth of aphids (Breton and Addicott 1992). We did not asses plant quality. However, Dolt (2001) found an increased above-ground plant biomass in fragments in the years 1996-1998. Furthermore, in fragments plant biomass tended to be larger in the edge zone than in the core area (Dolt 2001). Plant productivity may be an indirect indicator of plant quality as many aphids grow best under conditions of high nutrient transport (like in growing and wilting plants). Indeed, aphid density increased with plant biomass in experimental plots in 1997 (B. Braschler, unpubl. data). However, our results showed no consistent edge effect on aphid density in fragments.

The experimental fragmentation did not reduce the parasitation rate of aphids. This contrasts predictions from theoretical models (Holt 1996) and findings from other

fragmentation studies (Kruess and Tscharntke 1994, 2000). The isolation distance of fragments (5 m) used in our field experiment seems to be small for flying parasitoids. However, previous results showed that the abundance of foraging butterflies was negatively affected by this type of fragmentation (Zschokke et al. 2000). Furthermore, Goverde et al. (2002) found that the abundance of a bumblebee species was negatively affected by the fragmentation and that the bumblebee's foraging behaviour was changed in fragments. In another fragmentation experiment, ladybird beetles arrived later in fragments of 1 m^2 than in control plots (Kareiva 1984, 1987). In this experiment the isolation distance of 1 m between fragments was even smaller than that in our study. Thus, the discontinuity in favourable habitat appears to affect the movement and foraging pattern even in mobile organisms.

Ants are important mutualists of numerous aphid species in the grasslands examined. In our study, ants were more abundant in fragments than in control plots and a greater proportion of the aphid colonies was ant-attended in fragments. Ant-attended colonies in fragments were also more intensively visited by ants than colonies in control plots in one year. The importance of ants for aphids varies among species. Most species in our study are ant-tended but may also live without tending ants. *A. malvae* and some others are rarely or never visited by ants. The better services provided by ants in fragments such as the removal of honeydew and protection from predators (Sudd 1987) may contribute to the success of ant-tended aphid species. Furthermore, extrafloral nectaries of *Euphorbia cyparissias* L. were more frequently visited by ants in fragments than in control plots (B. Braschler, unpubl. data). This may indicate a greater demand for sugar resources by ants in fragments or, alternatively, be a side effect of the increased ant density. The increased demand for sugar should lead to a more intensive tending of the aphids (Offenberg 2000, 2001). However, non-attended aphid colonies were also more numerous in fragments. This suggests that other factors than enhanced ant services contributed to the increased aphid density found in fragments.

Our study shows that small-scale fragmentation can lead to an increased density of herbivores. It is noteworthy that this effect was found in slightly different aphid communities which consisted predominantly of specialists for single host plant species. Furthermore, the experimental fragmentation affected the mutualistic aphid-ant interaction. Not all aphid species were ant-attended. The effect on the mutualistic aphid-ant interaction may therefore change the competitive interaction between attended and non-attended aphids. Similarly, other studies demonstrated fragmentation effects on species interactions, mostly on parasitism and predation (e.g. Kareiva 1984, 1987, Kruess and Tscharntke 1994, 2000, Lei and Hanski 1997).

The observed fragmentation effects on aphid density might be a combined result of several distinct influences including a higher abundance of mutualistic ants, an increased plant productivity and altered abiotic factors in fragments. Other potential influences like reduced predator pressure could not be demonstrated but may also contribute to a higher aphid density in fragments.

Acknowledgements

We thank Ludwika Sygnarski for preparing the aphid specimens for species determination. Hans-Peter Rusterholz, Samuel Zschokke, Peter Stoll and two anonymous reviewers provided valuable comments on the manuscript. Numerous field assistants helped to maintain the field experiment. This work was part of the Swiss Priority Programme Environment supported by the Swiss National Science Foundation (grant 5001-44620 to B. Baur).

References

Addicott J.F (1978) Competition for mutualists: aphids and ants. Can J Zool 56:2093-2096.

Addicott JF (1979) A multispecies aphid-ant association: density dependence and species-specific effects. Can J Zool 57:558-569.

Binz A, Heitz C (1990) Schul- und Exkursionsflora für die Schweiz, mit Berücksichtigung der Grenzgebiete: Bestimmungsbuch für die wildwachsenden Gefässpflanzen. Schwabe.

Bolton B (1995). A new general catalogue of the ants of the world. Harvard Univ Press.

Breton LM, Addicott JF (1992) Does host-plant quality mediate aphid-ant mutualism? Oikos 63:253-259.

Cappuccino N (1987) Comparative population dynamics of two goldenrod aphids: spatial patterns and temporal constancy. Ecology 68:1634-1646

Cappuccino N, Martin M-A (1997) The birch tube-maker *Acrobasis betulella* in a fragmented habitat: the importance of patch isolation and edges. Oecologia 110:69-76.

Collinge SK (2000) Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. Ecology 81:2211-2226.

Cushman JH, Addicott JF (1989) Intra- and interspecific competition for mutualists: ants as a limited and limiting resource for aphids. Oecologia 79:315-321.

Davies KF, Margules CR (1998) Effects of habitat fragmentation on carabid beetles: Experimental evidence. J Anim Ecol 67:460-471.

Debinski, D. M. and Holt, R. D. (2000). A survey and overview of habitat fragmentation experiments. - Conserv. Biol. 14: 342-355.

Dixon AFG (1985) Aphid ecology. Blackie.

Dolt C (2001) Effects of small-scale grassland fragmentation on plants and plant-animal interactions. PhD thesis, Univ Basel.

Edson JL (1985) The influences of predation and resource subdivision on the coexistence of goldenrod aphids. Ecology 66:1736-1743.

Ellenberg H (1986) Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. 4., verbess. Aufl. Eugen Ulmer.

Goverde M, Schweizer K, Baur B, Erhardt A (2002) Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands. Biol Conserv 104:293-299.

Groppe K, Steinger T, Schmid B, Baur B, Boller T (2001) Effects of habitat fragmentation on choke disease (*Epichloë bromicola*) in the grass *Bromus erectus*. J Ecol 89:247-255.

Heinze K (1952) Polyvinylalkohol-Lactophenol-Gemisch als Einbettungsmittel für Blattläuse. Naturwissenschaften 39:285-286.

Holt RD (1996) Food webs in space: an island biogeographic perspective. In Polis GA, Winemiller KO (eds) Food webs : integration of patterns [and] dynamics. Chapman and Hall, pp. 313-323.

Holt RD, Robinson GR, Gaines S (1995) Vegetation dynamics in an experimentally fragmented landscape. Ecology 76:1610-1624.

Kareiva P (1984) Predator-prey dynamics in spatially structured populations: manipulating dispersal in a coccinellid-aphid interaction. In Levin SA, Hallam TG (eds) Mathematical Ecology 54. Springer-Verlag, pp. 368-389.

Kareiva P (1987) Habitat fragmentation and the stability of predator-prey interactions. Nature 326:388-390.

Kienzle U (1979) Sukzessionen in brachliegenden Magerwiesen des Jura und des Napfgebietes. PhD thesis, Univ Basel.

Kindlmann P, Dixon AFG (1992) Optimum body size: effects of food quality and temperature, when reproductive growth rate is restricted, with examples from aphids. J Evol Biol 5: 677-690.

Kruess A, Tscharntke T (1994) Habitat fragmentation, species loss, and biological control. - Science 264:1581-1584.

Kruess A, Tscharntke T (2000) Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. Oecologia 122:129-137.

Lacy RC, Lindenmayer DB (1995) A simulation study of the impacts of population subdivision on the mountain brushtail possum *Trichosurus caninus* Ogilby (Phalangeridae: Marsupialia) in South-eastern Australia: II. Loss of genetic variation within and between subpopulations. Biol Conserv 73:131-142.

Laurance WF, Yensen E (1991). Predicting the impacts of edge effects in fragmented habitats. - Biol Conserv 55:77-92.

Lei G-C, Hanski I (1997) Metapopulation structure of *Cotesia melitaearum*, a specialist parasitoid of the butterfly *Melitaea cinxia*. Oikos 78:91-100.

Offenberg J (2000) Correlated evolution of the association between aphids and ants and the association between aphids and plants with extrafloral nectaries. Oikos 91:146-152.

Offenberg J (2001) Balancing between mutualism and exploitation: the symbiotic interaction between *Lasius* ants and aphids. Behav Ecol Sociobiol 49:304-310.

Remaudière G, Remaudière M (1997) Catalogue des Aphididae du monde - catalogue of the world's Aphididae. Institut National de la Recherche Agronomique.

Robert Y (1987) Dispersion and migration. In Minks AK, Harrewijn P (eds) Aphids their biology, natural enemies and control, vol. A. Elsevier, pp. 299-312.

Robinson GR, Holt RD, Gaines MS, Hamburg SP, Johnson ML, Fitch HS, Martinko EA (1992). Diverse and contrasting effects of habitat fragmentation. Science 257:524-526.

Robinson GR, Quinn JF (1988) Extinction, turnover and species diversity in an experimentally fragmented California annual grassland. Oecologia 76:71-82.

Roland J, Kaupp WJ (1995) Reduced transmission of forest tent caterpillar (Lepidoptera: Lasiocampidae) nuclear polyhedrosis virus at the forest edge. Environ Entomol 24:1175-1178.

Sakata H, Hashimoto Y (2000) Should aphids attract or repel ants? Effect of rival aphids and extrafloral nectaries on ant-aphid interactions. Pop Ecol 42:171-178.

SAS Institute (1990) SAS/STAT user's guide: version 6. SAS Institute Inc.

SAS Institute (1998) Statview. SAS Institute Inc.

Satterthwaite FW (1946) An approximate distribution of estimates of variance components. Biometrics Bull 2:110-114.

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5:18-32.

Simberloff D (2000) What do we really know about habitat fragmentation. Tex J Sci 52 (Suppl.):5-22.

Sokal RR, Rohlf FJ (1995) Biometry. 3d ed. W. H. Freeman and Company.

Stadler B (1995) Adaptive allocation of resources and life-history trade-offs in aphids relative to plant quality. Oecologia 102:246-254.

Sudd JH (1987) Ant aphid mutualism. In Minks AK, Harrewijn P (eds) Aphids their biology, natural enemies and control, vol. A. Elsevier, pp. 355-365.

Völkl W (1992) Aphids or their parasitoids: Who actually benefits from ant-attendance. J Anim Ecol 61:273-281.

Zoller H (1947) Studien an *Bromus erectus*-Trockenrasengesellschaften in der Nordwestschweiz, speziell im Blauengebiet. Ber Geobot Inst ETH, Stift Rübel 1946:51-81.

Zschokke S, Dolt C, Rusterholz H-P, Oggier P, Braschler B, Thommen GH, Lüdin E, Erhardt A, Baur B (2000) Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation. Oecologia 125:559-572.

Appendix A. Aphid species and density (individuals/ 0.25 m^2) recorded in experimental plots in 1998. In a few cases the aphid species could not be determined (only nymphs or alatae were found). Frequency indicates in how many experimental plots (fragments and control plots) a particular species was recorded at the two study sites (N: Nenzlingen, 40 plots; V: Vicques, 32 plots). Aphid densities of single species were calculated on the basis of plots occupied by the particular species (means ± 1SD). The number of plots is given in parentheses. Ant species observed at aphid colonies: Lf: *Lasius flavus* (Fabricius), Lp: *L. paralienus* Seifert, M: *Myrmica* sp.

Aphid species	Host plants	Frequency		Aphid density				Ant species
		N	V	Fragments		Control plots		
Acyrthosiphon loti (Theobald, 1913)	*Lotus corniculatus*		1	-		0.01	(1)	-
A. malvae poterii Prior et Stroyan, 1964	*Sanguisorba minor*	13	6	1.50 ± 2.37	(13)	0.12 ± 0.10	(6)	-
Aphis acetosae Linnaeus, 1761	*Rumex acetosa*	1		0.30	(1)	-		Lp
A. confusa Walker, 1849	*Knautia arvensis*, *Scabiosa columbaria*	6		11.25 ± 9.93	(4)	13.79 ± 11.93	(2)	Lp
A. craccivora Koch, 1854	*Lotus corniculatus*	1	3	16.50 ± 29.12	(4)	-		Lp, M
A. euphorbiae Kaltenbach, 1843	*Euphorbia cyparissias*	1		3.64	(1)	-		Lp
A. helianthemi Ferrari, 1872	*Helianthemum nummularium*		2	7.96 ± 5.71	(2)	-		Lp, M
A. plantaginis Goeze, 1778	*Plantago lanceolata*	2		1.05	(1)	0.21	(1)	Lp
	Plantago media		1	0.89	(1)	-		Lp
A. pomi DeGeer, 1773	*Crataegus monogyna*		1	0.14	(1)	-		Lp
A. sanguisorbae Schrank, 1801	*Sanguisorba minor*	2		0.03 ± 0.02	(2)	-		Lp
Aphis sp.	*Salvia pratensis*	4		4.46 ± 7.12	(3)	0.07	(1)	Lp
Aphis sp.	*Senecio erucifolius*	1		-		0.25	(1)	-
Aphis sp.	*Origanum vulgare*		1	504	(1)	-		Lp
A. stachydis Mordvilko, 1929	*Betonica officinalis*	9	6	1.37 ± 1.67	(9)	12.78 ± 29.03	(6)	Lf, Lp
Brachycaudus sp. (alatae and nymphs)	unknown		1	0.05	(1)	-		Lp
Dysaphis (*Pomaphis*) *plantaginea* (Passerini, 1860)	*Plantago media*	1	5	0.07 ± 0.10	(3)	0.02 ± 0.01	(3)	-
Macrosiphum rosae (Linnaeus, 1758)	*Knautia arvensis*	6		22.15 ± 31.17	(5)	25.00	(1)	Lp
	Rosa sp.		1	-		0.10	(1)	-
Myzaphis rosarum (Kaltenbach, 1843)	*Rosa* sp.		1	0.01	(1)	-		-
Myzus (*Galiobium*) *langei* (Börner, 1933)	*Galium verum*		1	44.44	(1)	-		Lp
Myzus sp. (alatae)	unknown		1	-		0.01	(1)	-
Semiaphis sp.	unknown		1	-		0.06	(1)	Lp
unidentified species (escaped)	*Veronica* sp.	1		-		0.01	(1)	-
unidentified species (nymph)	*Hieracium pilosella*		1	-		0.01	(1)	-
unidentified species (alatae)	unknown		1	-		0.01	(1)	-

Appendix B. Plant taxa infested by aphids in Nenzlingen (N) and Vicques (V) in the years 1997-1999.

Plant species	1997		1998		1999	
Agrimonia eupatoria L.	N				N	V
Anthyllis vulneraria L.					N	
Betonica officinalis L.	N	V	N	V	N	V
Centaurea jacea L.		V				V
Chamaespartium sagittale P. Gibbs					N	
Crataegus monogyna Jacq.	N			V		
Daucus carota L.					N	V
Euphorbia cyparissias L.			N		N	
Galium verum L.	N			V	N	V
Genista tinctoria L.						V
Helianthemum nummularium Miller				V	N	
Hieracium pilosella L.				V	N	V
Hypericum perforatum L.	N	V			N	V
Knautia arvensis Duby	N	V	N		N	V
Lathyrus pratensis L.	N				N	
Lotus corniculatus L.	N	V	N	V	N	V
Ononis repens L.	N				N	
Origanum vulgare L.	N			V	N	V
Plantago lanceolata L.		V	N			
Plantago media L.	N		N	V	N	V
Prunella grandiflora Scholler		V			N	V
Prunus spinosa L.					N	V
Rosa sp.				V		
Rumex acetosa L.			N			
Salvia pratensis L.	N	V	N	V	N	
Sanguisorba minor Scop.	N		N	V	N	V
Scabiosa columbaria L.			N		N	
Senecio erucifolius L.			N			V
Thymus serpyllum L.					N	
Trifolium sp.					N	V
Veronica sp.	N		N		N	
Viola hirta L.					N	

Chapter III

Effects of experimental small-scale grassland fragmentation on spatial distribution, density, and persistence of ant nests

B. Braschler, B. Baur

Ecological Entomology 28: 651-658

B. Braschler, B. Baur

Department of Integrative Biology, Section of Conservation Biology (NLU), University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland

Abstract. 1. Grassland fragmentation is expected to influence the abundance of different invertebrate species to a different extent. Fragmentation-related effects are of particular importance in species that interact with many other species.

2. We examined the density and spatial distribution of nests of 15 ant species in experimentally fragmented calcareous grasslands at three sites in the Northern Swiss Jura mountains. Fragments of different size (0.25 m^2, 2.25 m^2 and 20.25 m^2) were isolated by a 5 m wide strip of frequently mown vegetation. Control plots of corresponding size were situated in adjacent undisturbed grassland.

3. Three years after initiation of the experiment, ant nest density did not differ between fragments and control plots. Six years after initiation of the experiment, however, ant nest density and forager abundance were higher in large fragments than in large control plots. Ant nests tended to occur more frequently along the edge of fragments than in the core area. Persistence time of nests of the most abundant species, *Lasius paralienus*, tended to be shorter in fragments than in control plots. Furthermore, persistence time was longer in nests situated close to the fragment edge than in nests in the core area.

4. Effects on nest density, edge effects on the spatial distribution of nests and the relationships between nest density and environmental factors were more pronounced when only nests of *L. paralienus* were considered. Implications of these findings for plant and other invertebrate species are discussed.

Key words. Abiotic factors, ants (Hymenoptera: Formicidae), calcareous grasslands, density, habitat fragmentation, nest dispersion, nest persistence

Introduction

Habitat fragmentation is considered as a major threat to biodiversity (Saunders *et al.*, 1991; Collinge, 2000; Simberloff, 2000). Fragmentation reduces the area suitable to the organisms and creates isolated subpopulations by disrupting the exchange of individuals and preventing gene flow (Lacy & Lindenmayer, 1995). Fragmentation also influences interactions among species (Kareiva, 1987; Kruess & Tscharntke, 1994; Groppe *et al.*, 2001; Goverde *et al.*, 2002; Braschler *et al.*, 2003) and ecological processes (Robinson *et al.*, 1992).

Previous research revealed species-specific reactions to habitat fragmentation: some species decreased in abundance, others became more abundant, while still others seemed to be

unaffected by the fragmentation of their habitat (Kareiva, 1984; Davies *et al.*, 2000; Zschokke *et al.*, 2000). Consequently, further work was dedicated to the identification of traits that allow to predict a species' response to fragmentation (Davies *et al.*, 2000). However, even within guilds, different species may show different responses towards habitat fragmentation.

In the present study, we examined effects of small-scale grassland fragmentation on the dynamics of ants, a group that is characterised by a variety of interactions with species from very different taxonomic groups (Hölldobler & Wilson, 1990). Ant communities are mainly structured by intra- and interspecific competition for suitable nest sites and food resources. An overdispersed or regular nest distribution, which can most frequently be observed in nature, is generally explained as a result of competition (Levings & Traniello, 1981; Ryti & Case, 1984, 1986; Hölldobler & Wilson, 1990). However, aggregated and random distributions of ant nests have also been reported (Ryti & Case, 1984; Herbers, 1985, 1989; Soares & Schoereder, 2001). An aggregated pattern can result from spatial heterogeneity of the substrate or colony budding (Soares & Schoereder, 2001). Ant nests may persist at the same place for a few days up to many years. The suitability of a nest site is determined by a range of abiotic and biotic environmental conditions including degree of shading (vegetation cover), soil moisture, soil depth, availability of nesting materials (stones, branches, litter, cavities etc.), temperature, availability of food resources in the neighbourhood and positions of neighbouring ant nests. Many of these factors may be affected by habitat fragmentation.

The present study was undertaken to examine the effect of small-scale habitat fragmentation on the spatial distribution and density of ant nests in nutrient-poor, semi-dry, calcareous grasslands in the Swiss Jura mountains. Fragmentation could influence ant nest distribution and density in several ways. In the present long-term fragmentation experiment, above-ground plant biomass increased in fragments (Zschokke *et al.*, 2000; Dolt, 2001). Increased shading of nests may lead to nest relocation (Carlson & Gentry, 1973; Smallwood, 1982). However, the increase in vegetation cover may also provide more food resources and thus support a higher ant density. On the other hand, ant density could be reduced in fragments as the surrounding (mown) isolation area offers little food. Furthermore, some ant species may benefit from the conditions prevailing in fragments and become stronger competitors, while others may suffer from the altered conditions. Any change in ant species composition may be reflected by a different nest distribution pattern.

We examined ant nest distribution 3 and 6 years after the initiation of the experiment. The following questions were addressed: (1) does the experimental fragmentation affect density, spatial distribution and persistence time of ant nests, (2) are the spatial distribution and

persistence time of nests influenced by the edge of fragments, and (3) do fragmentation effects increase with the duration of the experiment?

Material and methods

Study sites

Ant nest distribution was assessed in three calcareous grasslands situated near the villages of Nenzlingen (10 km S of Basel; 47˚ 34' N, 7˚ 35' E), Movelier (26 km SW of Basel) and Vicques (26 km SSW of Basel) in the Northern Swiss Jura mountains. Originally covered by beech forest, these grasslands have been grazed by cattle for many centuries, leading to the characteristic vegetation of the *Teucrio-Mesobrometum* (Ellenberg, 1986). A description of the sites is given in Baur *et al.* (1996) and Zschokke *et al.* (2000).

Fragmentation experiment

The experimental fragmentation of the grasslands was created in spring 1993 by mowing the vegetation around the fragments (Zschokke *et al.*, 2000). One experimental unit, called block, contained two small (0.5 x 0.5 m), one medium (1.5 x 1.5 m) and one large (4.5 x 4.5 m) fragment, all of them separated by a 5-m wide strip of mown vegetation, as well as the corresponding control plots, which were mirror-symmetrically arranged and surrounded by undisturbed vegetation (Fig. 1). Within a block, the positions of the different sizes of fragment-control plot pairs as well as the control and fragment halves were randomised. The experimental set-up consisted of 12 blocks (five in Nenzlingen, three in Movelier and four in Vicques) with 48 fragments (24 small, 12 medium and 12 large) and 48 corresponding control plots. The distances between blocks within the sites ranged from 25 to 135 m. The blocks were part of larger study areas (1.5 - 2 ha) that were enclosed by fences to exclude large herbivores. The experimental fragmentation had been maintained since April 1993 by frequently (6-12 times per year) mowing the area between the fragments in the period from March to October. The entire experimental area was mown in late autumn every year to prevent succession.

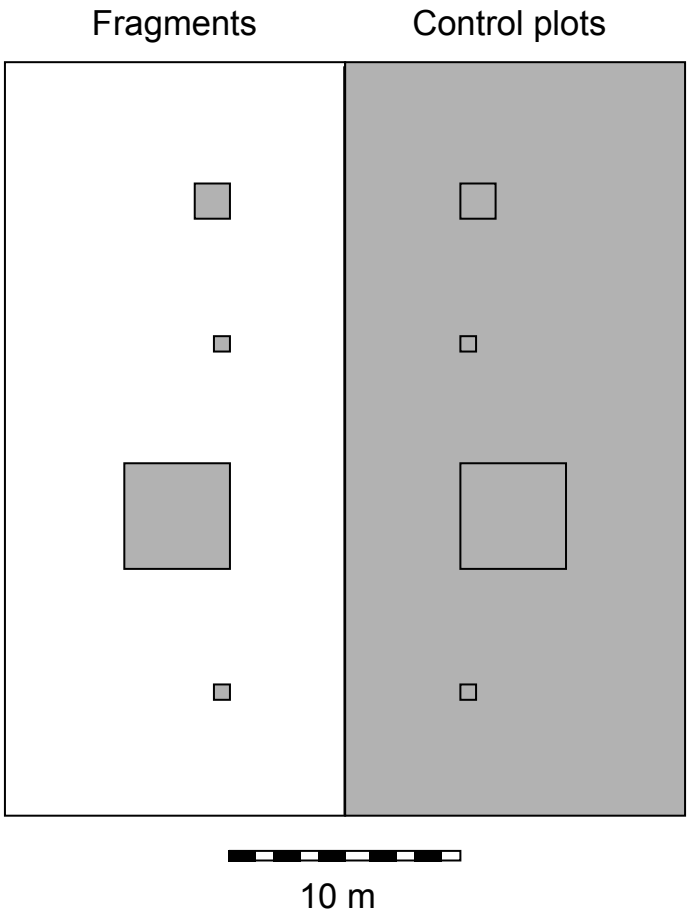


Fig. 1. Diagram of one block of the fragmentation experiment. A block contained two small (0.5 x 0.5 m), one medium (1.5 x 1.5 m) and one large (4.5 x 4.5 m) fragment and corresponding control plots. The isolation area between the fragments (shown in white) was frequently mown.

Field methods

Spatial distribution and density of ant nests

The positions of ant nests were mapped in all fragments and control plots between 12 March and 12 June 1996 (3 years after the initiation of the experimental fragmentation). Nests were identified by carefully searching the plots for visual signs and by following the workers at baits (sugar solution in plastic caps measuring 2.9 cm in diameter) back to their nests. Nest positions were again mapped in large fragments and control plots between 29 July and 16 October 1999 (6 years after initiation of the fragmentation). Fragments and control plots of the same block were examined on the same or succeeding day to avoid errors due to seasonal differences in ant activity.

Forager abundance

To examine the relationship between nest density and forager abundance, foragers were counted at baits the day before mapping the nest positions in 1999. We placed 181 baits (sugar solution in plastic caps) in each large fragment and control plot. After an exposition of 1 h, at each bait ants were counted for 2 min. Foragers of most species were observed at sugar baits including individuals of the predominantly subterranean species *Lasius flavus* (Fabricius) and *Solenopsis fugax* (Latreille). Additional baits were placed around the plots examined. These baits attracted foragers from the surroundings of the experimental plots and thus reduced the error of the focal count (i. e. number of foragers from nests in the plots).

Nest persistence

The positions of randomly-chosen nests of the most abundant species, *Lasius paralienus* Seifert, were checked every 3 weeks between 2 June and 28 October 1997. At the end of the survey only three ant colonies (5%) were still active. Nest persistence was only studied in Nenzlingen (39 nests in large and medium-sized fragments and 21 in control plots). Persistence time was defined as number of weeks active ants were observed at a nest site plus 1.5 weeks. In a few deserted nests, active ants were observed at a later date. In some cases the nest site was later used by another species. These cases were recorded as nest reopening.

Environmental factors

Above-ground plant biomass was estimated by clipping the plants at a height of 5 cm above ground level (to preserve rosettes) between 6 and 15 October in 1996 (Dolt, 2001). In small plots, the entire vegetation was collected. In large and medium plots, randomly chosen subsamples of 0.25 m^2 were harvested (20 subsamples in large plots and 5 subsamples in medium plots). In 1999, 17 subsamples of 0.0625 m^2 were harvested in large plots (H.-P. Rusterholz, unpubl. data). Plants were oven-dried (60˚C for 2 days and 80˚C for 2 hours) and weighed. In both years presence/absence lists of plant species were compiled for all experimental plots by examining each plot three times during the season.

To examine whether ant nest density was influenced by abiotic factors we used the indicator scores of Landolt (1977) calculated from presence/absence data of the plant species for temperature (scale from 1, indicator for cold conditions found only in alpine zones, to 5, thermophilous species), soil humidity (1, arid land plants to 5, wetland plants), soil humus content (1, species on soil without humus layer, to 5, species on soils with high humus content), light (scale from 1, species of deep shade, to 5, plants of full sun), soil acidity (a

gradient of soil acidity and lime content from 1, calcifuges (pH = 3 - 4.5), to 5, calcicoles (pH > 6.5)), and soil nutrients (1, species with little requirements for soil nitrogen to 5, species with high requirements for soil nitrogen).

Statistical analyses

Data were analysed in two steps. First, the nests of all species were considered. Second, only nests of the most abundant species, *L. paralienus*, were considered. In analyses on nest density also the second (*L. flavus*) and the third most abundant species (*Myrmica sabuleti* Meinert) were analysed separately. All other species were rare or did not occur in some of the study sites (Appendix). A two-way ANOVA was used to examine the effects of fragmentation and plot size on nest density in 1996. In 1999, unpaired t-tests were used to analyse differences in nest density between large fragments and control plots. As variances were unequal between groups approximate degrees of freedom were calculated following Satterthwaite (1946).

To examine the spatial distribution of ant nests in large fragments and control plots nearest-neighbour distances were calculated for both 1996 and 1999 (Clark & Evans, 1954). As the positions of nests in the surrounding area were not recorded in 1996, a modification was used (Donnelly, 1978). c-values were calculated from observed and expected distances (Clark & Evans, 1954). Positive c-values indicate overdispersion of nests while negative values indicate an aggregated nest distribution. Departure from zero (random distribution) was tested using one-sample *t*-tests with combined data from all fragments and all control plots. A two-way ANOVA was used to examine the effects of year and fragmentation on nearest-neighbour distances. For the analysis of *L. paralienus* nests only plots containing 5 and more nests were considered.

For each nest the distance to the nearest edge of the experimental plot was measured. A possible edge effect was examined by comparing the number of nests in edge zones of increasing width (10-70 cm, in steps of 10 cm) and in the remaining core area in large fragments with the number of nests in edge and core zones of control plots using 2 x 2 independence tests. Persistence time of *L. paralienus* nests was analysed by ANCOVA. Fragmentation was considered as fixed factor and nest distance to the nearest edge was entered as covariate.

To examine the relationships between nest density and plant biomass and species richness simple and quadratic regressions were calculated using residuals from ANOVAs (type III, factor size (medium or large), calculated separately for fragments and control plots) in

1996. In 1999, normal simple and quadratic regression analysis was used as nest density was only assessed in large plots.

Data on species richness of grasses and forbs were square root-transformed and those on plant biomass, forager density and nearest-neighbour distances were log-transformed. Data on ant nest density and nest distance to the edge were log(y+1)-transformed. Mean values ± 1 SE are presented throughout. The six Landolt indicator scores were all derived from the same plant species composition and thus cannot be considered independent. Therefore, a sequential Bonferroni correction with a significance level of $\alpha = 0.05/6$ was applied in tests using indicator scores. Statistical analyses were performed using SAS 8.2 (SAS Institute, 2000) for general linear models and StatView 5.0 (SAS Institute, 1998) for 2 x 2 tests of independence.

Results

Ant species richness and composition

In all, nests of 15 ant species belonging to 7 genera were found in the experimental plots (Appendix). Workers of *Formica pratensis* Retzius and *F. sanguinea* Latreille were observed to forage in the experimental plots, although no nests were found in these plots. Workers of 7 further species were observed in the surroundings of the experimental plots. In all sites, the most abundant species was *Lasius paralienus* followed by *L. flavus* and *Myrmica sabuleti*.

Ant nest density and forager abundance

In 1996, 3 years after the initiation of the experiment, ant nest density did not differ between fragments and control plots (ANOVA; all species: $F_{1,90} = 0.02$, $P = 0.90$; *L. paralienus*: $F_{1,90} = 0.04$, $P = 0.83$; *L. flavus*: $F_{1,90} = 0.15$, $P = 0.70$; *M. sabuleti*: $F_{1,90} = 1.51$, $P = 0.22$). Neither plot size nor the interaction fragmentation x plot size did affect nest density (ANOVA; $P > 0.25$ in all cases). In 1999, however, large fragments contained a higher density of *L. paralienus* nests than control plots (fragments: 0.54 ± 0.03 nests/m^2, control plots: 0.41 ± 0.05 nests/m^2; $t = 2.35$, d.f. = 16.5, $P = 0.0316$), while no significant difference in nest density was found when all species were considered (fragments: 0.83 ± 0.06 nests/m^2, control plots: 0.68 ± 0.07 nests/m^2; $t = 1.70$, d.f. = 22, $P = 0.10$) or when nests of *L. flavus* (fragments: 0.12 ±

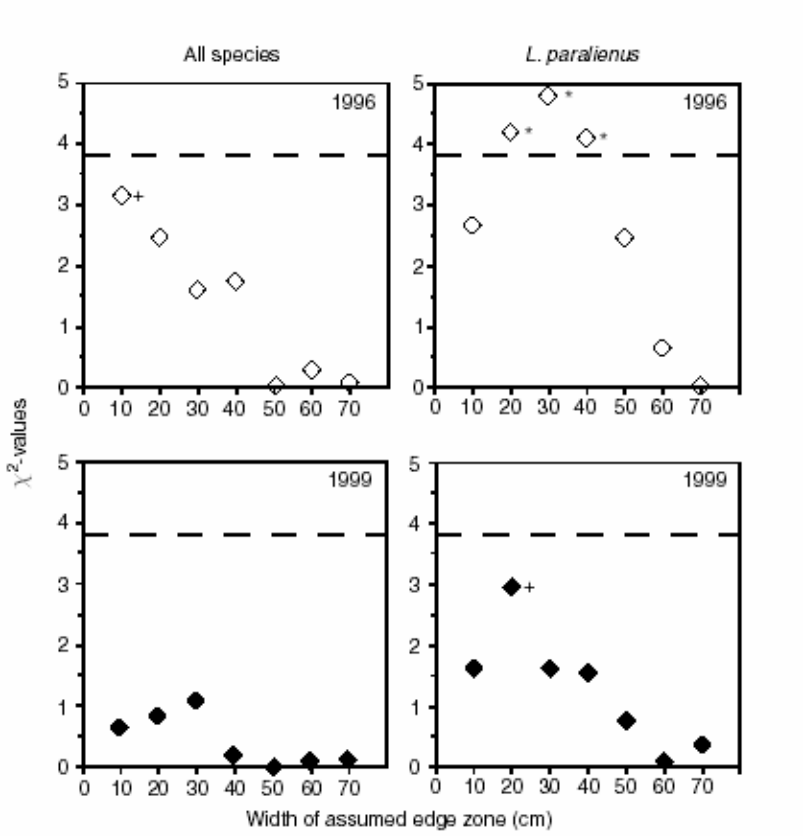


Fig. 2. χ^2-values resulting from 2 x 2 independence tests that examined the proportion of nests in the edge strip and the remaining interior area of fragments in relation to the proportion of nests in the assumed edge strip and core area of control plots. The width of the assumed edge zone was increased from 10 to 70 cm in steps of 10 cm. χ^2-values above the broken line indicate a significantly larger proportion of ant nests in the edge strip than in the core area of fragments compared to the distribution of nests in control plots. $^+$ $P < 0.1$, * $P < 0.05$.

0.13,control plots: 0.10 ± 0.19; $t = 0.45$, df = 22, $P = 0.66$) or *M. sabuleti* (fragments: 0.06 ± 0.02, control plots: 0.06 ± 0.02; $t = 0.00$, df = 22, $P > 0.99$) were considered. In 1999, forager abundance was larger in fragments (number of foragers counted per bait in 2 min; 1.29 ± 0.24) than in control plots (0.64 ± 0.13; $t = 2.53$, d.f. = 22, $P = 0.0191$). This was mainly a result of the higher forager abundance of the dominant species *L. paralienus* in fragments (1.17 ± 0.23) compared with that in control plots (0.52 ± 0.11; $t = 2.74$, d.f. = 22, $P = 0.0121$).

Spatial distribution of ant nests

In fragments and control plots ant nests were either overdispersed or randomly distributed (Table 1). The experimental fragmentation did not affect the nearest-neighbour distance

(ANOVA; $F_{1,44} = 0.21$, $P = 0.65$). Neither did the nearest-neighbour distance differ between years ($F_{1,44} = 1.83$, $P = 0.18$) nor was there an interaction between the two factors ($F_{1,44} = 0.31$, $P = 0.58$). A similar result was obtained when exclusively nests of *L. paralienus* were considered (fragmentation: $F_{1,38} = 0.03$, $P = 0.86$, year: $F_{1,38} = 0.00$, $P = 0.95$, fragmentation x year: $F_{1,38} = 1.01$, $P = 0.32$).

Considering the spatial distribution of ant nests in relation to the edge of large experimental plots, ant nests tended to occur more frequently in a 10 cm wide strip along the edge of the fragment than along the assumed edge of control plots in 1996 (Fig. 2). For *L. paralienus*, the effect was significant for 20-40 cm wide edge zones (Fig. 2). In 1999, the edge effect was less pronounced. *Lasius paralienus* nests tended to occur more frequently in 20 cm wide edge zones of fragments than in control plots (Fig. 2). This suggests that the edge affects the spatial distribution of ant nests over a distance of up to 40 cm.

Nest persistence in fragments and control plots

Nest persistence time of *L. paralienus* tended to be lower in fragments than in control plots ($F_{1,56} = 2.89$, $P = 0.0947$). Mean persistence time was 9.9 ± 0.9 weeks for *L. paralienus* nests in fragments and 12.0 ± 0.9 weeks for nests in control plots. There was a significant interaction between fragmentation and nest distance to the plot edge ($F_{1,59} = 5.04$, $P = 0.0287$). Nests situated close to the edge of fragments persisted longer than those in the core area of fragments ($r^2 = 0.12$, $F_{1,37} = 5.21$, $P = 0.0283$). No relationship between nest persistence time and distance to the assumed edge was found in control plots ($r^2 = 0.08$, $F_{1,37} = 1.57$, $P = 0.23$). In 44 of 114 (38.6%) abandoned nests, the site was at least temporarily reoccupied by either *L. paralienus* (21 nests, 18.4%) or another species (23 nests, 20.2%). Reopening frequency did not differ between fragments and control plots ($\chi^2 = 0.08$, d.f. = 2, $P = 0.96$).

Ant nest density and environmental factors

Above-ground plant biomass was larger in fragments than in control plots in 1996 (large plots: fragments: 284.7 ± 17.5 g/m^2, control plots: 234.6 ± 13.4 g/m^2, paired-$t = 4.53$, $P = 0.0009$; medium plots: fragments: 336.4 ± 29.4 g/m^2, control plots 261.8 ± 18.7 g/m^2, paired-$t = 3.74$, $P = 0.0033$; d.f. = 11 in both cases). In 1999, the difference was not significant (fragments: 472.1 ± 18.6 g/m^2, control plots: 422.6 ± 24.8 g/m^2, paired-$t = 2.13$, d.f. = 11, $P = 0.0564$). Plant biomass increased both in large fragments and control plots from 1996 to 1999 (paired-$t = 16.72$, d.f. = 11, $P < 0.0001$; control plots: paired-$t = 14.28$, d.f. = 11, $P < 0.0001$). Species

richness of grasses and that of forbs did not differ between fragments and control plots in either year. Plant species richness did not change between 1996 and 1999. Comparing Landolt's indicator scores in fragments and control plots yielded no significant differences after sequential Bonferroni correction in large and medium plots in 1996 and in large plots in 1999. However, fragments became dryer between 1996 and 1999 (Wilcoxon ranked sign: humidity: $P = 0.0076$, significant at $\alpha = 0.05$ after Bonferroni correction). In control plots Landolt indicator scores did not change over the same period.

Ant nest density of all species together was neither related to plant biomass nor to species richness of grasses or forbs in 1996. However, ant nest density tended to increase with species richness of grasses and decreased with species richness of forbs in fragments in 1999 (grass species richness: $y = -0.017 + 0.074x$, $r^2 = 0.25$, $t = 1.82$, $P = 0.0992$; forb species richness: $y = 0.527 - 0.043x$, $r^2 = 0.41$, $t = 2.63$, $P = 0.0253$; d.f. = 10 in both cases). No similar relationship was found in control plots in 1999. *Lasius paralienus* nest density tended to decrease with above-ground plant biomass and decreased with species richness of grasses and forbs in fragments in 1996 (plant biomass: $y = 2.44*10^{-6} - 0.464x$, $r^2 = 0.16$, $t = 2.01$, $P = 0.0580$; grass species richness: $y = 1.393*10^{-6} - 0.164x$, $r^2 = 0.20$, $t = 2.29$, $P = 0.0326$; forb species richness: $y = 1.328*10^{-6} + 0.102x$, $r^2 = 0.22$, $t = 2.43$, $P = 0.0242$; d.f. = 21 in all cases). In 1999, *L. paralienus* nest density in fragments was neither related to plant biomass nor to plant species richness. *Lasius paralienus* nest density in control plots was not related to plant biomass in either year. However, *L. paralienus* nest density in control plots tended to decrease with species richness of grasses and forbs in 1996 and increased with species richness of forbs in 1999 (grass species richness 1996: $y = 2.013*10^{-6} - 0.104x$, $r^2 = 0.13$, $t = 1.75$, d.f. = 21, $P = 0.0944$; forb species richness 1996: $y = 0.045 - 0.022x - 0.104x^2$, $r^2 = 0.15$, $t = 1.88$, d.f. = 21, $P = 0.0738$; forb species richness 1999: $y = -0.118 + 0.041x$, $r^2 = 0.35$, $t = 2.30$, d.f. = 10, $P = 0.0442$). Considering Landolt indicator scores, nest density of all species tended to increase with decreasing soil pH in fragments in 1999 ($r_s = -0.78$, $n = 12$, $P < 0.1$ after sequential Bonferroni correction). In contrast, *L. paralienus* nest density decreased with decreasing soil pH and tended to increase with light intensity in medium-sized fragments in 1996 (soil acidity: $r_s = 0.80$, $P < 0.05$; light: $r_s = 0.74$, $P < 0.1$; P- values after sequential Bonferroni correction, $n = 12$ in both cases). No correlation between ant nest density and any of the Landolt indicator scores was found in control plots in either year (after Bonferroni correction).

Table 1. Density and nearest-neighbour distances of ant nests in large fragments and control plots for nests of all ant species (All) and for nests of *L. paralienus* (Lp). Only plots containing 5 and more nests were considered. c-values were calculated after Clark & Evans (1954). Positive c-values indicate overdispersion while negative c-values indicate an aggregated nest distribution. One-group *t*-tests were used to examine deviations of c-values from zero (random distribution). Means ± 1 SE are shown. *n* indicates the number of experimental plots.

Year	Treatment		*n*	Number of nests/ m^2	Nearest-neighbour distance (cm)		c	*t*	*P*	Spatial distribution
					Observed	Expected				
1996	Fragments	All	12	0.74 ± 0.12	65.1 ± 4.0	64.1 ± 4.7	0.55 ± 0.13	1.61	0.13	Random
		Lp	10	0.65 ± 0.12	72.8 ± 6.3	68.8 ± 5.9	0.46 ± 0.27	1.72	0.12	Random
	Control plots	All	12	0.77 ± 0.10	73.2 ± 8.0	62.7 ± 5.2	0.99 ± 0.38	2.59	0.0253	Overdispersed
		Lp	9	0.61 ± 0.10	77.1 ± 5.8	69.6 ± 5.6	0.90 ± 0.33	2.69	0.0274	Overdispersed
1999	Fragments	All	12	0.83 ± 0.06	61.3 ± 3.9	56.3 ± 2.5	0.60 ± 0.29	2.11	0.0582	Overdispersed (tendency)
		Lp	12	0.54 ± 0.03	78.5 ± 4.6	68.7 ± 1.8	0.83 ± 0.32	2.59	0.0252	Overdispersed
	Control plots	All	12	0.68 ± 0.07	61.2 ± 4.4	62.8 ± 3.0	-0.17 ± 0.31	-0.56	0.59	Random
		Lp	11	0.44 ± 0.04	73.6 ± 7.9	77.8 ± 3.5	-0.22 ± 0.51	-0.44	0.67	Random

Discussion

The experimental fragmentation affected the density and spatial distribution of ant nests in several ways. Nest density of the most abundant species *L. paralienus* was higher in large fragments than in large control plots in 1999. Furthermore, ant nest distribution was influenced by the fragment edge. Fragmentation effects were most pronounced in nests of *L. paralienus*. This can be explained by species-specific habitat requirements. *Lasius paralienus* is a xerothermophilous species, which builds its nests in the soil or under stones (Seifert, 1992). Foragers frequently climb on plants and bushes attending aphid colonies and extrafloral nectaries (for details on the biology see Seifert (1992)).

In the experimental plots nests of 15 species were recorded (Appendix). Some of these species prefer cooler and moister sites for their nests than *L. paralienus*, while the majority prefer dry and warm nest sites. As a consequence, species-specific responses to the changed environmental conditions in the fragments can be expected.

The experimental fragmentation altered a variety of environmental factors that may determine the suitability of ant nest sites. Above-ground plant biomass was higher in fragments than in control plots in the years 1996-1999 (Dolt, 2001). More shading of nests through higher vegetation may lead to nest relocation in some species (Carlson & Gentry, 1973; Smallwood, 1982). A higher plant productivity may also increase herbivore and detrivore abundance and thus enhance food resources for ants. In the grasslands examined the abundance of some invertebrate groups was influenced by plant productivity and plant species richness (Braschler *et al.*, in press). Furthermore, the density of aphids, an important food resource for most ant species in the examined grasslands, was higher in fragments than in control plots (Braschler *et al.*, 2003). This could partly be a result of a higher density of tending ants as the proportion of aphid colonies with ant-attendance was increased in fragments. However, aphid colonies without ant-attendance were also more numerous in fragments than in control plots (Braschler *et al.*, 2003).

Effects of fragment edges on the nest distribution ranged from a few cm (nests of all species together) to a maximum of 40 cm (nests of *L. paralienus*). This corresponds with the findings of Zschokke *et al.* (2000) who recorded significant temperature changes over a distance of a few cm along the fragment edges. Most of the ant species present in the localities examined prefer dry and warm grasslands. This may explain both the slightly increased nest density in the edge zone of fragments and the higher ant density in fragments 6 years after the

initiation of the fragmentation experiment. Indicator scores of plants showed that the conditions in fragments became dryer during the experimental period of 6 years. *Lasius paralienus* nests situated near the edge of fragments persisted longer than those in the centre of fragments. This could be a result of a limited number of alternative nest sites or of favourable conditions in the edge zone of fragments. The latter explanation is supported by the higher nest density in this species in the edge zone of fragments.

There was no clear fragmentation effect on the nearest-neighbour distance between ant nests. Nests distribution in the experimental plots tended towards overdispersion. In the literature overdispersed, aggregated and random patterns of ant nest distribution have been reported (Levings & Traniello, 1981; Herbers, 1985, 1989; Soares & Schoereder, 2001; Cerda *et al.*, 2002). Overdispersion of ant nests is generally considered to result from competition for food between ant colonies (Traniello, 1989). Overdispersion of nests can result from space preemption when established colonies prey on founding queens and thus prevent the establishment of young colonies near old nests (Deslippe & Savolainen, 1995). Furthermore, asymmetric competition between colonies of different size can result in a reduced survival of small colonies near large colonies (Deslippe & Savolainen, 1995). Other factors like predation may also contribute to a regular nest distribution (Ryti & Case, 1986; Hölldobler & Wilson, 1990; Deslippe & Savolainen, 1995).

As ant colonies often persist for years, changes in nest densities are expected to take longer than changes in abundance in other arthropod groups. In contrast, behavioural patterns like nest relocation frequency and the small-scale distribution of ant nests may adjust faster to the altered conditions. In our field study, persistence time of *L. paralienus* nests tended to be shorter in fragments, though nests close to the edge persisted for longer than those in the core area of fragments. Nest density was affected by the fragmentation 6 years after the initiation of the experiment. The ability of ants to adjust their nest structure to changing environmental conditions and the potentially long life of ant colonies makes it necessary to study effects of habitat change on ant populations over several years.

Experimental studies on habitat fragmentation are highly biased with regard to taxa and type of habitat considered (Debinski & Holt, 2000). Regardless of their abundance and diversity, the response of grassland insects to fragmentation has hardly been examined (Steffan-Dewenter & Tscharntke, 2002). Ants with their crucial role in this ecosystem are of particular interest as changes in ant abundance are expected to affect a variety of other species. In the present fragmentation experiment, changes in the population dynamics of aphids - a group with a close association to ants - could partly be explained by changes in ant abundance

and ant-tending intensity of aphid colonies (Braschler *et al.*, 2003). Changes in ant density may further affect numerous prey species of the ants and may also influence ant services like seed distribution and pollination in some plant species. Furthermore, numerous arthropod species spend at least part of their life cycle in ant nests. A change in nest persistence time may affect guest species. Moreover, changes in nest persistence time or nest density may affect soil properties. Many of the observed changes in ant nest density, the spatial distribution of ant nests and nest persistence time were relatively small. However, they translated into strong differences in the number of ant foragers observed on baits and the number of ants tending aphids. Thus, even subtle changes in nest density may have a large impact on ant services.

Acknowledgements

We are grateful to C. Dolt and H.-P. Rusterholz for data on plant biomass and species composition and to S. Schüpbach and P. Leuenberger for field assistance. G. Armbruster, P. Stoll, S. Zschokke and an anonymous referee provided valuable comments on the manuscript. This work was part of the Priority Programme Environment of the Swiss National Science Foundation (grant 5001-44620 to B. Baur).

References

Baur B, Joshi J, Schmid B, Hänggi A, Borcard D, Stary J, Pedroli-Christen A, Thommen GH, Luka H, Rusterholz H-P, Oggier P, Ledergerber S, Erhardt A (1996) Variation in species richness of plants and diverse groups of invertebrates in three calcareous grasslands of the Swiss Jura mountains. Rev Suisse Zool 103:801- 833.

Braschler B, Lampel G, Baur B (2003) Experimental small-scale grassland fragmentation alters aphid population dynamics. Oikos 100:581-591.

Braschler B, Zschokke S, Dolt C, Thommen GH, Oggier P, Baur B. (2003) Grain-dependent relationships between plant productivity and invertebrate species richness and biomass in calcareous grasslands. Basic Appl Ecol 5:15-24.

Carlson DM, Gentry JB (1973) Effects of shading on the migratory behavior of the Florida harvestor ant, *Pogonomyrmex badius*. Ecology 54:452-453.

Cerda X, Dahbi A, Retana J (2002) Spatial patterns, temporal variability, and the role of multi-nest colonies in a monogynous Spanish desert ant. Ecol Entomol 27:7-15.

Clark PJ Evans FC (1954) Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445-453.

Collinge SK (2000) Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. Ecology 81:2211-2226.

Davies KF, Margules CR, Lawrence JF (2000) Which traits of species predict population declines in experimental forest fragments? Ecology 81:1450-1461.

Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. Conserv Biol 14:342-355.

Deslippe RJ, Savolainen R (1995) Mechanisms of competition in a guild of formicine ants. Oikos 72:67-73.

Dolt C (2001) Effects of small-scale grassland fragmentation on plants and plant-animal interactions. PhD thesis, Univ Basel, Switzerland.

Donnelly K (1978) Simulations to determine the variance and edge-effect of total nearest neighbor distance. In I Hodder (ed.) Simulation Methods in Archaeology, pp. 91-95. Cambridge Univ Press, London.

Ellenberg H (1986) Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. Eugen Ulmer, Stuttgart.

Goverde M, Schweizer K, Baur B, Erhardt A (2002) Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands. Biol Conserv 104:293-299.

Groppe K, Steinger T. Schmid B, Baur B, Boller T (2001) Effects of habitat fragmentation on choke disease (*Epichloë bromicola*) in the grass *Bromus erectus*. J Ecol 89:247-255.

Herbers JM (1985) Seasonal structuring of a north temperate ant community. Insectes Soc 32:224-240.

Herbers JM (1989) Community structure in north temperate ants: temporal and spatial variation. Oecologia 81:201-211.

Hölldobler B, Wilson EO (1990) The Ants. Springer-Verlag, Berlin.

Kareiva P (1984) Predator-prey dynamics in spatially structured populations: manipulating dispersal in a coccinellid-aphid interaction. In Levin SA, Hallam TG (eds) Mathematical Ecology, pp. 368-389. Springer-Verlag, Berlin.

Kareiva P (1987) Habitat fragmentation and the stability of predator-prey interactions. Nature 326:388-390.

Kruess A, Tscharntke T (1994) Habitat fragmentation, species loss, and biological control. Science, 264:1581-1584.

Lacy RC, Lindenmayer DB (1995) A simulation study of the impacts of population subdivision on the mountain brushtail possum *Trichosurus caninus* Ogilby (Phalangeridae: Marsupialia), in South-Eastern Australia. II. Loss of genetic variation within and between subpopulations. Biol Conserv 73:131-142.

Landolt E (1977) Ökologische Zeigerwerte zur Schweizer Flora. Ver Geobot Inst ETH, Stift Rübel, Zürich, 64:1-208.

Levings SC, Traniello JFA (1981) Territoriality, nest dispersion, and community structure in ants. Psyche 88:265-319.

Robinson GR, Holt RD, Gaines MS, Hamburg SP, Johnson ML, Fitch HS, Martinko EA (1992) Diverse and contrasting effects of habitat fragmentation. Science 257:524-526.

Ryti RT, Case TJ (1984) Spatial arrangement and diet overlap between colonies of desert ants. Oecologia 62:401-404.

Ryti RT, Case TJ (1986) Overdispersion of ant colonies: a test of hypotheses. Oecologia 69:446-453.

SAS Institute (1998) StatView. SAS Institute Inc., Cary, North Carolina.

SAS Institute (2000) SAS/STAT usoftware. Release 8.02. SAS Institute Inc., Cary, North Carolina.

Satterthwaite FW (1946) An approximate distribution of estimates of variance components. Biometrics Bull 2:110-114.

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5:18-32.

Seifert B (1992) A taxonomic revision of the palaearctic members of the ant subgenus *Lasius* s. str. (Hymenoptera: Formicidae). Abh Ber Naturkundemus Görlitz, 66/5:1-67.

Seifert B (1996) Ameisen beobachten, bestimmen. Naturbuch Verlag, Augsburg.

Simberloff D (2000) What do we really know about habitat fragmentation. Tex J Sci 52 (Suppl.):5-22.

Smallwood J (1982) Effect of shade and competition on emigration rate in the ant *Aphaenogaster rudis*. Ecology 63:124-134.

Soares SM, Schoereder JH (2001) Ant-nest distribution in a remnant of tropical rainforest in southeastern Brazil. Insectes Soc 48:280-286.

Steffan-Dewenter I, Tscharntke T (2002) Insect communities and biotic interactions on fragmented calcareous grasslands - a mini review. Biol Conserv 104:275-284.

Traniello JFA (1989) Foraging strategies of ants. Ann Rev Entomol 34:191-210.

Zschokke S, Dolt C, Rusterholz H-P, Oggier P, Braschler B, Thommen GH, Lüdin E, Erhardt A, Baur B (2000) Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation. Oecologia 125:559-572.

Appendix. Nest density of ant species in fragments and control plots in 1996 and 1999. The number of nests per m^2 (mean ± SE) and number of plots occupied (in parenthesis) are given. Nomenclature follows Seifert (1996). Sites: N: Nenzlingen, M: Movelier, V: Vicques. x indicates species nesting in experimental plots, + indicates species that occur in the site but not in the experimental plots. Densities are calculated on the basis of occupied plots. In 1999, only large plots were mapped.

	N	M	V	Density			
				1996		1999	
				Fragments	Control plots	Fragments	Control plots
Myrmicinae							
Myrmecina graminicola (Latreille 1802)	x		+	0.05 (1)	-	-	-
Myrmica ruginodis Nylander 1846	x	+		-	-	0.05 (1)	-
Myrmica scabrinodis Nylander 1846	x	x	x	-	0.05 ± 0.00 (2)	-	0.05 ± 0.00 (2)
Myrmica sabuleti Meinert 1860	x	x	x	0.57 ± 0.32 (12)	0.17 ± 0.05 (8)	0.10 ± 0.02 (7)	0.12 ± 0.02 (6)
Myrmica schencki Emery 1894	x	x	x	0.05 (1)	0.05 (1)	0.06 ± 0.01 (4)	0.05 (1)
Myrmica specioides Bondroit 1918	x		x	0.05 (1)	-	0.05 ± 0.00 (4)	0.05 ± 0.00 (2)
Solenopsis fugax (Latreille 1798)	x	+	x	0.05 (1)	0.25 ± 0.20 (2)	0.07 ± 0.02 (3)	0.05 ± 0.00 (4)
Tetramorium caespitum (Linnaeus 1758)	x	x	x	0.07 ± 0.03 (2)	0.32 ± 0.12 (2)	0.05 ± 0.00 (2)	0.07 ± 0.03 (2)
Dolichoderinae							
Tapinoma ambiguum Emery 1925			x	0.07 ± 0.03 (2)	0.10 (1)	0.15 (1)	0.08 ± 0.03 (3)
Tapinoma erraticum (Latreille 1798)	x	x		0.25 ± 0.20 (2)	0.16 ± 0.10 (4)	0.10 ± 0.00 (2)	0.06 ± 0.01 (4)
Formicinae							
Formica cunicularia Latreille 1798	x	x	x	0.07 ± 0.03 (2)	0.05 ± 0.00 (3)	0.05 (1)	0.07 ± 0.02 (3)
Formica rufibarbis Fabricius 1793	x	x	x	-	0.05 ± 0.00 (3)	0.10 (1)	0.05 (1)
Lasius flavus (Fabricius 1781)	x	x	x	0.28 ± 0.16 (8)	0.67 ± 0.43 (9)	0.17 ± 0.04 (9)	0.25 ± 0.10 (5)
Lasius niger (Linnaeus 1758)	x			-	0.05 (1)	-	0.05 (1)
Lasius paralienus Seifert 1992	x	x	x	2.04 ± 0.41 (32)	1.91 ± 0.33 (33)	0.54 ± 0.03 (12)	0.41 ± 0.05 (12)

Chapter IV

Experimental small-scale grassland fragmentation alters competitive interactions among ant species

B. Braschler, B. Baur

Oecologia 143: 291-300

Electronic Supplementary Material Supplementary material is available for this article at

http://dx.doi.org/10.1007/s00442-004-1778-x

B. Braschler, B. Baur

Department of Integrative Biology, Section of Conservation Biology (NLU), University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland

Abstract

Different species may respond differently to habitat fragmentation. Theory predicts that abundant generalist species should be less affected by fragmentation than specialist species. In ant communities, the most abundant species is often also behaviourally dominant. Thus, habitat fragmentation could alter competitive interactions between the dominant ant species and the other species. We tested this hypothesis in a long-term grassland fragmentation experiment. Fragments of different size (20.25 m^2 and 2.25 m^2) were isolated by a 5-m wide strip of frequently mown vegetation. Control plots were situated in adjacent undisturbed grassland. Ant density and species composition were assessed 3 years and 6 years after initiation of the experimental fragmentation. The effect of the dominant ant species on the resource use of the other species was examined at natural sugar resources (aphids and extrafloral nectaries) and at artificial sugar baits. *Lasius paralienus* was the most abundant ant species (72% of nests) in the grasslands examined. Species richness and forager density in the other species decreased with increasing density of *L. paralienus* in fragments but not in control plots. The overall forager density of the other species was positively related to their habitat niche overlap with *L. paralienus*. The density of foragers of the other species at sugar resources was not affected by *L. paralienus* forager density. The experimental fragmentation resulted in an increase in natural sugar resources in fragments. This may have reduced the intensity of interspecific competition for sugar resources. Our study shows that the grassland fragmentation altered interactions between the dominant *L. paralienus* and the other ant species.

Key words: Community composition, Dominance, *Euphorbia cyparissias*, Formicidae, Nest density

Introduction

Habitat fragmentation is considered as a major threat to biodiversity (Saunders et al. 1991; Collinge 2000; Simberloff 2000). Fragmentation reduces the area suitable to the organisms and creates isolated subpopulations by disrupting the exchange of individuals and preventing gene flow (Lacy and Lindenmayer 1995). Fragmentation affects species and their interactions on

different spatial scales, ranging from small breaks in an otherwise homogeneous habitat to widely scattered units of remnant habitat in a surrounding area (Lord and Norton 1990). The scale on which a given species responds strongest to habitat fragmentation depends on its biology and thus is species-specific. In the present paper we focus on the effects of habitat fragmentation on the scale of individual isolated fragments using a controlled field experiment.

Theory predicts that generalists should be less influenced by habitat fragmentation than specialists (Mac Nally and Brown 2001; Gibb and Hochuli 2002). Similarly, species of low trophic rank should be less affected than species of high trophic rank (Holt 1996; Davies et al. 2000; Tscharntke et al. 2002). Most of the common species have broad niches and can exist in disturbed habitat or matrix habitat. Consequently, these species are less affected by the isolation following fragmentation (Andrén 1994). Assuming that abundant species benefit from habitat fragmentation then their competitive strength may further increase in fragments. As a result the diversity and density of the other species would decline in fragments. Several studies have shown that habitat fragmentation can alter biotic interactions (Steffan-Dewenter and Tscharntke 1999; Groppe et al. 2001; Goverde et al. 2002; Braschler et al. 2003). For example, interspecific competition might be more intensive in fragments than in undisturbed habitat, because edge effects further reduce the area of undisturbed habitat in fragments. Furthermore, it is often more difficult to emigrate from fragments than to disperse in continuous habitat.

In the present paper we examined the effect of experimental small-scale grassland fragmentation on competitive interactions among ant species. Ant communities are assumed to be structured mainly by intra- and interspecific competition for resources such as food or suitable nest sites (Hölldobler and Wilson 1990). In dry, calcareous and nutrient poor grasslands of the Swiss Jura mountains the majority of ant species are generalist consumers constructing soil nests. An important food resource of these ant species is honeydew from plant-sucking insects but arthropod prey is also required (Seifert 1996). Some species complement their diet by foraging for nectar. The relative importance of the different food resources in the diet varies between species (S1). A few, mostly rare species have more specialised diets. Species with a high overlap either in nest site requirements or diet are expected to compete for these resources (Ryti and Case 1984, 1986; Hölldobler and Wilson 1990).

Ant communities often consist of one or few dominant species, a few subdominant species, several competitively inferior species and some rare specialists (Andersen 1992). Dominant ant species are often very abundant in a given habitat. In the grasslands examined,

Lasius paralienus Seifert, a xerothermophilous species, building nests in the soil or under stones, is the most abundant ant (Braschler and Baur 2003). *Lasius paralienus* foragers frequently climb on plants and bushes attending aphid colonies and extrafloral nectaries (for details on the biology see Seifert (1992)). As a generalist it has a food overlap with several other ant species. Thus, when the competitive strength of *L. paralienus* increases in fragments, negative effects on the resource use and population density in other ants can be expected.

In this paper we tested this hypothesis in a grassland fragmentation experiment that ran for 7 years. In particular, we addressed the following questions: (1) Does fragmentation affect the interaction of the dominant species *L. paralienus* with other ant species? (2) Are species with similar preferences for nest sites and food as *L. paralienus* more affected by the dominant species than those with different nest site and food requirements? And (3) does the density of *L. paralienus* affect the resource use in other ant species?

Material and Methods

Study sites

The fragmentation experiment was carried out in three calcareous grasslands situated in the region of Basel (47° 34' N, 7° 35' E) in the Northern Swiss Jura mountains: in Nenzlingen (13 km S of Basel), Vicques (26 km SSW of Basel) and Movelier (26 km SW of Basel). Originally covered by beech forest, these grasslands have been grazed by cattle for many centuries, leading to the characteristic vegetation of the *Teucrio-Mesobrometum* (Ellenberg 1986). Site descriptions can be found in Baur et al. (1996) and Zschokke et al. (2000).

Fragmentation experiment

The experimental fragmentation of the grasslands was created in spring 1993 by mowing the vegetation around the experimental fragments. One experimental unit, called block, contained one large (4.5 x 4.5 m), one medium (1.5 x 1.5 m) and two small (0.5 x 0.5 m) fragments, all of them separated by a 5 m wide strip of mown vegetation, as well as the corresponding control plots, which were mirror-symmetrically arranged and surrounded by undisturbed vegetation (Fig. 1). Within each block, the positions of the different sizes of fragment-control plot pairs as well as the control and fragment halves were randomised. The distances between blocks within the sites ranged from 25 to 135 m. The distance between sites ranged from 9 to 19 km. The blocks were part of larger study areas (1.5 - 2 ha) that were enclosed by fences to exclude large herbivores. The experimental fragmentation was maintained from April 1993 to November 1999 by frequently (6-12 times per year) mowing the area between the fragments in

the period from March to October. The entire experimental area was mown in late autumn every year to prevent succession. In the present study, only the large and medium fragments and control plots were considered. The experimental set-up thus consisted of 12 blocks (five in Nenzlingen, four in Vicques and three in Movelier) with 24 fragments (12 large and 12 medium) and 24 corresponding control plots.

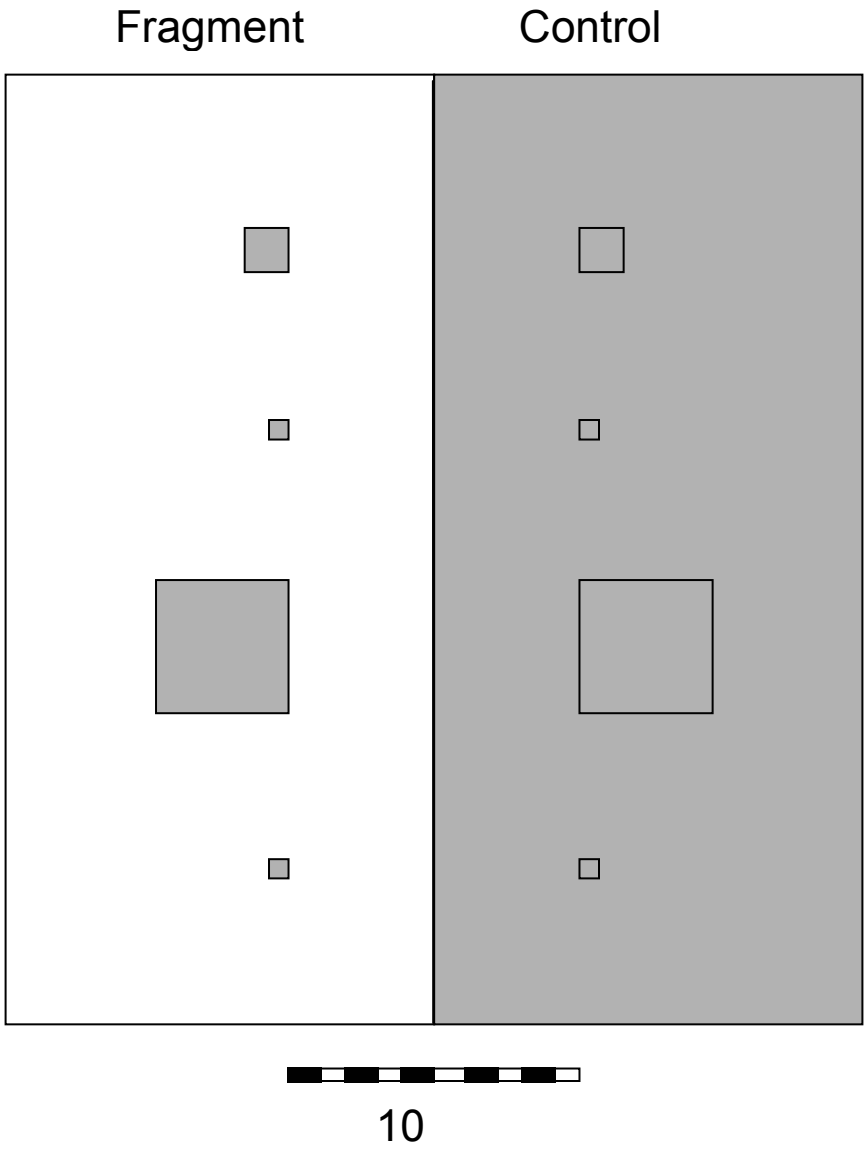


Fig. 1. Diagram of one block of the fragmentation experiment. A block contained two small (0.5 x 0.5 m), one medium (1.5 x 1.5 m) and one large (4.5 x 4.5 m) fragment and corresponding control plots. In the present study, only the large and medium fragments and control plots were used. The isolation area between the fragments (shown in white) was frequently mown.

Field methods

Density of ant nests

Ant nest density was assessed in large and medium fragments and control plots between 12 March and 12 June 1996 (3 years after the initiation of the experimental fragmentation). Nests were identified by carefully searching the plots for visual signs and by following the workers at baits (sugar solution in plastic caps) back to their nests. Fragments and control plots of the same block were examined on the same or succeeding day to avoid errors due to seasonal differences in ant activity.

Abundance of ant workers

In 1999 (6 years after the initiation of the experimental fragmentation), two pitfall traps were placed in each large and medium-sized fragment and control plot. The traps were cylindrical plastic beakers 6.7 cm in diameter and 7 cm deep filled with 10% glycerol solution. The animals were removed every second week between 6 May and 12 August.

Effects of L. paralienus *on resource use by other ant species*

Ant visitors were observed at an artificial and two natural carbohydrate resources. In 1999, 181 baits (sugar solution in plastic caps measuring 2.9 cm in diameter) were placed uniformly at a distance of 25 cm in each large experimental plot on single days between 28 July and 15 October. Ants were counted at each bait during 2 min, 1 hour after the bait was set. Fragments and control plots of the same block were examined on the same day. Additional baits placed around the plots attracted foragers from the surroundings and thus reduced the error of the focal count (i. e. number of foragers from nests in the plots). Some baits were displaced and emptied by crickets, reducing the number of counts to 155 in one plot and to 172 - 181 per plot in the other plots.

Ants of several species regularly visit extrafloral nectaries of plants, e.g. inflorescences of *Euphorbia cyparissias* L. in Nenzlingen and Vicques. Ants were counted at each extrafloral nectary of all flowering *E. cyparissias* for 2 min. in large and medium plots. To estimate the size of this resource the number of nectaries of each inflorescence was counted. Data were obtained between 13 and 28 May 1998 and between 7 and 19 May 1999.

Most of the ant species in the grasslands examined collect honeydew of aphids. The number of ants visiting aphid colonies were counted in large and medium plots in Nenzlingen

and Vicques. Aphid colonies were examined in 27 subplots of 50 x 50 cm in large plots and in three subplots in medium plots (in both cases one third of the plot area). Both the number of aphids in that colony was counted and the number of ants attending this aphid colony in 2 min. was counted. Data were obtained between 18 and 30 May 1998 and between 1 and 24 July 1999.

To prevent disturbance, ants were only observed but not collected at the food resources. Thus, identification was not always possible at the species level. We therefore assigned all ants other than *L. paralienus* to the group "other species". In only one plot a nest of *L. niger*, a species that looks similar to *L. paralienus*, was found.

Statistical analyses

ANOVAs with the fixed factors treatment (fragment or control plot), plot size (large or medium, where applicable) and the random factor site were used to compare nest density, worker abundance, resource use and availability of resources in fragments and control plots. These analyses were performed separately for each year. The relationships between nest density or abundance of *L. paralienus* foragers with species richness, nest density or abundance of foragers of the other ant species were examined in two steps. First, we performed ANOVAs with the random factor site and the fixed factor size (where applicable) separately for fragments and control plots of each year. Second, residuals from these ANOVAs were used to calculate partial regressions. This approach combines the advantages of an ANOVA to eliminate the variation by the confounding factors site and plot size with the advantage of regression (analysis of the shape of the relationship). Ant species richness and density are expected to increase with habitat quality. However, the strength of competitive interactions can also vary with habitat quality leading to an overall nonlinear response. In the present paper we studied both the effects of habitat characteristics and of competition on ant communities. Therefore, we used both simple and quadratic regression for the analyses. When the quadratic term was significant the quadratic regression is reported while when both the quadratic and the simple regression were not significant only the simple regression is given.

Niche overlap indices between *L. paralienus* and all other species were calculated to assess whether there is any relationship between the niche overlap in habitat requirements or food preference with the dominant species *L. paralienus* and the abundance of the other ant species. Data on resource use of single ant species were compiled from the literature (see S1

details and references). Niche overlap was calculated using the formula by Pianka (Krebs 1999):

$$O_{jk} = (\sum_i^n (p_{ij} * p_{ik}))/\sqrt{(\sum_i^n p_{ij}^2 * \sum_i^n p_{ik}^2)}$$

where O_{jk} is the measure of niche overlap between species j and species k. p_{ij} is the proportion that resource i is of the total resources used by species j and p_{ik} is the proportion that resource i is of the total resources used by species k. n is the total number of resource states. Simple and quadratic regression analyses were used to examine the relationship between the number of ant nests or worker abundance of each species in all fragments combined and in all control plots combined with the niche overlap indices.

To examine the effect of *L. paralienus* abundance on the resource use by other species estimates of two natural resources (flowering *Euphorbia cyparissias* plants and aphid colonies) were pooled. This yielded a more comprehensive picture of above-ground carbohydrate resource use by ants. An aphid colony was considered as one resource unit that equals one flowering *E. cyparissias* plant. As aphids were only assessed in subsamples measuring 33% of the total area of a plot the number of aphid colonies was multiplied by 3. In a second estimate information on aphid colony size and number of nectaries per flower were considered. In this estimate each single aphid and each nectary were considered as a resource unit. Data from the two years were analysed separately. Similar analyses were conducted to examine the effect of *L. paralienus* abundance on the percentage of sugar baits visited by the other ant species.

Data on ant nest density, abundance at the resources and resource abundance were log (y + 1)-transformed. Data on ant forager abundance (number of workers captured in pitfall traps) were squareroot (y + 0.5)-transformed. Statistical analyses were performed using proc mixed of SAS v 8.2 (SAS Institute 1999) for mixed model ANOVAs and StatView 5.0 (SAS Institute 1998) for all other statistics. Means ± 1 SE are presented throughout.

Results

Species richness and composition

Ant species richness did not differ between fragments and control plots (nests in 1996: fragments: 2.3 ± 0.3, control plots: 2.3 ± 0.3; $F_{1,43} = 0.03$, $P = 0.86$; pitfall traps in 1999: fragments: 8.5 ± 0.4, control plots: 8.1 ± 0.4; $F_{1,20} = 0.05$, $P = 0.83$). Similarly, neither

diversity expressed as Shannon-Wiener index nor equitability differed between fragments and control plots (in all cases $P > 0.20$).

In the three most abundant ant species, nest density did not differ between fragments and control plots in 1996 (number of nests per m^2; *L. paralienus*: fragments: 0.89 ± 1.51, control plots: 0.79 ± 0.14; $F_{1,43} = 0.36$, $P = 0.55$; *L. flavus*: fragments: 0.09 ± 0.06, control plots: 0.08 ± 0.04; $F_{1,43} = 0.03$, $P = 0.87$; *Myrmica sabuleti*: fragments: 0.12 ± 0.05, control plots: 0.06 ± 0.02; $F_{1,43} = 1.16$, $P = 0.29$). In the remaining species nest density was too low for a species-specific analysis.

Abundance of ant workers in pitfall traps was assessed 6 years after the initiation of the experiment in 1999. In none of the 17 species examined a significant difference in abundance between fragments and control plots was found after sequential Bonferroni correction.

Table 1. Nest density, number of workers sampled per pitfall trap and number of foragers recorded per natural food resource (nectaries of flowering *Euphorbia* plants or aphids combined for analyses) or artificial food resource (sugar baits). Means ± 1 SE are given. Values in brackets indicate the percentage of *L. paralienus* on the total figures.

	Year	Fragments	Control plots	Overall
Nest density (m^{-2})	1996	1.01 ± 0.17 (76.1)	1.15 ± 0.16 (67.6)	1.08 ± 0.12 (72.2)
Foraging density (workers collected per pitfall trap)	1999	94.19 ± 7.23 (67.0)	104.88 ± 7.69 (65.9)	99.53 ± 5.28 (66.4)
Use of natural resources (number of foragers per unit of resource (*E. cyparissias* nectary or aphid))	1998	0.11 ± 0.04 (91.2)	0.07 ± 0.02 (91.0)	0.09 ± 0.02 (91.1)
	1999	0.05 ± 0.00 (86.1)	0.05 ± 0.01 (76.3)	0.05 ± 0.01 (81.3)
Use of artificial resources (number of foragers per bait)	1999	1.33 ± 0.26 (90.0)	0.65 ± 0.13 (80.8)	0.99 ± 0.16 (87.0)

Abundance of L. paralienus

Lasius paralienus was the most abundant species both in nest counts (1996) and in pitfall traps (1999) (Table 1). The proportion of *L. paralienus* was even higher when foragers at food resources were considered (Table 1). In 1999, a larger proportion of *L. paralienus* workers visited natural resources (*Euphorbia* nectaries and aphids combined) than were found in pitfall traps both in fragments and control plots (fragments: 86.1 ± 4.7 % (at resources) vs. 61.2 ± 5.3 % (in pitfall traps), paired-$t_{17} = 6.11$, $P < 0.0001$; control plots: 76.3 ± 7.1 % vs. 59.5 ± 5.6 %, paired-$t_{17} = 3.18$, $P = 0.0058$). Similarly, among the ants foraging at artificial sugar baits *L. paralienus* occurred in a larger proportion than expected from the proportion of *L. paralienus* workers found in pitfall traps (fragments: 89.1 ± 1.9 % vs. 59.3 ± 7.3 %, paired-$t_{11} = 4.43$, $P = 0.0010$; control plots: 77.7 ± 5.0 % vs. 59.4 ± 6.9 %, paired-$t_{11} = 3.46$, $P = 0.0053$). This indicates that *L. paralienus* was both numerically and functionally the dominant ant species in the plots examined. The figures for *L. paralienus* worker abundance in pitfall traps presented in this paragraph (resource use) differ slightly from those presented in Table 1 (data from all pitfall traps).

Effect of L. paralienus *abundance on the remaining ant species*

Considering nest counts, species richness of ants decreased with increasing *L. paralienus* nest density in fragments, while no such relationship was found in control plots (Fig. 2). Similarly, ant species richness represented by workers captured in pitfall traps, tended to decrease with increasing abundance of *L. paralienus* workers in fragments (Fig. 2). No relationship between ant species richness and *L. paralienus* worker abundance was found in control plots.

The relationship between nest density of *L. paralienus* and that of the other species was U-shaped in fragments (Fig. 3). No relationship was found in control plots. The abundance of workers in the other species decreased with increasing abundance of *L. paralienus* workers in fragments, while no relationship between the two variables was found in control plots (Fig. 3).

Nest density of both the second and the third most abundant ant species tended to decrease with increasing nest density of *L. paralienus* in fragments, but not in control plots (*L. flavus* in fragments: $t_{19} = 1.89$, $P = 0.074$; in control plots: $t_{19} = 0.33$, $P = 0.75$; *M. sabuleti* in fragments: $t_{19} = 1.88$, $P = 0.076$; in control plots: $t_{19} = 0.69$, $P = 0.50$).

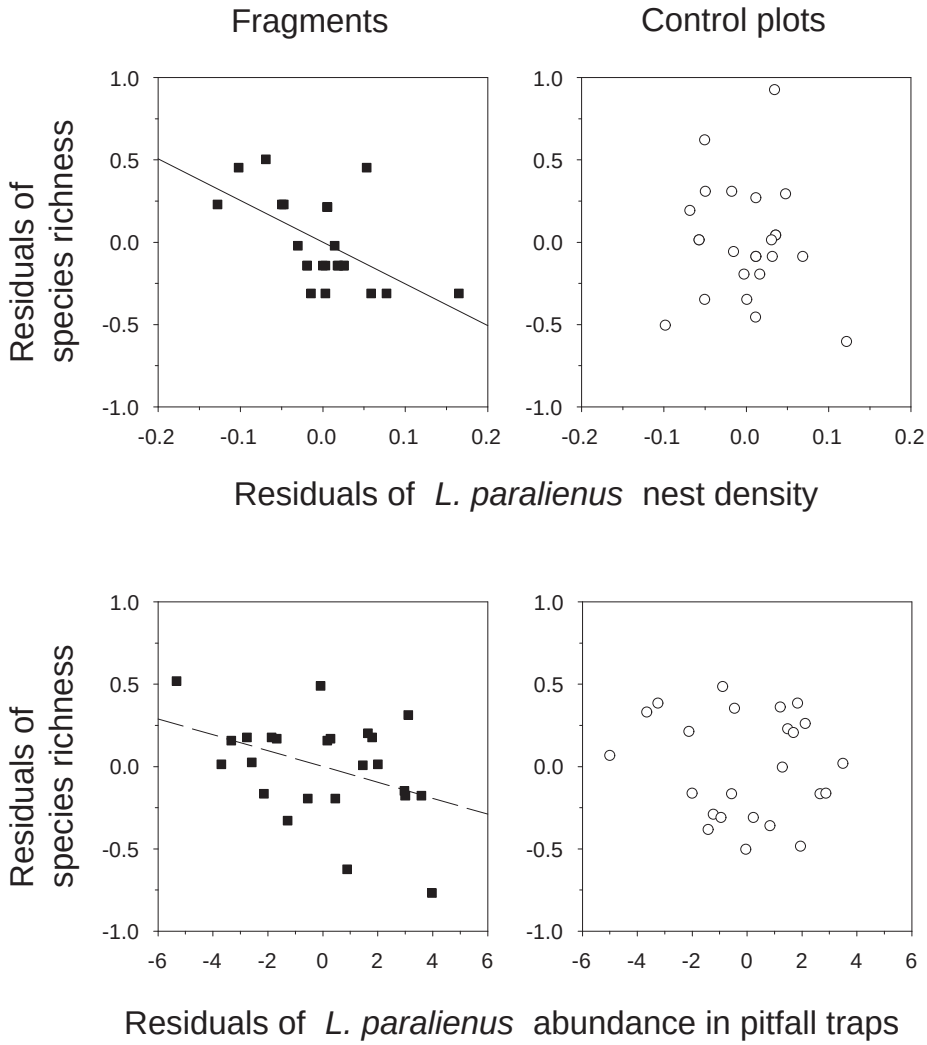


Fig. 2. Relationship between the abundance of the dominant species *Lasius paralienus* and species richness of the other ants in fragments and control plots. The abundance of *L. paralienus* is indicated by the residuals of the number of ant nests found in 1996 (upper plots) and by the residuals of number of workers captured in pitfall traps in 1999 (lower plots). Plots show the residuals from ANOVAs with the random factor site and the fixed factor plot size that were separately calculated for fragments and control plots. Partial regressions are shown as full line when $P < 0.05$ and as dashed line when $P < 0.1$. $N = 24$ in all cases. The regressions are: fragments 1996: $y = 4.219 * 10^{-6} - 2.532x$; $r^2 = 0.32$, $t = -3.21$, $P = 0.0040$; control plots 1996: $y = 1.521 * 10^{-6} - 0.674x$; $r^2 = 0.01$, $t = -0.45$, $P = 0.65$; fragments 1999: $y = 1.707 * 10^{-6} - 0.048x$; $r^2 = 0.16$, $t = -1.94$, $P = 0.067$; control plots 1999: $y = 2.507 * 10^{-6} - 0.018x$; $r^2 = 0.02$, $t = -0.56$, $P = 0.58$.

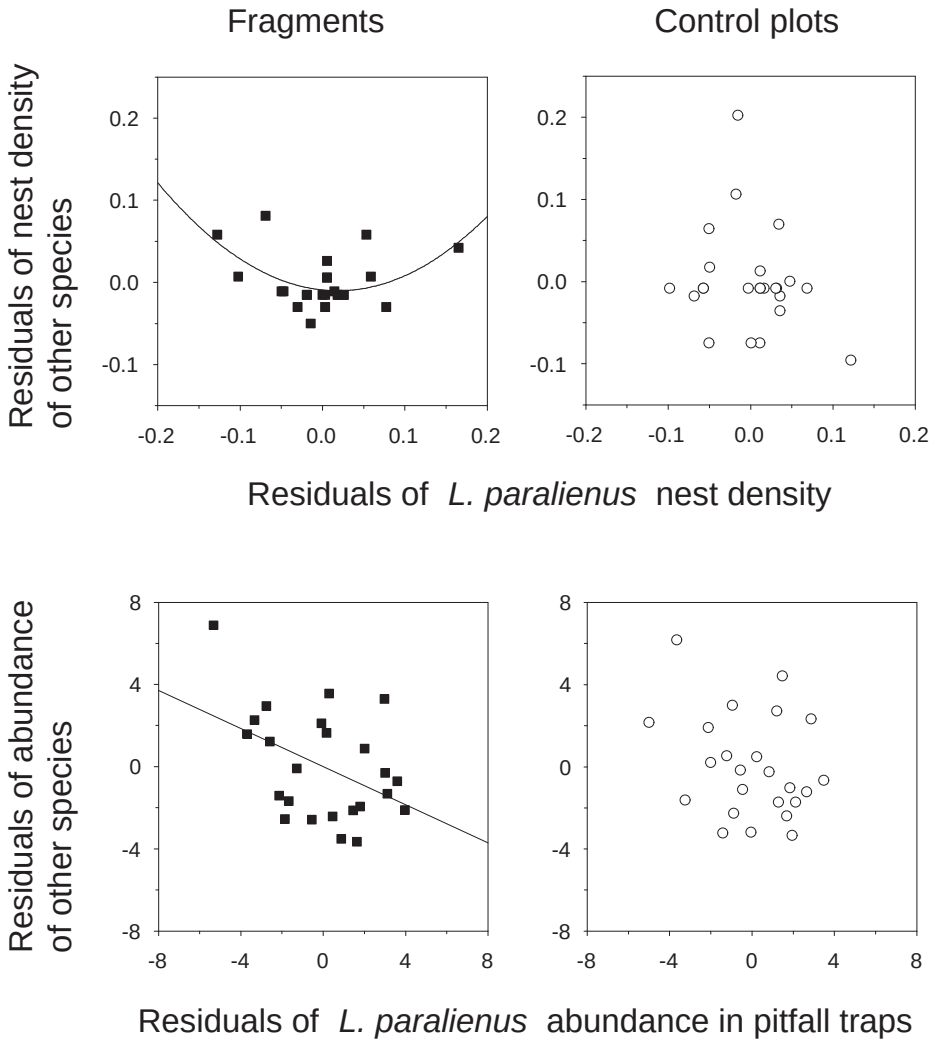


Fig. 3. Relationship between the abundance of the dominant species *Lasius paralienus* and that of the other ant species in fragments and control plots. Abundances are indicated by the residuals of the number of ant nests found in 1996 (upper plots) and by the residuals of the number of workers captured in pitfall traps in 1999 (lower plots). Plots show residuals from ANOVAs with the random factor site and the fixed factor plot size that were separately calculated for fragments and control plots. Partial regressions are shown when $P < 0.05$. For the quadratic regression the *t* and *P*-values refer to the quadratic term. $N = 24$ in all cases. The regressions are: fragments 1996: $y = -0.009 – 0.102x + 2.752x^2$; $r^2 = 0.31$, $t = 3.00$, $P = 0.0069$; control plots 1996: $y = -1.894 * 10^{-6} – 0.273x$; $r^2 = 0.05$, $t = -1.05$, $P = 0.31$; fragments 1999: $y = 4.468 * 10^{-7} – 0.464x$; $r^2 = 0.20$, $t = -2.18$, $P = 0.0422$; control plots 1999: $y = -2.364 * 10^{-6} – 0.325x$; $r^2 = 0.08$, $t = -1.30$, $P = 0.21$.

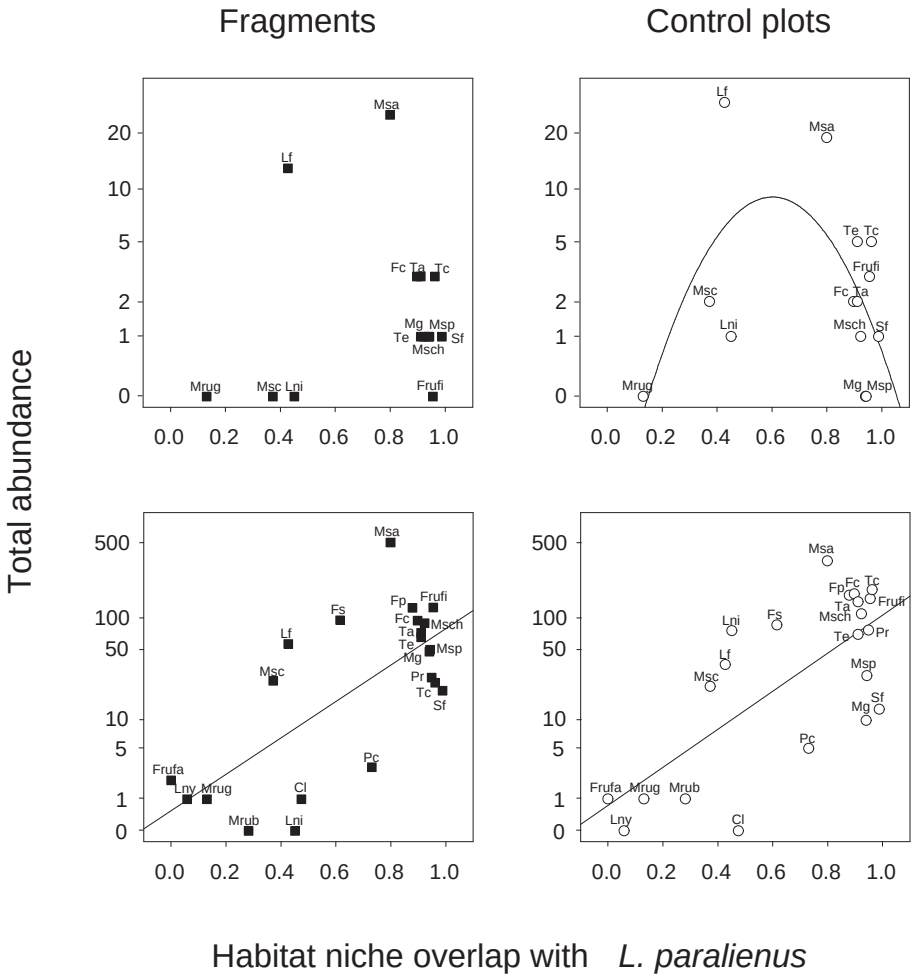


Fig. 4. Relationship between number of nests (upper plots), number of workers captured (lower plots) and the species habitat niche overlap with the dominant species *Lasius paralienus*. Only significant regressions are shown ($P < 0.05$). For the quadratic regressions the *t* and *P*-values refer to the quadratic term. The regressions are: fragments 1996: $y = -0.693 + 4.217x - 3.236x^2$; $r^2 = 0.23$, $t = -1.61$, $P = 0.14$; control plots 1996: $y = -0.761 + 5.847x - 4.878x^2$; $r^2 = 0.35$, $t = -2.41$, $P = 0.0349$; fragments 1999: $y = 0.193 + 1.714x$; $r^2 = 0.50$, $t = 4.49$, $P = 0.0002$; control plots 1999: $y = 0.241 + 1.793x$; $r^2 = 0.52$, $t = 4.65$, $P = 0.0002$. Species are indicated as follows: Cl: *Camponotus ligniperda*, Fc: *Formica cunicularia*, Fp: *F. pratensis*, Frufa: *F. rufa*, Frufi: *F. rufibarbis*, Fs: *F. sanguinea*, Lf: *Lasius flavus*, Lni: *L. niger*, Lny: *Leptothorax nylanderi*, Mg: *Myrmecina graminicola*, Mrub: *Myrmica rubra*, Mrug: *M. ruginodis*, Msa: *M. sabuleti*, Msc: *M. scabrinodis*, Msch: *M. schencki*, Msp: *M. specioides*, Pr: *Polyergus rufescens*, Pc: *Ponera coarctata*, Sf: *Solenopsis fugax*, Ta: *Tapinoma ambiguum*, Te: *T. erraticum*, Tc: *Tetramorium caespitum*.

No relationship between the total number of nests of each ant species in the experimental plots and its habitat niche overlap with the dominant *L. paralienus* was found in fragments (Fig. 4). In control plots, however, the species' abundance was related to their habitat niche overlap with *L. paralienus* (Fig. 4). The relationship was hump-shaped as both the second and the third most abundant species (*L. flavus* and *M. sabuleti*) have an intermediate habitat overlap with *L. paralienus*. In contrast, species with a high habitat overlap with *L. paralienus* were less abundant. Considering the number of workers collected in pitfall traps, the species' abundance was positively correlated with habitat niche overlap with *L. paralienus* both in fragments and control plots (Fig. 4). This indicates that the species composition was strongly influenced by habitat characteristics.

No relationship between the food niche overlap with *L. paralienus* and the abundance of single species was found.

Effect of L. paralienus *on resource use by other species*

The experimental grassland fragmentation affected the abundance of food resources for ants. Natural resource density was higher in fragments than in control plots (flowering *Euphorbia* plants per m^2 and aphid colonies per m^2 combined for analysis; in 1998: fragments: 3.2 ± 0.6, control plots: 1.6 ± 0.3, $F_{1,31} = 5.42$, $P = 0.0266$; in 1999: fragments: 16.3 ± 2.6, control plots: 7.0 ± 0.7, $F_{1,31} = 18.78$, $P = 0.0001$). A similar result was found when single nectaries and aphids were considered as resource units.

L. paralienus visited more baits in fragments than in control plots (fragments: 36% ± 4%, control plots: 22% ± 3%, $F_{1,20} = 8.45$, $P = 0.0087$). In the remaining ant species, no difference in the number of baits visited was found between fragments and control plots (fragments: 9% ± 2%, control plots: 9% ± 2%, $F_{1,20} = 0.01$, $P = 0.94$). In both years, neither *L. paralienus* nor the other ant species differed between fragments and control plots regarding the percentage of natural resources used (flowering *Euphorbia* plants and aphid colonies combined for analysis; $P > 0.23$ in all cases). However, as a consequence of enhanced food abundance in fragments, the total number of *L. paralienus* foragers that were recorded at flowering *Euphorbia* plants and at aphid colonies was still larger in fragments than in control plots (number of workers visiting *Euphorbia* plants or aphids per m^2; in 1998: fragments: 9.0 ± 3.7, control plots: 1.8 ± 1.0, $F_{1,31} = 6.93$, $P = 0.0131$; in 1999: fragments: 13.9 ± 2.6, control plots: 3.8 ± 0.7, $F_{1,31} = 21.80$, $P < 0.0001$). A similar result was obtained for foragers of the other ant

species (in 1998: fragments: 0.20 ± 0.09, control plots: 0.04 ± 0.03, $F_{1,31} = 4.61$, $P = 0.0397$; in 1999: fragments: 1.5 ± 0.5, control plots: 0.5 ± 0.1, $F_{1,31} = 4.22$, $P = 0.0486$).

Neither the percentage of baits visited by foragers of the other species nor the number of foragers of the other species per bait were related to bait use by *L. paralienus* ($P > 0.31$ in all cases). No relationship between the percentage of *Euphorbia* plants and aphid colonies visited by *L. paralienus* and that visited by the foragers of the other species was found either in fragments or in control plots in 1998. In 1999, however, the percentage of *Euphorbia* plants and aphid colonies visited by the other species tended to decrease with the percentage visited by foragers of *L. paralienus* in control plots ($t_{13} = 2.06$, P = 0.060) but not in fragments ($t_{13} = 1.19$, $P = 0.26$). No relationship between the percentage of resources used by *L. paralienus* and by the other species was found when single nectaries or single aphids were considered as resource unit ($P > 0.15$ in all cases).

Discussion

The present study showed that *Lasius paralienus* was the most abundant species in the grasslands examined. The species' relative abundance was even greater at sugar resources than in pitfall traps. Sugar baits were attractive to almost all of the species caught in pitfall traps. In contrast, not all species found in pitfall traps forage for nectar or tend aphids. This indicates that *L. paralienus* was both numerically and functionally dominant and excluded most other ant species from the natural resources examined. Even species known to forage for nectar like *M. sabuleti* and *M. schencki* were never observed at *E. cyparissias* nectaries. However, a few individuals of these species were found to forage on extrafloral nectaries of *Vicia* sp. in the plots.

In the present study two methods were used to assess ant species richness and density. In some ant species colonies, which are the reproductive units of ants, can be split into several nests (Hölldobler and Wilson 1990). However nest density is frequently assumed to correlate with colony density. In contrast, pitfall traps yield information about forager density and individuals from species that have their nests in the surroundings but forage in the experimental plots. Forager density determines the strength of interaction with other organisms. Pitfall traps are widely used in studies on ant diversity (Agosti et al. 2000). However, their use has been questioned because different species differ in trapability (Seifert

1990). This limits the use of pitfall traps when comparing the absolute abundances of different species, although the design of our field experiment allows comparisons between fragments and control plots. In the present study ant species composition assessed by nest counts and pitfall traps was compared for large plots in 1999. Individuals of all species with nests in the plots were caught by pitfall traps and foragers of additional species whose nests were located in the surroundings. Only a few species with large foragers moved large distances to forage in fragments. The high species richness found in pitfall traps was most probably a result of long exposition of the traps (14 weeks).

Numbers are of central importance in determining the outcome of competitive interactions in ants (Hölldobler and Wilson 1990; Holway 1998; Holway and Case 2001). Dominance at food resources by the most abundant ant species has been shown in several studies covering a range of habitats (Andersen 1992). In our experiment, ant species richness of other ant species in fragments was negatively correlated with the density of the dominant species. No similar relationship was found in control plots. This indicates an increased effect of *L. paralienus* density on the ant species composition in fragments. The composition of the ant community in control plots may be the result of past competition that is no longer apparent. However, the changed conditions in fragments alter the relative competitive strength of some species and thus the community composition in the fragments is no longer at equilibrium. This imbalance results in the now apparent competitive interactions.

Non-dominant species in control plots may reduce or even escape competition by using less preferred resources. These alternative resources may have been affected by the experimental grassland fragmentation. In our experiment, the density of *L. paralienus* did not affect the food resource use in other ant species. This contrasts findings of Andersen (1992) and Andersen and Patel (1994) who found negative relationships between the abundance of dominant ants and the abundance and species richness of other ant species at tuna baits in Australian savannahs. In our experiment the increased density of natural sugar resources in fragments could have reduced the competition for them. The increase in natural sugar resources was mainly due to the enhanced aphid density in fragments and may in part have been a result of changes in the ant-aphid interaction. The proportion of ant-attended aphids was larger in fragments than in control plots and tended aphids were more intensively visited in one out of three years of study (Braschler et al. 2003). Other ant food resources like arthropod prey have not been examined.

Although ant communities are commonly considered to be mainly structured by competition, other mechanisms may contribute, e. g. habitat specialisation (Johnson 2001;

Soares et al. 2001; Ribas and Schoereder 2002). In our experiment, species showing a high habitat niche overlap with the dominant *L. paralienus* were more frequently found in pitfall traps than species with a low niche overlap. This indicates that the ant community in the grasslands examined was mainly structured by habitat characteristics. However, species richness in single fragments decreased with the density of the dominant species. Thus, competitive interactions may have shaped the ant community on a small-scale, while external factors may become more important on a larger scale.

The negative relationship between the density of *L. paralienus* workers and that of other ant species in pitfall traps might be a result of competition for suitable nest sites rather than for food. The suitability of a habitat for ants is primarily determined by temperature and humidity, with most ant species preferring relatively warm and dry localities (Hölldobler and Wilson 1990; Seifert 1996). Both factors were affected by the experimental grassland fragmentation. Temperature was increased in the edge zone of fragments (Zschokke et al. 2000) and the fragments soil tended to become drier in the course of the experiment (Braschler and Baur 2003). Ant diversity can be expected to increase when unsuitable cold and moist habitat becomes warmer and drier and thus favourable for more species. However, weak competitors can only coexist with stronger competitors when they are able to use patches with suboptimal conditions. In uniformly favourable habitat, competitive exclusion of weak competitors through the dominant species is expected (Connell 1978; Andersen 1992). The negative linear relationships between *L. paralienus* forager density and species richness and forager density of the other species may thus be interpreted as the declining part of a hump-shaped relationship where ant diversity originally increases with habitat quality but declines under favourable conditions due to competitive exclusion of weak competitors. Hump-shaped relationships between the density of a dominant species and species richness and density of the remaining species have been predicted for sessile organisms like plants and corals (Connell 1978). For terrestrial invertebrates such hump-shaped relationships were observed for ants, whose nests can be compared to sessile organisms (Andersen 1992). Both competitive interactions and habitat characteristics affected ant community composition in the study sites. The relationship between measurements of habitat quality (e.g. productivity) and species richness and density has been best studied in plants. Positive linear relationships between plant diversity and productivity or hump-shaped relationships between diversity and productivity as a consequence of increased competition at higher productivities are most often predicted. However, also negative linear and U-shaped relationships have been widely reported in the

literature (Mittelbach et al. 2001). Similarly, a wide range of responses in different habitats can be expected for ants.

A high overlap in resource use was found between most of the ant species occurring in the grasslands examined. However, the species differ in their effectiveness to use the common resources and in the use of additional resources (S1). Ant species may also differ in their impact on ecosystem services like enriching soil with nutrients. While, some interactions with other taxa are species-specific, many interactions can involve a large number of ant species, e. g. tending of aphids, visiting extrafloral nectaries and distributing seeds with elaiosomes. However, ant species differ also with regard to the benefit they provide to other taxa in a partnership (Addicott 1978, 1979). *Lasius paralienus* is a generalist species that is involved in numerous interactions with other taxa. However, to what degree *L. paralienus* is able to provide ecosystem services remains to be examined. For example, ants pollinate flowers of *E. cyparissias* while visiting the extrafloral nectaries and they disperse *E. cyparissias* seeds (Schürch et al. 2000).

Flowering *Euphorbia* plants and aphid colonies represent food resources at certain places for some time. Ants have been shown to return to stable food resources over a time span of some days to several weeks. The flowering period of *E. cyparissias* overlaps with the period aphids are available. The quality of these two resources was not compared but the attractivity for ants can be expected to differ (Engel et al. 2001). *Euphorbia* nectar is also consumed by a range of winged insects that are potential competitors for the ants (Pfunder and Roy 2000). Winged insects were more effective pollinators of *E. cyparissias* than ants (Schürch et al. 2000). Ants may repel other insects. Thus, a change in ant densities at *Euphorbia* flowers could indirectly affect pollination success. Furthermore, ants may provide protection against some groups of herbivorous insects (Oliveira and Brandão 1991; Engel et al. 2001). The degree of this protection may partly depend on ant density. However, species-specific characters like the ants' body size, their aggressiveness and time of foraging also influence the degree of protection. Thus, a change in ant species composition may affect the protection of plants from herbivores.

The present study showed that grassland fragmentation alters interactions between the dominant *L. paralienus* and the other ant species. As ants interact with many other organisms and the outcome of these interactions frequently depends on the species involved, the observed changed interactions between ant species may also affect other invertebrates and plants.

Acknowledgements

We thank N. Minoretti for field assistance and B. Seifert and R. Neumeyer for their help with ant determination. Samuel Zschokke and two anonymous referees provided constructive comments on the manuscript. Financial support was received from the Swiss National Science Foundation (grant 5001-44620 to B. Baur).

References

Addicott JF (1978) Competition for mutualists: aphids and ants. Can J Zool 56:2093-2096

Addicott JF (1979) A multispecies aphid-ant association: density dependence and species-specific effects. Can J Zool 57:558-569

Agosti D, Majer JD, Alonso LE, Schultz TR (eds) (2000) Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington

Andersen AN (1992) Regulation of "momentary" diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. Am Nat 140:401-420

Andersen AN, Patel AD (1994) Meat ants as dominant members of Australian ant communities: an experimental test of their influence on the foraging success and forager abundance of other species. Oecologia 98:15-24

Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366

Baur B, Joshi J, Schmid B, Hänggi A, Borcard D, Stary J, Pedroli-Christen A, Thommen GH, Luka H, Rusterholz HP, Oggier P, Ledergerber S, Erhardt. A (1996) Variation in species richness of plants and diverse groups of invertebrates in three calcareous grasslands of the Swiss Jura mountains. Rev Suisse Zool 103:801- 833

Braschler B, Baur B (2003) Effects of experimental small-scale grassland fragmentation on spatial distribution, density and persistence of ant nests. Ecol Entomol 28:651-658

Braschler B, Lampel G, Baur B (2003) Experimental small-scale grassland fragmentation alters aphid population dynamics. Oikos 100:581-591

Collinge SK (2000) Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. Ecology 81:2211-2226

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302-1310

Davies KF, Margules CR, Lawrence JF (2000) Which traits of species predict population declines in experimental forest fragments? Ecology 81:1450-1461

Ellenberg H (1986) Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. Eugen Ulmer, Stuttgart

Engel V, Fischer MK, Wäckers FL, Völkl W (2001) Interactions between extrafloral nectaries, aphids and ants: are there competition effects between plant and homopteran sugar sources? Oecologia 129:577-584

Gibb H, Hochuli DF (2002) Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biol Conserv 106:91-100

Goverde M, Schweizer K, Baur B, Erhardt A (2002) Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands. Biol Conserv 104:293-299

Groppe K, Steinger T, Schmid B, Baur B, Boller T (2001) Effects of habitat fragmentation on choke disease (*Epichloë bromicola*) in the grass *Bromus erectus*. J Ecol 89:247-255.

Hölldobler B, Wilson EO (1990) The Ants. Springer, Berlin Heidelberg New York

Holt RD (1996) Food webs in space: an island biogeographic perspective. In Polis GA, Winemiller KO (eds) Food webs: integration of patterns dynamics. Chapman and Hall, New York, pp. 313-323

Holway DA (1998) Factors governing rate of invasion: a natural experiment using Argentine ants. Oecologia 115:206-212

Holway DA, Case TJ (2001) Effects of colony-level variation on competitive ability in the invasive Argentine ant. Anim Behav 61:1181-1192

Johnson RA (2001) Biogeography and community structure of North American seed-harvester ants. Annu Rev Entomol Syst 46:1-29

Krebs CJ (1999) Ecological Methodology. 2nd ed. Benjamin/Cummings, Menlo Park

Lacy RC, Lindenmayer DB (1995) A simulation study of the impacts of population subdivision on the mountain brushtail possum *Trichosurus caninus* Ogilby (Phalangeridae: Marsupialia), in South-Eastern Australia. II. Loss of genetic variation within and between subpopulations. Biol Conserv 73:131-142

Lord JM, Norton DA (1990) Scale and the spatial concept of fragmentation. Conserv Biol 4: 197-202

Mac Nally R, Brown GW (2001) Reptiles and habitat fragmentation in the box-ironbark forests of central Victoria, Australia: predictions, compositional change and faunal nestedness. Oecologia 128:116-125

Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L (2001) What is the observed relationship between species richness and productivity? Ecology 82: 2381-2396

Oliveira PS, Brandão CRF (1991) The ant community associated with extrafloral nectaries in the Brazilian cerrados. In Huxley CR, Cutler DF (eds) Ant-plant interactions. Oxford Univ Press, Oxford, pp. 198-211

Pfunder M, Roy BA (2000) Pollinator-mediated interactions between a pathogenic fungus, *Uromyces pisi* (Pucciniaceae), and its host plant, *Euphorbia cyparissias* (Euphorbiaceae). Am J. Bot 87:48-55

Ribas CR, Schoereder JH (2002) Are all ant mosaics caused by competition? Oecologia 131:606-611

Ryti RT, Case TJ (1984) Spatial arrangement and diet overlap between colonies of desert ants. Oecologia 62:401-404

Ryti RT, Case TJ (1986) Overdispersion of ant colonies: a test of hypotheses. Oecologia 69:446-453.

SAS Institute (1998) StatView. SAS Institute Inc., Cary

SAS Institute (1999) SAS/STAT software: Release 8.02. SAS Institute Inc., Cary

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5:18-32

Schürch S, Pfunder M, Roy BA (2000) Effects of ants on the reproductive success of *Euphorbia cyparissias* and associated pathogenic rust fungi. Oikos 88:6-12

Seifert B (1990) Wie wissenschaftlich wertlose Fangzahlen entstehen - Auswirkungen artspezifischen Verhaltens von Ameisen an Barberfallen direkt beobachtet. Entomol Nachr Ber 34:21-27

Seifert B (1992) A taxonomic revision of the Palaearctic members of the ant subgenus *Lasius* s. str. (Hymenoptera: Formicidae). Abh Ber Naturkundemus Görlitz 66:1-66

Seifert B (1996) Ameisen beobachten, bestimmen. Naturbuch Verlag, Augsburg

Simberloff D (2000) What do we really know about habitat fragmentation. Tex J Science 52 (Suppl.):5-22

Soares SM, Schoereder JH, DeSouza O (2001) Processes involved in species saturation of ground-dwelling ant communities (Hymenoptera, Formicidae). Austral Ecol 26:187-192

Steffan-Dewenter I, Tscharntke T (1999) Effects of habitat isolation on pollinator communities and seed set. Oecologia 121:432-440

Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002) Characteristics of insect populations on habitat fragments: a mini review. Ecol Res 17:229-239

Zschokke S, Dolt C, Rusterholz HP, Oggier P, Braschler B, Thommen GH, Lüdin E, Erhardt A, Baur B (2000) Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation. Oecologia 125:559-572

S1. Habitat and food preferences of the ant species and presence at the investigation sites (N = Nenzlingen, M = Movelier and V = Vicques). Habitats are: F = forest, H = forest edge or hedgerow, W = wetlands or tall forbs, MG = moist grasslands, SD = semidry grasslands (including those with shrubs), D = dry grasslands (including those with shrubs), R = rock, gravel or bare soil, U = urban habitats. Food resources are: N = nectar or other plant juices, HS = honeydew from subterranean plant-suckers, HA = honeydew from above-ground plant-suckers, PS = subterranean prey, SP = small above-ground prey or carrion, MP = medium-sized above-ground prey or carrion, LP = large above-ground prey or carrion, S = seeds without elaiosomes, E = seeds with elaiosomes. Values refer to the proportion of the resource used (0.05 was used as minimum value). Data from studies in Central European countries (Switzerland (a, b, k, p, q), Austria (i), France (f, l) and Germany (c, r, s, t, u, v, w)) were preferentially used to minimize geographical differences in niche use.

Species	Site			Habitats								Food resources									References
	N	M	V	F	H	W	MG	SD	D	R	U	N	HS	HA	PS	SP	MP	LP	S	E	
Camponotus ligniperda (Latreille 1802)		x		0.40	0.20			0.20	0.20			0.10		0.50		0.10	0.15	0.15			a, c, k, v
Formica cunicularia Latreille 1798	x	x	x		0.05	0.05	0.05	0.40	0.35	0.10		0.05		0.50		0.10	0.20	0.10		0.05	a, f, h, i, k, q, v
F. pratensis Retzius 1783	x		x	0.05	0.10			0.05	0.80			0.05		0.50		0.10	0.20	0.10		0.05	b, d, h, k, q, v
F. rufa Linnaeus 1758	x			0.40	0.60							0.05		0.60		0.05	0.15	0.10		0.05	b, c, d, j, k, v, x
F. rufibarbis Fabricius 1793	x	x	x				0.05	0.40	0.50	0.10		0.05		0.50		0.10	0.20	0.10		0.05	h, i, k, v
F. sanguinea Latreille 1798		x	x	0.14	0.14	0.14	0.14	0.15	0.15	0.14		0.05		0.50		0.10	0.20	0.10		0.05	a, c, d, h, i, k, v
Lasius flavus (Fabricius 1781)	x	x	x	0.05	0.05	0.05	0.30	0.45	0.05	0.05			0.75		0.25						a, c, h, i, k, o, v
L. niger (Linnaeus 1758)	x			0.05	0.10	0.05	0.10	0.40	0.05	0.05	0.20		0.25	0.45	0.10	0.10	0.05			0.05	a, c, d, f, h, i, k, n, o, s, u, v

L. paralienus Seifert 1992 #	x	x	x					0.25	0.55	0.20		0.15	0.15	0.40	0.05	0.15	0.05		0.05	i, q, u, v
Leptothorax nylanderi (Förster 1850)	x			0.70	0.20		0.05		0.05			0.15				0.80			0.05	i, k, v
Myrmecina graminicola (Latreille 1802)	x		x	0.10	0.10		0.05	0.20	0.40	0.10	0.05				0.40	0.40	0.20			a, i, v
Myrmica rubra (Linnaeus 1758)		x		0.05	0.05	0.20	0.25	0.15	0.05	0.05	0.20	0.15	0.05	0.35	0.05	0.10	0.15	0.10	0.05	a, d, h, i, k, m, v, w
M. ruginodis Nylander 1846	x	x		0.60	0.05	0.10	0.10	0.10	0.05			0.10	0.05	0.10	0.05	0.15	0.30	0.20	0.05	a, i, m, t, v, w
M. sabuleti Meinert 1860	x	x	x	0.05	0.15			0.45	0.30	0.05		0.10	0.05	0.20	0.05	0.20	0.25	0.10	0.05	a, h, i, m, t, v, w
M. scabrinodis Nylander 1846	x	x	x	0.05		0.25	0.25	0.40	0.05			0.05	0.05	0.05	0.05	0.30	0.35	0.10	0.05	a, c, h, i, m, t, v, w
M. schencki Emery 1894	x	x	x	0.05	0.10		0.05	0.30	0.50			0.15	0.05	0.05	0.05	0.15	0.30	0.20	0.05	a, i, m, t, v, w
M. specioides Bondroit 1918	x		x	0.05	0.05			0.30	0.60					0.05	0.05	0.30	0.45	0.15	0.05	f, h, m, t, k, v, w
Polyergus rufescens (Latreille 1798) $	x		x					0.33	0.67			0.05		0.50		0.10	0.20	0.10	0.05	a, d, c, h, k, v
Ponera coarctata (Latreille 1802)	x	x		0.15	0.05			0.20	0.20	0.20	0.20				0.95	0.05				c, g, h, k, v
Pyramica baudueri (Emery 1875) ¥	x														1.00					e, g
Solenopsis fugax (Latreille 1798)	x	x	x		0.05			0.20	0.60	0.15			0.20		0.80					a, c, f, g, h, i, k, v
Tapinoma ambiguum Emery 1925 †			x	0.05		0.05	0.10	0.35	0.40	0.05		0.10				0.40	0.30	0.15	0.05	(a, h), i, r, v

T. erraticum (Latreille 1798) †	x	x		0.05		0.05	0.10	0.35	0.40	0.05		0.10			0.35	0.30	0.20		0.05	(a, h), k, l, r, v
Tetramorium caespitum (Linnaeus 1758)	x	x	x	0.05		0.05	0.05	0.15	0.45	0.15	0.10		0.25		0.05	0.15			0.55	a, c, d, f, h, i, k, v

L. paralienus was not distinguished from the sibling species *L. alienus* and *L. psammophilus* until recently.

† The two *Tapinoma* species are frequently not distinguished in the literature (references in brackets), but seem to have very similar habitat requirements (r, v). Therefore the same niche was assumed for both species.

$ The slave-making species *Polyergus rufescens* does not forage. Therefore, the food preferences of the two slave species *F. cunicularia* and *F. rufibarbis* were used for niche calculation.

¥ No information on habitats available.

References are: a Agosti (1983); b Agosti and Cherix (1994); c Bellmann (1995); d Carroll and Janzen (1973); e Dejean (1985); f Du Merle et al. (1978); g Emery (1876); h Gallé (1986); i Glaser (1998); j Hölldobler and Wilson (1990); k Kutter (1977); l Lachaume and Meudec (1987); m Lepidopterologen-Arbeitsgruppe (1991); n Pontin (1961); o Pontin (1963); p Savolainen and Vepsäläinen (1988); q Schürch et al. (2000); r Seifert (1984); s Seifert (1988a); t Seifert (1988b); u Seifert (1992); v Seifert (1996); w Wardlaw et al. (1998); x Wellenstein (1952).

References for S1

Agosti D (1983) Faunistisch-ökologische Untersuchungen über Ameisen (Hymenoptera: Formicidae) im Randen, (Kt. Schaffhausen). Diploma thesis, ETH Zürich

Agosti D, Cherix D (1994) Rote Liste der gefährdeten Ameisenarten in der Schweiz. In Duelli P (ed.) Rote Liste der gefährdeten Tierarten in der Schweiz. Bundesamt für Umwelt, Wald und Landschaft, Bern, pp. 45-47

Bellmann H (1995) Bienen, Wespen, Ameisen: Hautflügler Mitteleuropas. Franckh-Kosmos Verlag, Stuttgart

Carroll CR, Janzen DH (1973) Ecology of foraging by ants. Ann Rev Ecol Syst 4:231-257

Dejean A (1985) Etude eco-ethologique de la predation chez les fourmis du genre *Smithistruma* (Formicidae-Myrmicinae - Dacetini) II. Attraction des proies principales (collemboles). Insectes Soc 32:158-172

Du Merle P, Jourdheuil P, Marro JP, Mazet R (1978) Evolution saisonnière de la myrmécofaune et de son activité dans un milieu forestier: Les interactions clairière - lisière-forêt. Ann Soc Entomol France 14:141-157

Emery C (1876) Über hypogäische Ameisen. Stett Entomol Zeit 37:71-76

Gallé L (1986) Habitat and niche analysis of grassland ants (Hymenoptera: Formicidae). Entomol Gen 11:197-211

Glaser F (1998) Die Ameisenfauna des Arzler Kalvarienberges bei Innsbruck (Tirol, Österreich) (Hymenoptera, Formicidae). Ber Naturw-Med Ver Innsbruck 85:257-286

Hölldobler B, Wilson EO (1990) The Ants. Springer, Berlin

Kutter H (1977) Hymenoptera: Formicidae. Schweizerische Entomologische Gesellschaft, Zürich.

Lachaume A, Meudec M (1987) L'exploitation de l'habitat chez la fourmi *Tapinoma erraticum* (Formicidae - Dolichoderinae). Bull Soc Zool France 111:221-224

Lepidopterologen-Arbeitsgruppe (1991) Tagfalter und ihre Lebensräume: Arten, Gefährdung, Schutz : Schweiz und angrenzende Gebiete. Schweizerischer Bund für Naturschutz, Basel

Pontin AJ (1961) Population stabilization and competition between the ants *Lasius flavus* (F.) and *L. niger* (L.). J Anim Ecol 30:47-54

Pontin AJ (1963) Further considerations of competition and the ecology of the ants *Lasius flavus* (F.) and *L. niger* (L.). J Anim Ecol 32:565-574

Savolainen R, Vepsäläinen K (1988) A competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos 51:135-155

Schürch S, Pfunder M, Roy BA (2000) Effects of ants on the reproductive success of *Euphorbia cyparissias* and associated pathogenic rust fungi. Oikos 88:6-12

Seifert B (1984) A method for differentiation of the female castes of Tapinoma ambiguum Emery and Tapinoma erraticum (Latr.) and remarks on their distribution in Europe north of the Mediterranean region (Insecta, Hymenoptera, Formicidae). Faun Abh Staatl Mus Tierkd Dresd 11:151-155

Seifert B (1988a) A revision of the European species of the ant subgenus Chthonolasius (Insecta, Hymenoptera, Formicidae). Entomol Abh Staatl Mus Tierkd Dresd 51:143-180

Seifert B (1988b) A taxonomic revision of the *Myrmica* species of Europe, Asia Minor, and Caucasia (Hymenoptera, Formicidae). Abh Ber Naturkundemus Görlitz 62:1-75

Seifert B (1992) A taxonomic revision of the Palaearctic members of the ant subgenus *Lasius* s. str. (Hymenoptera: Formicidae). Abh Ber Naturkundemus Görlitz 66:1-66

Seifert B (1996) Ameisen beobachten, bestimmen. Naturbuch Verlag, Augsburg

Wardlaw JC, Elmes GW, Thomas JA (1998) Techniques for studying *Maculinea* butterflies: II. Identification guide to *Myrmica* ants found on *Maculinea* sites in Europe. J Insect Conserv 2:119-127

Wellenstein G (1952) Zur Ernährungsbiologie der Roten Waldameise (*Formica rufa* L.). Zeit Pflanzenkr Pflanzenschutz 59:430-451

Chapter V

Grain-dependent relationships between plant productivity and invertebrate species richness and biomass in calcareous grasslands

B. Braschler, S. Zschokke, C. Dolt, G. H. Thommen, P. Oggier, B. Baur

Basic and Applied Ecology 5: 15-24

B. Braschler, S. Zschokke, C. Dolt, G. H. Thommen, P. Oggier, B. Baur

Department of Integrative Biology, Section of Conservation Biology (NLU), University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland

Abstract

The relationships among productivity, species richness and consumer biomass are of fundamental importance for understanding determinants of biodiversity. These relationships may depend on grain size. We examined the relationships between productivity (above-ground phytomass) and plant species richness and between productivity and species richness and biomass of gastropods and grasshoppers using sampling units of different sizes (0.5, 2.75 and 23 m^2) in nutrient-poor, calcareous grasslands in north-western Switzerland in two successive years. Species richness of forbs had a unimodal relationship with productivity in sampling units of 0.5 m^2 and was negatively correlated with productivity at the other two plot sizes in one year. In the other year, forb species richness tended to decrease with productivity in sampling units of 23 m^2. No similar relationship was found for grasses. Gastropod biomass had a unimodal relationship with productivity at 0.5 m^2 in the first year. Grasshopper species richness was correlated with forb species richness at plot sizes of 2.75 and 23 m^2. This study demonstrates that patterns detected between productivity and diversity and between productivity and biomass of consumers depend on the grain size used in the investigation and vary among years.

Die Zusammenhänge zwischen Produktivität, Artenreichtum und Biomasse von Konsumenten sind wichtig, um zu verstehen, was Biodiversität beeinflußt. Diese Zusammenhänge können von der Größe der Untersuchungsfläche abhängig sein. Wir untersuchten während zwei aufeinanderfolgenden Jahren die Zusammenhänge zwischen Produktivität (oberirdische Pflanzenbiomasse) und Artenreichtum von Gefäßpflanzen, sowie zwischen Produktivität und Artenreichtum und Biomasse von Schnecken und Heuschrecken bezüglich dreier räumlicher Skalen (0.5, 2.75 und 23 m^2) in Kalkmagerrasen in der Nordwestschweiz. Der Zusammenhang zwischen dem Artenreichtum von Kräutern und der Produktivität war unimodal in Flächeneinheiten von 0.5 m^2 und negativ in Flächeneinheiten von 2.75 und 23 m^2 im ersten Jahr und war tendenziell negativ in Flächeneinheiten von 23 m^2 im zweiten Jahr, während kein solcher Zusammenhang bei Gräsern gefunden wurde. Der Zusammenhang zwischen Produktivität und Biomasse von Schnecken war unimodal in Flächeneinheiten von 0.5 m^2 im ersten Jahr. Außerdem bestand ein Zusammenhang zwischen dem Artenreichtum von Kräutern und Heuschrecken in Flächeneinheiten von 2.75 und 23 m^2. Diese Arbeit zeigt, daß Zusammenhänge zwischen Produktivität und Diversität sowie zwischen Produktivität und

Biomasse von Konsumenten von der Größe der Untersuchungsfläche abhängen und zwischen Jahren variieren.

Key words: above-ground plant biomass - biodiversity - grasshoppers - Swiss Jura mountains - terrestrial gastropods

Introduction

The patterns and theories of biodiversity provide a sound, scientific basis for the study and management of natural resources (Huston 1994, Rosenzweig 1995). Of particular interest are the relationships among resource productivity and the diversity of plants and coexisting consumer species. Basically, two types of productivity-diversity relationships have been proposed: (1) monotonic, where diversity increases (but may level off) as productivity increases, and (2) unimodal, where diversity increases with productivity at low levels, but eventually decreases at high productivity (Waide et al. 1999, Mittelbach et al. 2001). Numerous authors attributed the decreased diversity at high productivities to increased competitive exclusion under these conditions and argued that high productivity may lead to a decrease in spatial heterogeneity of limiting resources (e.g. Tilman & Pacala 1993, Rosenzweig 1995). However, there are several alternative explanations for the occurrence of unimodal curves (Abrams 1995, Aarssen 2001). Besides productivity, disturbance, spatial heterogeneity and large-scale processes (both in time and space) are major factors regulating small-scale species richness in plant communities (Huston 1994, Grace 1999). However, the relationships between species richness and productivity, disturbance and spatial heterogeneity may have different shapes and may be expressed differently when the data are collected at different grain sizes.

It has been suggested that plant diversity should be important for animal diversity (herbivores and detrivores; e.g. Southwood 1973, Tilman 1988, Knops et al. 1999). Correlative and experimental studies showed that increasing plant diversity increases arthropod herbivore diversity (Lawton 1983, Siemann 1998). However, these studies were often confounded by changes in plant community composition that correlate with changes in plant diversity (Siemann et al. 1998). The current debate on most aspects of diversity regulation suffers from a failure to explicitly consider the relationship between the spatial scales (grain or geographical extent) at which phenomena (e.g. species richness) are evaluated and the spatial scales at which the hypothesised causes of these phenomena operate (Huston 1999, Whittaker et al.

2001). Critical questions concern the appropriate grain size for looking at the effects of local processes and how regional processes are manifested at the grain sizes normally used in ecological measurements.

Biodiversity patterns are strongly affected by the size of the mapping unit. Usually only a small portion of any landscape or habitat patch can be sampled. The minimum mapping unit is not only a problem for vascular plant diversity, it might be quite different in various animal groups as a result of species-specific mobilities and habitat requirements. Thus, a grain size suitable for the assessment of plant diversity might not be suitable for the assessment of invertebrate diversity. To circumvent this problem sampling methods at multiple grain sizes are required.

The present study examines the relationships among productivity, plant species richness and species richness and biomass of gastropods and grasshoppers in calcareous grasslands at three grain sizes in two successive years. Nutrient-poor dry calcareous grasslands are among the most diverse plant communities in Europe (Fischer & Stöcklin 1997, Baur et al. 1996). These extensively used semi-natural habitats are highly threatened by non-sustainable agriculture and abandonment (Fischer & Stöcklin 1997).

The species composition of invertebrate communities in grasslands is affected by numerous abiotic and biotic factors (Siemann 1998). In many cases these factors can be related to obvious proximal habitat components such as the structure and species composition of vegetation on which they live (e.g. in caterpillars and leafhoppers) or to soil conditions (e.g. in ground beetles). The relative contribution of environmental factors (including the vegetation community) in determining the species composition of invertebrate communities may vary among different animal groups. One might expect that a relationship between productivity and invertebrate diversity exists in groups with a close association to plants (e.g. specialised herbivores), whereas such a relationship might be less obvious in groups consisting of generalist feeders including detrivores. The invertebrates considered in the present study represent different groups (detrivores and generalist herbivores: gastropods; generalist herbivores: grasshoppers). Moreover, the relationship between plant productivity and invertebrate diversity might occur at a different spatial scale than the relationship between productivity and plant diversity and it might vary among animal groups due to differences in mobility.

In the present study, we addressed the following questions: (1) Does the size of the sampling unit affect the possible relationships among productivity and species richness of

plants and invertebrates in nutrient-poor, calcareous grasslands, and (2) at which grain size is invertebrate biomass related to plant productivity and plant species richness.

Materials and Methods

Study sites

Species diversity and abundance of different groups of organisms were assessed in three calcareous grasslands situated near the villages of Nenzlingen (10 km S of Basel), Movelier (26 km SW of Basel) and Vicques (26 km SSW of Basel) in the northern Swiss Jura mountains. Originally covered by beech forest, these grasslands have been grazed by cattle for many centuries, leading to the characteristic vegetation of the *Teucrio-Mesobrometum* (Ellenberg 1986). For a detailed description of the sites see Zschokke et al. (2000).

In spring 1993, 12 experimental blocks measuring 29 x 32 m were set-up (five blocks in Nenzlingen, three in Movelier and four in Vicques) to examine small-scale effects of grassland fragmentation (Zschokke et al. 2000). The distances between the centres of the blocks ranged from 25 to 135 m within each site; the distances between sites were between 9 and 19 km. At each site the entire investigation area was fenced to exclude large herbivores. The grasslands were mown at the end of October and the plant biomass was removed.

For the present study we exclusively used data collected in the undisturbed control plots of each block in 1996 and 1997. Each block contained two small (0.5 x 0.5 m), one medium (1.5 x 1.5 m) and one large (4.5 x 4.5 m) plots of undisturbed grassland.

Field methods

Productivity and abiotic environmental factors

Above-ground plant biomass was used as a measure of productivity. The plants were clipped at a height of 5 cm above ground level (to preserve rosettes) between 6 and 15 October both in 1996 and 1997. In small plots, the entire vegetation was collected. In the other plots, subsamples covering 0.25 m^2 (5 subsamples in medium plots and 20 subsamples in large plots) were randomly chosen and the plants harvested. The samples were oven-dried (60 C for 2 days and 80 C for 2 hours) and weighed.

To relate plant productivity to abiotic environmental factors we used the indicator scores of Landolt (1977) for soil humidity (1, arid land plants to 5, wetland plants) and soil nutrients

(1, species with little requirements for soil nitrogen to 5, species with high requirements for soil nitrogen). Indicator values of species were weighted by their abundance in each block. Ground air temperature was measured using Tinytalk temperature loggers (Gemini Data Loggers, Chichester, U.K.). In each block, two loggers were placed in the vegetation. Temperature was recorded every 10 minutes from 22 September to 4 October 1995 (autumn), from 23 January to 6 February 1996 (winter), from 7 May to 19 May 1996 (spring) and from 16 July to 28 July 1996 (summer). From these data we calculated the average temperature over all four seasons.

Species richness, density and biomass of invertebrates

Diversity and abundance data on forbs, grasses, gastropods and grasshoppers were recorded in four permanent plots (two small, one medium and one large plot; see above) in each block. This resulted in sampling areas of 0.5 m^2 (area of both small plots within a block combined), 2.25 m^2 and 20.25 m^2 per block. No plants or animals were removed from the plots.

To estimate the abundance of the various plant species, the number of grass and graminoid culms and the number of rooting shoots and rosettes of herbaceous plants were counted in each plot in 1996. Trees and shrubs were regularly removed and are therefore not considered. Each plot was examined three times: in May/June, June/July and August/September. The term 'grasses' includes all true grasses (Poaceae) as well as sedges (*Carex* sp.) and rushes (Juncaceae). In 1997, the abundance of plant species was assessed in four subsamples of 0.5 x 0.5 m in large plots and two subsamples in medium plots. In small plots plant species abundance was assessed in the whole area.

In the evening of a rainy day, sheets of cardboard (measuring 10 x 10 cm) were placed 50 cm apart in the vegetation of the plots. In the morning of the following day the cardboard sheets were checked for gastropods (Oggier et al. 1998). Specimens were identified in the field. Field work was done in autumn when most gastropod species are active in grasslands. Gastropod biomass was calculated using size-dry weight relationships obtained from Mason (1970), South (1992) and B. Baur (unpubl. data).

The entire vegetation of the plots was carefully searched for grasshoppers (including bush crickets and true crickets). Plants were slightly moved with a bamboo rod for an easier detection of the insects. Inactive and moving individuals were identified in situ. Monitoring was repeated three times between July and early September 1996 and two times in August in

1997. Grasshopper biomass was calculated using size-dry weight relationships obtained from Sage (1982). Data on body length were obtained from Bellmann (1993).

Data analysis

Data collected in 1996 were used to determine species-area curves. The first three points of the species-area curves (0.5, 2.75 and 23 m^2) are based on the average species richness of each group in small plots combined, small and medium plots combined and all plots of a block combined. The following points (multiples of 23 m^2 up to the whole area sampled (276 m^2)) are based on a rarefaction analysis (cf. Simberloff 1978). We randomly chose subsamples of blocks and counted the number of species occurring in these blocks. Simulations were repeated 100'000 times. As 'regional' species pool we considered all species recorded in the three grasslands in 1993-1996 (Baur et al. 1996, Zschokke et al. 2000).

Possible relationships among plant biomass and diversity of plants and invertebrates were analysed in two steps. First, the effect of locality (n = 3) on species richness and diversity was evaluated. Second, the relationships among plant biomass and species richness and diversity of grasses, forbs, gastropods and grasshoppers were examined for sampling areas of different size using blocks (n = 12) as units.

One-way ANOVAs were used to examine possible site effects on plant biomass, species richness and diversity (Shannon-Wiener index) of all groups of organisms considered. Tukey-Kramer tests were applied to examine differences between pairs of sites.

To examine possible relationships between plant biomass and species richness of grasses, forbs, all plants combined, gastropods and grasshoppers and density and biomass of gastropods and grasshoppers we used partial regressions to eliminate the confounding factor site. In a first step we calculated ANOVAs (type III) with the random factor site and the variables listed above as dependents. The ANOVAs were calculated separately for the three grain sizes and the two years to avoid autocorrelation. Data on plant biomass were log-transformed, those on species richness of grasses, forbs and all plants combined were square root-transformed and those on species richness, density and biomass of gastropods and grasshoppers were square root (y + 0.5)-transformed. In a second step the residuals of all dependent variables were used to calculate regressions. The degrees of freedom for these partial regressions were reduced by 2 as these degrees of freedom were used in the ANOVAs ($df_{corrected} = 8$). We used the regression coefficient divided by the corrected standard error of the regression as a test value, which is assumed to follow a t-distribution under H_0. The

corrected standard error was calculated as $SE_{corrected} = \sqrt{(SE_{old}^2 * 10/ 8)}$. Quadratic regressions are presented when the quadratic term was significant, else linear regressions are presented.

A similar technique was used to calculate partial correlations between species richness of grasses or forbs and species richness of gastropods or grasshoppers. We used the residuals of the ANOVAs described above to calculate the correlations. The t-value corresponding to the r-value of the correlation was calculated as $t = r * \sqrt{((n-2)/ (1-r^2))}$. The degrees of freedom were reduced by 2 as described above.

Results

Among-site differences in productivity and species richness

Productivity, measured as above-ground plant biomass, ranged from 152 to 303 g dry weight per m^2 (grand mean = 237 g) among blocks in 1996 and from 158 to 366 g per m^2 (grand mean = 260 g) in 1997. The three sites differed in plant biomass in 1996 (Table 1). Nenzlingen and Movelier had a larger plant biomass than Vicques in 1996. In 1997 there were no significant among-site differences in plant biomass. Above-ground plant biomass was correlated between 1996 and 1997 at all grains considered (0.5 m^2: $r = 0.78$, $P = 0.0019$; 2.75 m^2: $r = 0.76$, $P = 0.0026$; 23 m^2: $r = 0.63$, $P = 0.0268$; $n = 12$ in all cases).

Species richness of grasses and species richness and diversity of gastropods differed among sites in 1996 (Table 1). In contrast, grasshopper species richness and diversity did not differ among sites (Table 1). Species richness of grasses and forbs were positively correlated between years (grasses: 0.5 m^2: $r = 0.65$, $P = 0.0204$; 2.75 m^2: $r = 0.61$, $P = 0.0320$; 23 m^2: $r = 0.84$, $P = 0.0002$; forbs: 0.5 m^2: $r = 0.80$, $P = 0.0011$; 2.75 m^2: $r = 0.58$, $P = 0.0456$; 23 m^2: $r = 0.87$, $P < 0.0001$; $n = 12$ in all cases). Gastropod species richness was not correlated between 1996 and 1997. In contrast, species richness of grasshoppers was correlated between years in sampling areas of 23 m^2 ($r = 0.68$, $n = 12$, $P = 0.0139$).

Above-ground plant biomass decreased with increasing average air temperature in the vegetation ($r_s = -0.77$, $n = 12$, $P = 0.0107$). Furthermore, above-ground plant biomass was positively correlated with indicators of soil humidity and nutrient content (soil humidity: $r_s = 0.60$, $n = 12$, $P = 0.0461$; nutrients: $r_s = 0.69$, $n = 12$, $P = 0.0217$).

Species-area curves and 'regional' species pool

The species-area curves of grasses levelled off at an area of approximately 100 m^2, those of gastropods and grasshoppers reached a plateau at an area of about 200 m^2, whereas the species-area curve of forbs still increased when cumulative data of all sampling plots were considered (276 m^2; Fig. 1). The 'regional' species pools of all groups except grasses contained species not found in the plots examined.

Table 1. Among-site comparisons of above-ground plant biomass and species richness and diversity (Shannon-Wiener index) of grasses, forbs, gastropods and grasshoppers in 1996. Mean values of blocks ± 1 SD are shown, F- and P-values result from one-way ANOVAs. Means with different letters are significantly different by Tukey-Kramer tests.

	Nenzlingen (n = 5)	Movelier (n = 3)	Vicques (n = 4)	$F_{2,9}$	P
Above-ground plant biomass (g / m^2)					
	268.9 ± 27.5 [a]	248.3 ± 5.5 [a]	189.0 ± 33.6 [b]	10.20	0.0049
Species richness (number of species)					
Grasses	18.2 ± 1.6 [a]	17.3 ± 0.6 [a,b]	13.5 ± 2.9 [b]	6.47	0.0181
Forbs	39.6 ± 9.6 [a]	50.3 ± 4.0 [a]	45.2 ± 5.0 [a]	2.11	0.18
Gastropods	5.2 ± 0.8 [a,b]	6.7 ± 0.6 [b]	4.0 ± 0.8 [a]	10.04	0.0051
Grasshoppers	7.0 ± 1.9 [a]	9.0 ± 1.7 [a]	6.8 ± 0.5 [a]	2.20	0.17
Diversity (Shannon-Wiener index)					
Grasses	1.47 ± 0.32 [a]	1.46 ± 0.18 [a]	1.40 ± 0.13 [a]	0.10	0.91
Forbs	2.78 ± 0.23 [a]	2.91 ± 0.20 [a]	2.94 ± 0.24 [a]	0.64	0.55
Gastropods	1.23 ± 0.18 [a]	1.58 ± 0.05 [b]	1.30 ± 0.15 [a,b]	5.38	0.0289
Grasshoppers	1.46 ± 0.37 [a]	1.60 ± 0.29 [a]	1.51 ± 0.09 [a]	0.21	0.81

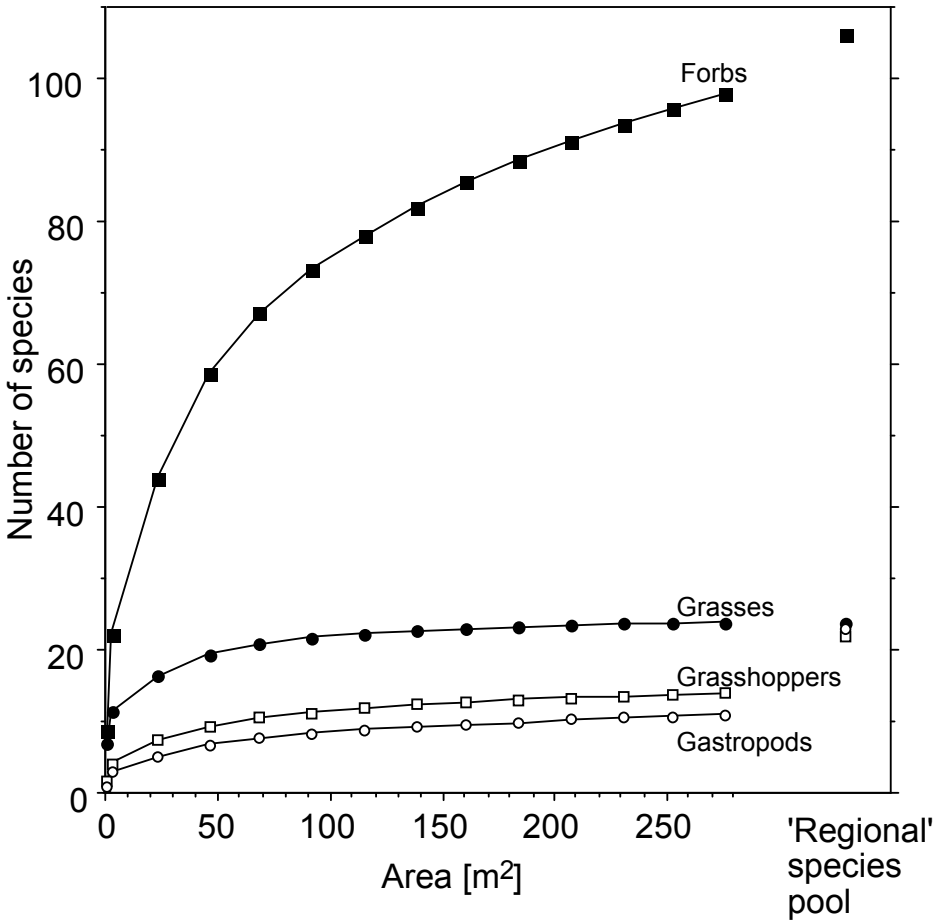


Fig. 1. Species-area curves of plants and two groups of invertebrates in calcareous grasslands in north-western Switzerland in 1996.

Species richness in sampling areas of different size is shown in Table 2. Small sampling areas (0.5 m^2) contained 19-22 % of the species recorded in the total sampling area of 23 m^2 in all groups except in grasses, where small sampling areas contained 43 %. Sampling areas of 2.75 m^2 contained 70 % of the grass species found in the total area of 23 m^2. The corresponding figures were 60 % for gastropods, 58 % for grasshoppers and 51 % for forbs. In all groups, species richness varied considerably among blocks (Table 2). Data from 1997 allowed similar analyses only in gastropods and grasshoppers. Sampling areas of 0.5 m^2 contained 20 % of gastropod and 10 % of grasshopper species recorded in areas of 23 m^2. For sampling areas of 2.75 m^2 the corresponding figures were 42 % for gastropods and 35 % for grasshoppers.

Productivity and species richness

Plant biomass was not affected by the size of the sampling plots (1996: 0.5 m^2: 227 ± 62g/m^2; 2.75 m^2: 256 ± 57 g/m^2; 23 m^2: 237 ± 44 g/m^2; $F_{2,33}$ = 0.82, P = 0.45; 1997: 0.5 m^2: 244 ± 41 g/m^2; 2.75 m^2: 263 ± 76 g/m^2; 23 m^2: 260 ± 57 g/m^2; $F_{2,33}$ = 0.35, P = 0.71). Species richness of grasses was independent of plant biomass. However, species richness of forbs showed a unimodal relationship with plant biomass in sampling areas of 0.5 m^2 and decreased with plant biomass in areas of 2.75 and 23 m^2 in 1996 (Fig. 2). In 1997, species richness of forbs tended to decrease with productivity in areas of 23 m^2. The relationship between species richness of all plants together and productivity was similar to that between forbs and productivity at all grain sizes examined (Fig. 2). Gastropod species richness tended towards a unimodal relationship with productivity at 0.5 m^2 in 1996 (Fig. 2) and towards a positive relationship at the same grain size in 1997. Species richness of grasshoppers tended to decrease with plant biomass in areas of 2.75 m^2 in 1996 (Fig. 2).

Table 2. Species richness of grasses, forbs, gastropods and grasshoppers in sampling areas of different size in 1996. Mean values ± 1 SD with ranges in brackets are given (n = 12 in each case).

	Sampling area (m^2)		
	0.5	2.75	23
Grasses	7.1 ± 2.5	11.5 ± 2.3	16.4 ± 2.8
	[4 - 13]	[8 - 16]	[10 - 20]
Forbs	8.8 ± 3.6	22.4 ± 6.7	44.2 ± 8.0
	[3 - 14]	[13 - 34]	[32 - 54]
Gastropods	1.0 ± 1.3	3.1 ± 1.8	5.2 ± 1.3
	[0 - 4]	[0 - 6]	[3 - 7]
Grasshoppers	1.6 ± 1.1	4.3 ± 1.7	7.4 ± 1.7
	[0 - 3]	[1 - 7]	[5 - 10]

Grasshopper species richness was positively correlated with species richness of forbs in areas of 2.75 m^2 ($r = 0.69$, $df = 8$, $t = 2.99$, $P = 0.0174$) and 23 m^2 ($r = 0.76$, $df = 8$, $t = 3.68$, $P = 0.0062$), whereas gastropod species richness was neither correlated with species richness of forbs nor with that of grasses.

Plant productivity and invertebrate density and biomass

Gastropod density tended towards a unimodal relationship with productivity at 0.5 m^2 in 1996 ($y = 0.532 + 1.162x - 58.031x^2$; $r^2 = 0.46$, $df = 8$, $t = 2.27$, $P = 0.0528$) and tended to increase with productivity at the same grain size in 1997 ($y = -1.942 * 10^{-5} + 5.075x$; $r^2 = 0.34$, $df = 8$, $t = 2.04$, $P = 0.0760$). Grasshopper density tended towards unimodal relationships with plant biomass in plots of 0.5 m^2 ($y = 0.419 + 2.292x - 45.739x^2$; $r^2 = 0.44$, $df = 8$, $t = 1.86$, $P = 0.0994$) and 2.75 m^2 ($y = 0.303 - 3.583x - 29.87x^2$; $r^2 = 0.46$, $df = 8$, $t = 1.94$, $P = 0.0878$) in 1996. Gastropod biomass showed a unimodal relationship with productivity in plots of 0.5 m^2 ($y = 0.231 - 0.404x - 25.156x^2$; $r^2 = 0.44$, $df = 8$, $t = 2.35$, $P = 0.0470$) and grasshopper biomass showed a trend towards a unimodal relationship with productivity at 2.75 m^2 ($y = 0.047 - 0.462x - 4.671x^2$; $r^2 = 0.46$, $df = 8$, $t = 2.22$, $P = 0.0570$) in 1996. Grasshopper density was not affected by the size of the sampling plots (Table 3). Gastropod density tended to be higher in sampling areas of 0.5 m^2 and 2.75 m^2 than in areas of 23 m^2 (Table 3).

Table 3. Densities of gastropods and grasshoppers (ind./m^2) in sampling areas of different size in two successive years. Mean values ± 1 SD are given (n = 12 in each case).

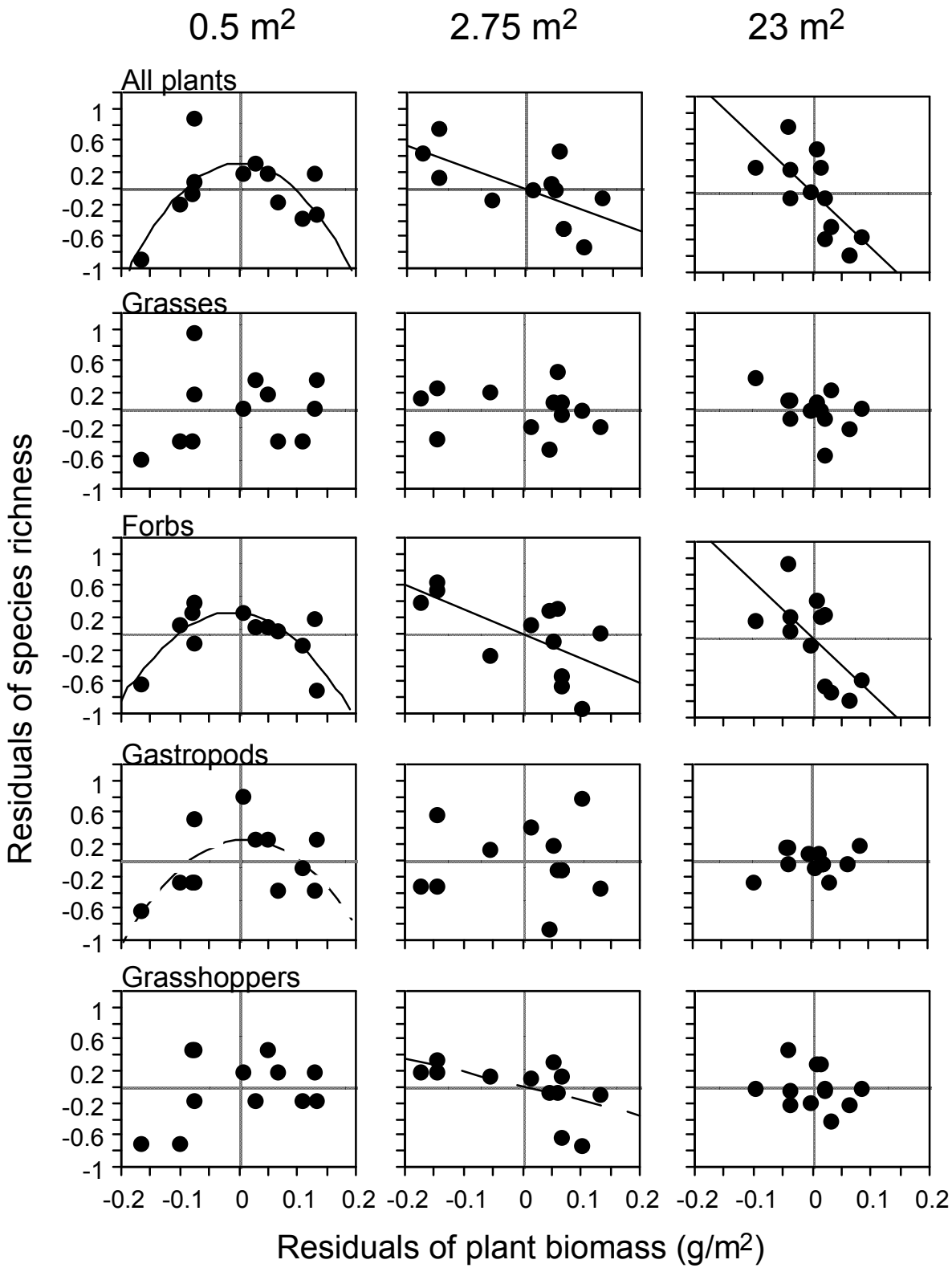
Year	Group	Sampling area (m^2)		
		0.5	2.75	23
1996	Gastropods	2.5 ± 3.3	2.2 ± 1.6	1.2 ± 0.7
	Grasshoppers	4.0 ± 3.0	4.6 ± 2.4	3.3 ± 1.3
1997	Gastropods	2.5 ± 2.1	2.0 ± 1.0	1.4 ± 0.7
	Grasshoppers	1.5 ± 1.9	1.6 ± 1.0	1.3 ± 0.6

► Fig. 2. Scale-dependent relationships between above-ground plant biomass and species richness of all plants, grasses, forbs, gastropods and grasshoppers in 1996. Regressions were calculated with residuals from ANOVAs with the random factor site. Regressions are shown when $P \leq 0.05$ as full lines and $P \leq 0.1$ as dashed lines. For unimodal relationships the significance tests refer to the quadratic term. Regression lines are: all plants, 0.5 m^2: $y = 0.339 - 0.02x - 37.003x^2$, $r^2 = 0.48$, $t = 2.53$, $P = 0.0354$; all plants, 2.75 m^2: $y = -1.233 * 10^{-5} - 2.7x$, $r^2 = 0.43$, $t = 2.44$, $P = 0.0408$; all plants, 23 m^2: $y = -1.809 * 10^{-5} - 6.904x$, $r^2 = 0.47$, $t = 2.65$, $P = 0.0294$; forbs, 0.5 m^2: $y = 0.282 - 0.615x - 30.816x^2$, $r^2 = 0.53$, $t = 2.87$, $P = 0.0210$; forbs, 2.75 m^2: $y = -1.266 * 10^{-5} - 3.047x$, $r^2 = 0.42$, $t = 2.38$, $P = 0.0442$; forbs, 23 m^2: $y = 1.741 * 10^{-5} - 6.962x$, $r^2 = 0.42$, $t = 2.40$, $P = 0.0432$; gastropods, 0.5 m^2: $y = 0.271 + 0.607x - 29.571x^2$, $t = 1.94$, $P = 0.0890$; grasshoppers, 2.75 m^2: $y = -6.93 * 10^{-6} - 1.829x$, $r^2 = 0.33$, $t = 1.96$, $P = 0.0852$ (df = 8 in all cases).

Discussion

An important step in understanding the productivity-diversity relationship is the careful examination of the spatial and ecological scales at which patterns are detected (Rosenzweig 1995). The present study showed that relationships between productivity, species richness and biomass of invertebrates varied among animal groups, different local spatial scales and years.

There is a wide agreement that diversity of plant species in grasslands is influenced by productivity (Mittelbach et al. 2001). The present study showed a unimodal relationship between productivity and forb species richness in small plots of nutrient-poor calcareous grasslands in one of two years confirming the findings of earlier studies in grasslands (Waide et al. 1999). For vascular plants at geographical scales smaller than continents, unimodal relationships occur most frequently (Mittelbach et al. 2001). However, most of the studies reviewed by Mittelbach et al. (2001) compared productivity in several types of grassland. A unimodal relationship may result from a series of linear relationships including absence of a relationship in differently productive communities if the slope of the relationship decreases with mean productivity. Thus, a unimodal relationship seems more probable in studies covering several plant communities. Furthermore, different studies applied different methods, potentially confounding a review on scale-dependence of the productivity-diversity relationship. In a recent study that considered both grain size and extent, the relationship between productivity and plant species density (number of species per m^2) depended on both (Gross et al. 2000). In our study, the unimodal relationship between productivity and forb


0.5 m2
2.75 m2
23 m2
All plants
Grasses
Forbs
Gastropods
Grasshoppers
Residuals of species richness
Residuals of plant biomass (g/m2)
1
0.6
0.2
-0.2
-0.6
-1
-0.2
-0.1
0
0.1
0.2

species richness was only observed at the smallest grain size examined, whereas at the other two grain sizes a negative relationship was observed in one year and a trend towards a negative relationship at 23 m^2 in the second year. Scale-dependence of the productivity-diversity relationship can result when the differences in species composition increase with productivity (Chase & Leibold 2002). Higher dissimilarity between local species compositions with increasing productivity could result from a larger degree of heterogeneity in environmental factors (including productivity itself) at higher average productivities, both spatially and temporarily. A test of these hypotheses is beyond of the scope of our study (three sites, two years).

It has been argued that species richness at one scale is primarily determined by the number of available species at the next larger scale. In our study, the 'regional' species pool of all groups except grasses contained species not found in the sampling plots. The increase in species richness at the regional level can partly be explained by an enhanced habitat diversity. Our sampling plots were chosen to represent homogeneous grassland vegetation. However, slightly different managed grassland areas in the neighbourhood, exposed limestone bedrock, isolated rocks and vegetation adjacent to forest edge contained additional species.

Plant species richness and above-ground biomass are relatively simple to measure in grasslands, even for small sampling areas. However, assessing the relationships between plant productivity and species richness and biomass of invertebrate groups remains a problem for several reasons. Firstly, there is no simple scaling function of plant productivity that applies to the biomass of different invertebrate groups. Secondly, different invertebrate species may show different patterns of microdistribution in the grasslands. Different species react differently to the spatial heterogeneity in the physical environment (e.g. soil depth, moisture and structure). Furthermore, species differ in their abilities of using resources and in their metabolic requirements. Thus, rather than one factor or mechanism determining the patterns of invertebrate species richness, it may be the cumulative or interactive effect of different factors. An inappropriate size of sampling units may give misleading results.

In our study, grasshopper species richness was affected by both plant biomass and forb species richness. Plant species richness is expected to affect species richness of herbivorous insects as they often are specialist feeders (Knops et al. 1999). However, this explanation probably does not explain the observed relationships between forb species richness and that of grasshoppers as they are generalist feeders. It is possible that forb species richness is an indicator of structural diversity of the grasslands examined. In an experiment with manipulated

plant species richness, Siemann et al. (1998) found that not only the diversity of herbivorous arthropods but also that of predacious arthropods was affected by plant species richness.

Individuals of terrestrial gastropods occur often aggregated within population. The size of these aggregations vary with the scale of structural heterogeneity of the habitat. Patches of high soil moisture may contribute to an overlap of aggregations of different species, whereas different food and resting-site preferences and species interactions (e.g. interspecific competition) may cause a separation of interspecific aggregations. The combination of these partly subtle influences and interactions - most of them working at different spatial scales - could cause the observed patterns of distribution of individuals.

The relationships among productivity and species richness and density of gastropods and grasshoppers differed between the two groups. In plots of 0.5 m^2, gastropods, mainly detrivores and generalist herbivores, showed a trend towards a unimodal relationship with plant productivity in one year and tended to increase with plant productivity in the other year, but appeared not to be directly affected by species richness of forbs or grasses. In contrast, species richness of grasshoppers, a group of generalist herbivores, tended to decrease with plant productivity, but was positively correlated with species richness of forbs in plots of 2.75 m^2 in one year. Furthermore, ants, a group of general feeders without strong plant-associations, was neither influenced by productivity nor by species richness of forbs or grasses in 1996 (B. Braschler, unpubl. data). In contrast, the density of aphids, a group of specialised herbivores, was positively correlated with species richness of forbs and tended to be correlated with species richness of grasses in plots of 23 m^2 in 1997 (B. Braschler, unpubl. data). These findings support the hypothesis that productivity and plant diversity have a higher impact on the diversity of invertebrates with close associations to plants than on that of invertebrates with no direct association to plants.

The invertebrate groups examined also differed in mobility. Most grasshopper species can be considered as rather mobile compared to gastropod species. Nonetheless, the grasshoppers seemed to be affected by plant richness and biomass even at the grain size of 2.75 m^2.

It is generally recognised that area and environmental heterogeneity have strong effects on species richness (Huston 1994, Rosenzweig 1995). Determining the causes of variation in species diversity and productivity requires linking the scales at which variation is measured to the scales at which the processes hypothesised to affect diversity and productivity actually operate. Theoretical and empirical approaches suggest that the form of the relationship between species richness and productivity depends both on the grain size and the geographical

extent of the study. Considerable controversy remains concerning the general form of the relationship, which organisms fit particular relationships, the spatial scale at which these patterns occur, and what mechanisms produce these pattern. The present study showed that productivity-species richness patterns in grassland invertebrates depend on plot size even in very small areas.

Acknowledgements. We thank M Wurtz and numerous students for field assistance. H-P Rusterholz, P Stoll, A Baur, A Erhardt and two anonymous reviewers provided constructive comments on the manuscript and E Lüdin helped with the statistical analyses. Financial support was received from the Swiss National Science Foundation (grants to B Baur).

References

Aarssen LW (2001) On correlations and causations between productivity and species richness in vegetation: predictions from habitat attributes. Basic Appl Ecol 2:105-114.

Abrams P (1995) Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? Ecology 76:2019-2027.

Baur B, Joshi J, Schmid B, Hänggi A, Borcard D, Stary J, Pedroli-Christen A, Thommen GH, Luka H, Rusterholz H-P, Oggier P, Ledergerber S, Erhardt A (1996) Variation in species richness of plants and diverse groups of invertebrates in three calcareous grasslands of the Swiss Jura mountains. Rev Suisse Zoologie 103:801-833.

Bellmann H (1993) Heuschrecken beobachten – bestimmen. Naturbuch Verlag, Augsburg.

Chase JM, Leibold MA (2002) Spatial scale dictates the productivity-biodiversity relationship. Nature 2002:427-430.

Ellenberg H (1986) Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. Eugen Ulmer, Stuttgart.

Fischer M, Stöcklin J (1997) Local extinctions of plants in remnants of extensively used calcareous grasslands 1950-85. Conserv Biol 11:727-737.

Grace JB (1999) The factors controlling species density in herbaceous plant communities: an assessment. Persp Plant Ecol Evol Syst 2:1-28.

Gross KL, Willig MR, Gough L, Inouye R, Cox SB (2000) Patterns of species density and productivity at different spatial scales in herbaceous plant communities. Oikos 89:417-427.

Huston MA (1994) Biological diversity: the coexistence of species on changing landscapes. Cambridge Univ Press, Cambridge.

Huston MA (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86:393-401.

Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E, Groth J (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecol Lett 2:286-293.

Landolt E (1977) Ökologische Zeigerwerte zur Schweizer Flora. Ver Geobot Inst ETH, Stift Rübel, in Zürich 64:1-208.

Lawton JH (1983) Plant architecture and the diversity of phytophageous insects. Ann Rev Entomol 28:23-39.

Mason CF (1970) Snail populations, beech litter production, and the role of snails in litter decomposition. Oecologia 5:215-239.

Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L (2001) What is the observed relationship between species richness and productivity? Ecology 82:2381-2396.

Oggier P, Zschokke S, Baur B (1998) A comparison of three methods for assessing the gastropod community in dry grasslands. Pedobiologia 42:348-357.

Rosenzweig ML (1995) Species diversity in space and time. Cambridge Univ Press, Cambridge.

Sage RD (1982) Wet and dry-weight estimates of insects and spiders based on length. Am Midl Nat 108:407-411.

Siemann E (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. Ecology 79:2057-2070.

Siemann E, Tilman D, Haarstad J, Ritchie M (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. Am Nat 152:738-750.

Simberloff D (1978) Use of rarefaction and related methods in ecology. In Dickson KL, Cairns J, Livingston RJ (eds) Biological data in water pollution assessment: quantitative and statistical analyses. American Society for Testing and Materials, Philadelphia, pp. 159-176.

South A (1992) Terrestrial slugs. Chapman and Hall, London.

Southwood TRE (1973) The insect/plant relationship - an evolutionary perspective. In van Emden HF (ed) Insect-plant relationships. Blackwell Science, Oxford, pp. 3-30.

Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton Univ Press, Princeton.

Tilman D, Pacala S (1993) The maintenance of species richness in plant communities. In Ricklefs RE, Schluter D (eds) Species diversity in ecological communities: historical and geographical perspectives. Univ Chicago Press, Chicago, pp. 13-25.

Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, Parmenter R (1999) The relationship between productivity and species richness. Ann Rev Ecol Syst 30:257-300.

Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. J Biogeogr 28:453-470.

Zschokke S, Dolt C, Rusterholz H-P, Oggier P, Braschler B, Thommen GH, Lüdin E, Erhardt A, Baur B (2000) Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation. Oecologia 125:559-572.

Appendix

Species list. Figures indicate the particular blocks (1-12) in which a species was found (Nenzlingen: 1-5, Movelier: 6-8, Vicques: 9-12). Plants were only identified in 29 % of the area of the blocks in 1997.

1996: Grasses: *Agrostis stolonifera* L.: 8; *A. tenuis* Sibth.: 1-12; *Anthoxanthum odoratum* L.: 1-5, 7; *Avenula pubescens* Dumortier: 1-3, 5; *Brachypodium pinnatum* P. B.: 1-12; *Briza media* L.: 1-12; *Bromus erectus* Hudson: 1-12; *Carex caryophyllea* La Tourrette: 1-2, 4-12; *C. flacca* Schreber: 1-12; *C. pilulifera* L.: 8; *Cynosurus cristatus* L.: 1-9, 11-12; *Dactylis glomerata* L.: 1-10, 12; *Danthonia decumbens* DC.: 1-2, 4-12; *Festuca ovina* L.: 1-2, 4-12; *F. pratensis* Hudson: 1-9, 11; *F. rubra* L.: 1-3, 5; *Holcus lanatus* L.: 1-5; *Koeleria pyramidata* P. B.: 2, 4-12; *Lolium perenne* L.: 1-3, 5-7, 9; *Luzula campestris* DC.: 1-9, 11; *Phleum pratense* L.: 4, 6-9, 11-12; *Poa compressa* L.: 6-7, 12; *P. pratensis* L.: 1-9, 12; *P. trivialis* L.: 1, 3, 5, 9; **Forbs:** *Achillea millefolium* L.: 1-2, 4-7, 9-12; *Acinos arvensis* Dandy: 9, 11; *Agrimonia eupatoria* L.: 1-12; *Ajuga reptans* L.: 4; *Alchemilla* agg. L.: 8; *Allium oleraceum* L.: 8-9; *Anacamptis pyramidalis* Rich.: 7; *Anthericum ramosum* L.: 6; *Anthyllis vulneraria* L.: 1-2, 10; *Asperula cynanchica* L.: 9-11; *Bellis perennis* L.: 1-2, 4; *Betonica officinalis* L.: 1-2, 4-12; *Campanula glomerata* L.: 6-8; *C. rotundifolia* L.: 2, 8, 10-11; *Carlina acaulis* L.: 6-7; *C. vulgaris* L.: 11; *Centaurea jacea* L.: 1-2, 4-12; *Centaurium erythraea* Rafn: 9, 11; *Cerastium fontanum* Baumg.: 1-7; *Chamaespartium sagittale* P. Gibbs: 7-12; *Cirsium acaule* Scop.: 1-12; *Colchicum autumnale* L.: 5; *Convolvulus arvensis* L.: 10; *Crepis biennis* L.: 3; *C. taraxifolia* Thuill.: 8; *Daucus carota* L.: 1-2, 4, 6-12; *Euphorbia cyparissias* L.: 2-5, 9-12; *E. verrucosa* L.: 8; *Galium album* Miller: 10-11; *G. pumilum* Murray: 7; *G. verum* L.: 1-3, 5-6, 9-12; *Genista tinctoria* L.: 10; *Gentiana verna* L.: 7; *Gentianella ciliata* Borkh.: 7; *G. germanica* Börner: 7-8; *Geranium dissectum* L.: 3; *Gymnadenia conopsea* R. Br.: 6-8; *Helianthemum nummularium* Miller: 2, 4, 6-12; *Hieracium pilosella* L.: 1-2, 4-12; *Hippocrepis comosa* L.: 4, 9-10; *Hypericum perforatum* L.: 1-2, 4-5, 7-12; *Hypochoeris radicata* L.: 2, 6-10; *Knautia arvensis* Duby: 1-3, 6, 9-11; *Lathyrus pratensis* L.: 1-3, 6-8; *Leontodon hispidus* L.: 2, 6-11; *Leucanthemum vulgare* Lam: 1-2, 4, 6-8, 10, 12; *Linum catharticum* L.: 1-12; *Lotus corniculatus* L.: 1-12; *Medicago lupulina* L.: 1-4, 6-7, 9-11; *Ononis repens* L.: 5-12; *Orchis militaris* L.: 6; *O. ustulata* L.: 6-7; *Origanum vulgare* L.: 1-2, 10, 12; *Pimpinella saxifraga* L.: 1-2, 9-12; *Plantago lanceolata* L.: 1-12; *P. major* L.: 1; *P. media* L.: 1-2, 4-12; *Platanthera chlorantha* Rchb.: 8; *Polygala amarella* Crantz: 8-9; *P. comosa* Schkuhr: 2, 8-10; *Potentilla*

erecta Räuschel: 2-3, 5-8, 10-12; *P. neumanniana* Rchb.: 4, 6-12; *P. reptans* L.: 5; *P. sterilis* Garcke: 1-5, 9; *Primula veris* Hudson: 1-2, 6-8; *Prunella grandiflora* Scholler: 1-2, 4, 6-12; *P. vulgaris* L.: 1-12; *Ranunculus bulbosus* L.: 1-12; *R. repens* L.: 2, 12; *Rumex acetosa* L.: 1-2; *Salvia pratensis* L.: 1-2, 9-11; *Sanguisorba minor* Scop.: 1-12; *Scabiosa columbaria* L.: 1-2, 6-7, 10; *Sedum sexangulare* Grimm: 1, 9-11; *Senecio erucifolius* L.: 2-3, 7-8; *Silaum silaus* Sch. et Th.: 7-8; *Spiranthes spiralis* Chevallier: 7; *Succisa pratensis* Moench: 6-8; *Taraxacum officinale* Weber: 3; *Tetragonolobus maritimus* Roth: 6-8; *Teucrium chamaedrys* L.: 2-4, 6-12; *Thlaspi perfoliatum* L.: 7; *Thymus serpyllum* L.: 1-2, 4, 6-11; *Trifolium campestre* Schreber: 1-4, 9-12; *T. medium* L.: 1-3, 5-12; *T. montanum* L.: 3-12; *T. ochroleucon* Hudson: 1-12; *T. pratense* L.: 1-12; *T. repens* L.: 1-12; *Veronica arvensis* L.: 1-3, 5, 8; *V. chamaedrys* L.: 1-3, 5, 9; *V. officinalis* L.: 1-12; *V. prostrata* L.: 2; *V. serpyllifolia* L.: 1-3, 5, 8, 11; *Vicia cracca* L.: 7; *V. hirsuta* S. F. Gray: 1-2, 4-12; *V. sativa* L.: 1-3, 5, 12; **Gastropods:** *Arion lusitanicus* Mabile 1868: 3; *Cochlicopa lubrica* (O. F. Müller 1774): 1-2, 4, 6-8, 10-12; *Deroceras reticulatum* (O. F. Müller 1774): 1-9, 12; *Helicella itala* (L. 1758): 9; *Limax* spp.: 1-6, 8; *Punctum pygmaeum* (Draparnaud 1801): 7-8, 12; *Pupilla muscorum* (L. 1758): 1-2, 9-11; *Succinea oblonga* (Draparnaud 1801): 6; *Trichia plebeia* (Draparnaud 1805): 1-8, 10-12; *Vertigo pygmaea* (Draparnaud 1801): 1-8, 10-12; *Vitrina pellucida* (O. F. Müller 1774): 6-8; **Grasshoppers:** *Chorthippus biguttulus* (L. 1758): 1-12; *C. parallelus* (Zetterstedt 1821): 1-12; *Decticus verrucivorus* (L. 1758): 10, 12; *Gomphocerippus rufus* (L. 1758): 1-2, 4-8, 12; *Euthystira brachyptera* (Ocskay 1826): 1-3, 6-8; *Gryllus campestris* L. 1758: 2; *Metrioptera bicolor* (Philippi 1830): 1-12; *M. brachyptera* (L. 1761): 8; *M. roeselii* (Hagenbach 1822): 3, 6-8; *Omocestus rufipes* (Zetterstedt 1821): 1, 7-12; *Pholidoptera griseoaptera* (De Geer 1773): 2, 4, 7; *Platycleis albopunctata* (Goeze 1778): 2, 4, 6-11; *Stenobothrus lineatus* (Panzer 1796): 1-5, 7-12; *Tettigonia viridissima* L. 1758: 2, 9.

1997: Grasses: *Agrostis stolonifera* L.: 8; *A. tenuis* Sibth.: 1-12; *Anthoxanthum odoratum* L.: 1-5; *Avenula pubescens* Dumortier: 1, 3, 5; *Brachypodium pinnatum* P. B.: 1-6, 8, 10-12; *Briza media* L.: 1-12; *Bromus erectus* Hudson: 1-12; *Carex caryophyllea* La Tourrette: 1, 4-5, 7-11; *C. flacca* Schreber: 2, 4-12; *Cynosurus cristatus* L.: 1-6, 8-9, 12; *Dactylis glomerata* L.: 1-8; *Danthonia decumbens* DC.: 4-5, 8-12; *Festuca ovina* L.: 1-2, 4-10, 12; *F. pratensis* Hudson: 1-7, 9; *F. rubra* L.: 2; *Holcus lanatus* L.: 1-3, 5; *Koeleria pyramidata* P. B.: 2, 6-10; *Lolium perenne* L.: 3, 6; *Luzula campestris* DC.: 1-5; *Phleum pratense* L.: 6, 11; *Poa compressa* L.: 6-7, 12; *P. pratensis* L.: 1-4, 7-9, 12; *P. trivialis* L.: 3, 5, 9; **Forbs:** *Achillea millefolium* L.: 1-2, 5, 7, 11; *Acinos arvensis* Dandy: 9; *Agrimonia eupatoria* L.: 2-8, 10-12; *Asperula cynanchica* L.: 8, 10-11; *Aster amellus* L.: 6; *Bellis perennis* L.: 1; *Betonica officinalis* L.: 1, 4-12;

Campanula glomerata L.: 6-7; *Carlina acaulis* L.: 10; *Centaurea jacea* L.: 2, 4, 7, 9-12; *Centaurium erythraea* Rafn: 12; *Chamaespartium sagittale* P. Gibbs: 4-5, 7-12; *Cirsium acaule* Scop.: 1-2, 4-8, 10, 12; *Daucus carota* L.: 1-2, 6-12; *Euphorbia cyparissias* L.: 1-2, 4-5, 9-12; *Galium album* Miller: 10; *G. pumilum* Murray: 6-7; *G. verum* L.: 1, 6-7, 9, 11-12; *Genista tinctoria* L.: 10; *Gentianella germanica* Börner: 7-8; *Geranium dissectum* L.: 3; *Helianthemum nummularium* Miller: 2, 4, 7-8, 12; *Hieracium pilosella* L.: 1-12; *Hippocrepis comosa* L.: 10; *Hypericum perforatum* L.: 2-4, 6-7, 10, 12; *Hypochoeris radicata* L.: 3, 6-8, 10; *Knautia arvensis* Duby: 1-4, 6, 9-10; *Lathyrus pratensis* L.: 1-5, 7; *Leontodon hispidus* L.: 2, 5-9, 11-12; *Leucanthemum vulgare* Lam: 1-2, 4, 6-8; *Linum catharticum* L.: 2, 6-7, 9-12; *Lotus corniculatus* L.: 1-2, 4, 6-12; *Medicago lupulina* L.: 1-2, 8, 11; *Ononis repens* L.: 6-12; *Origanum vulgare* L.: 1, 10; *Pimpinella saxifraga* L.: 1, 9-10; *Plantago lanceolata* L.: 3-4, 6-9, 11-12; *P. media* L.: 2, 4, 6-7, 9-12; *Polygala comosa* Schkuhr: 8, 10; *Potentilla erecta* Räuschel: 2, 5-8, 10-12; *P. neumanniana* Rchb.: 2, 6-7, 9-12; *P. sterilis* Garcke: 2, 4-5; *Primula veris* Hudson: 1-2, 6-7, 9, 11; *Prunella grandiflora* Scholler: 4, 6-11; *P.* spp.: 1-11; *P. vulgaris* L.: 1-2, 6-8, 12; *Ranunculus acris* L.: 7; *Salvia pratensis* L.: 1-2, 9-11; *Sanguisorba minor* Scop.: 1-12; *Scabiosa columbaria* L.: 1-2, 6, 8; *Sedum sexangulare* Grimm: 2, 11; *Senecio erucifolius* L.: 8, 12; *Silaum silaus* Sch. et Th.: 7; *Succisa pratensis* Moench: 1, 6-8; *Tetragonolobus maritimus* Roth: 6-8; *Teucrium chamaedrys* L.: 7, 9-12; *T. montanum* L.: 11; *Thlaspi perfoliatum* L.: 1; *Thymus serpyllum* L.: 1-4, 6-9, 11; *Trifolium medium* L.: 1; *T. montanum* L.: 4, 7-8, 10, 12; *T. pratense* L.: 1-10, 12; *Veronica arvensis* L.: 1; *V. chamaedrys* L.: 1-5, 7-8, 11; *V. officinalis* L.: 1-3, 5-6, 9-12; *V. serpyllifolia* L.: 1, 11; *Vicia hirsuta* S. F. Gray: 5-8, 10-12; *V. sativa* L.: 1-2, 10; **Gastropods:** *Abida secale* (Draparnaud 1801): 4; *Arion hortensis* Férussac 1819: 2-3; *Arion lusitanicus* Mabile 1868: 2, 5-6, 8; *Candidula unifasciata* (Poiret 1801): 10-11; *Cochlicopa lubrica* (O. F. Müller 1774): 1, 4, 6-7, 9, 12; *Deroceras reticulatum* (O. F. Müller 1774): 1-12; *Helicella itala* (L. 1758): 2, 4, 6-11; *Helix pomatia* L. 1758: 6-7; *Punctum pygmaeum* (Draparnaud 1801): 3; *Pupilla muscorum* (L. 1758): 9; *Trichia plebeia* (Draparnaud 1805): 2, 4-12; *Vertigo pygmaea* (Draparnaud 1801): 2-4, 7, 9-11; *Vitrina pellucida* (O. F. Müller 1774): 2, 5-6, 8; **Grasshoppers:** *Chorthippus biguttulus* (L. 1758): 1-4, 7-12; *C. dorsatus* (Zetterstedt 1821): 8; *C. parallelus* (Zetterstedt 1821): 1-6, 8, 10, 12; *Decticus verrucivorus* (L. 1758): 9; *Gomphocerippus rufus* (L. 1758): 1-8, 12; *Euthystira brachyptera* (Ocskay 1826): 1-8; *Metrioptera bicolor* (Philippi 1830): 1-12; *M. brachyptera* (L. 1761): 7; *M. roeselii* (Hagenbach 1822): 3; *Omocestus rufipes* (Zetterstedt 1821): 2, 9-12; *Platycleis albopunctata* (Goeze 1778): 2, 8-11; *Stenobothrus lineatus* (Panzer 1796): 2, 4-5, 7, 9-10, 12.

General discussion and conclusions

The aim of this thesis was to examine the effects of an experimental small-scale grassland fragmentation on invertebrate population dynamics. Invertebrates, in particular insects, fulfil important functions in most terrestrial ecosystems and make up a large part of the biodiversity. Even so they have only rarely been the focus of studies examining the effects of habitat fragmentation on biodiversity (Debinski and Holt 2000; Steffan-Dewenter and Tscharntke 2002; Tscharntke et al. 2002). In this thesis I tested predictions from theory on the effects of habitat fragmentation on biodiversity by using different insect groups and gastropods as model organisms. In this way I hope to have contributed to our understanding of how habitat fragmentation affects this often neglected part of biodiversity.

The response to habitat fragmentation varied among the different groups of organisms examined and even within groups. Similar species-specific responses have been reported from other fragmentation studies (Kareiva 1984; Davies and Margules 1998). In a study on Australian forest beetles, Davies et al. (2000) even report that closely related species differ in their response to fragmentation. In the present experiment most common species that were affected by the fragmentation were more abundant in the fragments than in control plots. The exceptions were the butterflies whose abundances were lower in fragments than in control plots (**Chapter I**). Considering ants, none of the common species differed in abundance between fragments and control plots 3 years after the initiation of the experimental fragmentation, but 3 years later the most abundant species was even more abundant in fragments than in control plots (**Chapter III**). Ants may have reacted slower to the fragmentation than some other groups of insects as ant abundance was measured as nest density. Ant nests can persist for several weeks to many years, though in some species nests are frequently relocated. Furthermore, the founding of a new nest at locations with many already established nests is rarely successful (Deslippe and Savolainen 1995). The relevant generation time in ants (i. e. that of nests) is thus longer than that of solitary grassland insects.

In vascular plants (**Chapter I**) and ants (**Chapter III**) the increase in abundance in some species were in part the result of edge effects. Plants growing in the edge zone of fragments may profit from reduced competition for light and nutrients. Above-ground plant biomass was

increased in fragments in the period 1996-1999 (**Chapter I**; Dolt 2001; H.-P. Rusterholz unpubl. data). This increase in productivity was mainly an edge effect. Similarly, thermophilic ants may profit from the slightly increased temperature in the edge zone of fragments and also indirectly from a higher food supply in fragments mediated through the increased plant productivity. At least one important food resource of the ants, namely mutualistic aphids, was more abundant in plots with a higher plant biomass. Consumer diversity and biomass were also related to plant productivity in other invertebrate groups in the examined grasslands (**Chapter V**). However, the shape of the relationship varied among groups of organisms and depended on the scale of the sampling units.

Because the response of species to habitat fragmentation varies so much, several hypotheses have been proposed to predict a species' response to fragmentation. Among the most frequently suggested hypotheses are the following. Species have been assumed to be particularly vulnerable to fragmentation when they are: (1) Naturally rare (Davies et al. 2000), in particular when they have not only a small but also a fluctuating population size (Kruess and Tscharntke 1994; Holt 1996), (2) when species are habitat specialists or specialist feeders (Zabel and Tscharntke 1998; Steffan-Dewenter and Tscharntke 2000), (3) when they have a large body size (Davies et al. 2000), (4) when they are already living in strongly isolated populations (Davies et al. 2000), and (5) when they belong to higher trophic groups (Kruess and Tscharntke 1994; Holt 1996; Zabel and Tscharntke 1998). Consequently, naturally abundant and generalist species that easily migrate between patches and are herbivores rather than predators should be most likely to benefit from fragmentation. In this thesis some of the predictions could be confirmed. However, the mechanisms that caused these results differed in some cases from the predictions of the theory.

Contrasting results were obtained considering the natural abundance of particular species. Most of the common plant and grasshopper species that showed a difference in abundance between fragments and control plots were indeed more abundant in fragments (**Chapter I**). In ants, the species that is naturally the most abundant in the examined grasslands became even more abundant in the fragments (**Chapter III**). However, the increase in ant density was observed 6 years after the initiation of the fragmentation. Three years after the initiation of the fragmentation no difference in ant nest density between fragments and control plots was found. In aphids, one of the two most abundant species benefited from fragmentation, while the other was not affected by the fragmentation (**Chapter II**). The common butterfly species were all negatively affected by the fragmentation as were the rare butterfly species (**Chapter I**). In other groups some rare species exclusively or mainly occurred

in control plots, while others were exclusively or mostly found in fragments (**Chapters I- III**). However, the results from rare species are descriptive as in this group there were not enough data for separate analyses. As biodiversity is largely composed of rare species their reaction to habitat fragmentation is of particular concern for conservation efforts.

The species reaction to the experimental fragmentation was not explicitly examined with regard to the degree of habitat or food specialisation. In the few other studies that examined the relationship between food specialisation of insects and their response to fragmentation the outcome varied. In a study considering insects on stinging nettles, monophagous herbivores were more often absent from small patches than polyphagous herbivores thus supporting theoretical expectations (Zabel and Tscharntke 1998). In another study, monophagous butterfly species increased in abundance in small plots while the density of oligophagous and polyphagous species decreased with plot area (Steffan-Dewenter and Tscharntke 2000).

The influence of body size was not examined in the present experiment. However, body size was not correlated with response to fragmentation or the effect of body size was unclear in other studies on fragmentation effects on insect diversity (Davies et al. 2000; Steffan-Dewenter and Tscharntke 2000; Tscharntke et al. 2002).

Contrary to theoretical expectations, it was the most mobile animal group considered, namely butterflies, that showed the most negative response to fragmentation (**Chapter I**). Furthermore, bumblebees changed their foraging patterns and visited fragments less frequently than control plots (Goverde et al. 2002). In contrast, the common gastropods species seemed to be unaffected by the fragmentation despite of the low mobility of the small snails (**Chapter I**). However, a more detailed study using mark-recapture techniques showed that three out of six snail species examined were less abundant in fragments than in control plots (Oggier 1999). Many ant and grasshopper species also used the matrix and thus were probably less affected by isolation.

Aphids, a group of herbivorous insects, benefited from the fragmentation as predicted by theory (**Chapter II**). This corresponds well with other studies showing that herbivorous insect density increased in fragments because of a reduced predation or parasitation pressure (Kareiva 1987; Kruess and Tscharntke 1994; Zabel and Tscharntke 1998; Davies et al. 2000). Indeed, the hypothesis that species at the top of the food chain may be most likely to be absent from small fragments thus releasing their prey species from predation pressure may to date be the best supported hypothesis. However, in our fragmentation experiment the increase in aphid density was not a result from reduced parasitation pressure but rather a result of changes in plant productivity and a higher degree of ant-tending in fragments. Thus, contrary to theoretical

predictions, the herbivore density increased as a result of an increased resource availability (bottom-up effect) rather than as a result of release from top-down control.

Not only species richness and abundance but also interactions between species and between groups of organisms were affected by the experimental fragmentation. Considering ants, the relationship between the density of the most abundant species and species richness and density of other ant species was negative in fragments while no relationship was found in control plots (**Chapter IV**). The frequency of ant-tending of aphids was increased in fragments (**Chapter II**). Similarly, the reluctance of pollinators like butterflies and bumblebees to cross the mown isolation area led to fewer pollinator visits in fragments and to a higher degree of visiting of nearby flowers in fragments (Goverde et al. 2002; H.-P. Rusterholz unpubl. data).

Studies examining the effects of habitat fragmentation on biodiversity have often concentrated on easy to assess measurements like species richness of certain indicator groups, most often plants and vertebrates. If mechanisms were studied in greater detail then often experimental systems involving only a small number of species were used. The results presented in this thesis show the value of field studies that simultaneously examine several groups of organisms and thus allow to compare the response of the different groups and to relate them to characteristics that differ between groups. By studying overall abundances of aphids and ants in the fragments and control plots general trends for these groups could be demonstrated. When examining the responses of single species of those groups and of interactions among species and among different groups of organisms to the fragmentation mechanisms can be detected that may help to explain species-specific responses even in closely related species or in members of the same guild. Studies that are restricted to species richness or overall density would fail to detect effects on small-scale spatial distribution like the edge effect on ant nest distribution reported in **Chapter III**. Similarly, studies restricted to a single survey would miss many responses. Neither the effect of the experimental fragmentation on ant nest persistence within a season nor the effect on overall ant nest density that only occurred at the end of the fragmentation experiment would have been detected using a short-term single survey experimental design. However, such subtle responses to fragmentation can, when involving groups of organisms that interact with many other groups of organisms, have a large impact on the whole ecosystem in the long-term. In groups like the aphids that consistently had a higher density in fragments than in control plots the multiple surveys increase our confidence that the observed increase in density is indeed a result of the fragmentation.

Most fragmentation studies measure species richness as an indicator for the changes imposed by the fragmentation. However, species extinction takes time. In many recently created fragments small populations will survive for some time but are doomed to go extinct at a later time. Thus, recently created fragments as used in many fragmentation studies have an extinction debt. This may also be the case in many small nature reserves that contain small remnant populations of protected species. Also it is the naturally rare species that are at the highest risk of extinction. Those rare species, however, are easily missed in surveys even though they are often of high conservation concern. Species richness may thus be of limited value as an indicator of disturbance in short-term ecological studies using recently created fragments. In the present experiment grassland invertebrates and plants in small fragments were examined over seven growing seasons. Even though many of these organisms have generation times that are short as compared to forest trees or vertebrates that are often the focus of fragmentation studies, no decrease of species richness in fragments could be demonstrated for most of the examined groups (**Chapters I-III**). However, even though species richness was not (yet) affected by the experimental fragmentation, the density of several of the examined groups and interactions among the species were strongly affected by the fragmentation (**Chapters II-IV**). In the long-term the altered interactions among species and among different groups of organisms may lead to changes in species composition and species richness.

The present experiment has shown the beginning of community disassembly following fragmentation. In order to understand the mechanisms through which man-made environmental change like habitat fragmentation affects single species we have to look at interactions and at ecosystem functioning. While ecosystem services may be more difficult to measure than species richness they may actually react to disturbance much faster as they are affected by the relative abundance of the involved species and by changes in behavioural patterns. For policy makers it is often the ecosystem services of an ecosystem that are easiest to translate into monetary value. To protect a species in its own right will fail to rally a majority of people in the case of many small invertebrates. It is thus necessary to also demonstrate the value of a diverse ecosystem per se to convince more people that the threat to biodiversity through manmade environmental change is truly a threat. For this purpose ecologists need to further examine how biodiversity is naturally created, how it persists, how it is related to ecosystem functioning and through which factors it is threatened. Many questions remain unresolved regarding the relationship between the diversity of different groups and the relative properties of naturally diverse ecosystems compared to impoverished systems. With my thesis I hope to

contribute to our understanding of the manifold ways one of the most striking changes in our landscape, namely habitat fragmentation, affects invertebrates in calcareous grasslands, one of the most diverse ecosystems in Europe. Patterns observed in this small-scale experiment may also be at work at a larger scale and in other groups of organisms. However, the variation in response to fragmentation among different groups of organisms that could be demonstrated in this thesis shows the need for careful testing of the hypothesis when considering different habitats and species.

References

Davies KF, Margules CR (1998) Effects of habitat fragmentation on carabid beetles: experimental evidence. J Anim Ecol 67:460-471.

Davies KF, Margules CR, Lawrence JF (2000) Which traits of species predict population declines in experimental forest fragments? Ecology 81:1450-1461.

Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. Conserv BioL 14:342-355.

Deslippe RJ, Savolainen R (1995) Mechanisms of competition in a guild of formicine ants. Oikos 72:67-73.

Dolt C (2001) Effects of small-scale grassland fragmentation on plants and plant-animal interactions. Dissertation. Univ Basel, Basel, Switzerland.

Goverde M, Schweizer K, Baur B, Erhardt A (2002) Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands. Biol Conserv 104:293-299.

Holt RD (1996) Food webs in space: an island biogeographic perspective. In Polis GA, Winemiller KO (eds) pp. 313-323. Food webs: integration of patterns dynamics. Chapman and Hall, New York, New York, USA.

Kareiva P (1984) Predator-prey dynamics in spatially structured populations: manipulating dispersal in a coccinellid-aphid interaction. In Levin SA, Hallam TG (eds) pp. 368-389. Mathematical Ecology. Springer-Verlag, Berlin, Germany.

Kareiva P (1987) Habitat fragmentation and the stability of predator-prey interactions. Nature 326:388-390.

Kruess A, Tscharntke A (1994) Habitat fragmentation, species loss, and biological control. Science 264:1581-1584.

Oggier P (1999) Effects of habitat fragmentation on the population dynamics of land snail species. PHD Thesis. Univ Basel, Basel, Switzerland.

Steffan-Dewenter I, Tscharntke T (2000) Butterfly community structure in fragmented habitats. Ecol Lett 3:449-456.

Steffan-Dewenter I, Tscharntke T (2002) Insect communities and biotic interactions on fragmented calcareous grasslands - a mini review. Biol Conserv 104:275-284.

Tscharntke T, Steffan-Dewenter I, Kruess, A, Thies C (2002) Characteristics of insect populations on habitat fragments: a mini review. Ecol Res 17:229-239.

Zabel J, Tscharntke T (1998) Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? Oecologia 116:419-425.

Contributions to each chapter

Chapter I **Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation**

Idea: B. Baur
Field work: C. Dolt (plants); H.-P. Rusterholz (butterflies); P. Oggier (gastropods); B. Braschler (ants); G. H. Thommen (grasshoppers); S. Zschokke (temperature)
Species determinations: C. Dolt (plants); H.-P. Rusterholz (butterflies); P. Oggier (gastropods); B. Braschler (ants); G. H. Thommen (grasshoppers); B. Seifert & C. Baroni-Urbani (some verifications of ant determinations)
Statistical analyses: S. Zschokke; E. Lüdin
Writing: S. Zschokke; B. Baur; includes contributions from all authors

Chapter II **Experimental small-scale grassland fragmentation alters aphid population dynamics**

Idea: B. Baur (fragmentation experiment); B. Braschler (aphids)
Field work: B. Braschler
Species determinations: G. Lampel (aphids); B. Braschler (ants, plants)
Statistical analyses: B. Braschler; B. Baur (advice), E. Lüdin (advice)
Writing: B. Braschler; B. Baur (partial rewriting/ corrections)

Chapter III **Effects of small-scale grassland fragmentation on spatial distribution, density, and persistence of ant nests**

Idea: B. Baur (fragmentation experiment); B. Baur & B. Braschler (ants)
Field work: B. Braschler (ants); C. Dolt (plants 1996); H.-P. Rusterholz (plants 1999)
Species determinations: B. Braschler (ants); C. Dolt (plants 1996); H.-P. Rusterholz (plants 1999); R. Neumeyer & B. Seifert (some verifications of ant determinations)
Statistical analyses: B. Braschler; B. Baur (advice)
Writing: B. Braschler; B. Baur (partial rewriting/ corrections)

Chapter IV Experimental small-scale grassland fragmentation alters competitive interactions among ant species

Idea: B. Baur (fragmentation experiment); B. Baur & B. Braschler (ants)
Field work: B. Braschler (mapping of ant nests, ant counts at ressources); B. Baur (pitfall traps); N. Minoretti (field assistant for pitfall traps)
Species determinations: B. Braschler; R. Neumeyer & B. Seifert (some verifications)
Statistical analyses: B. Braschler; B. Baur (advice)
Writing: B. Braschler; B. Baur (partial rewriting/ corrections)

Chapter V Grain-dependent relationships between plant productivity and invertebrate species richness and biomass in calcareous grasslands

Idea: B. Baur
Field work: C. Dolt (plants); G. H. Thommen (grasshoppers); P. Oggier (gastropods 1996); B. Braschler (gastropods 1997); S. Zschokke (temperature)
Species determinations: C. Dolt (plants); G. H. Thommen (grasshoppers); P. Oggier (gastropods 1996); B. Braschler (gastropods 1997); B. Baur (some verifications of gastropod determinations)
Statistical analyses: B. Braschler; S. Zschokke (species-area curves, partial preparation of 1996 data for analysis); B. Baur & E. Lüdin (advice)
Writing: B. Braschler (most); B. Baur (first draft of introduction; partial rewriting of the whole manuscript); S. Zschokke (first draft of experimental design and field methods)

Curriculum vitae

General information

Name: Brigitte Michèle Braschler

Date of birth: 3 March 1971

Nationality: Swiss citizen

Place of origin: Freienbach SZ

Education

1997–2003
PhD thesis

Department of Integrative Biology, Section of Conservation Biology (NLU), University of Basel, Switzerland

'Effects of experimental small-scale grassland fragmentation on the population dynamics of invertebrates'

Supervisor: Prof. Dr. Bruno Baur
Coreferee: PD Dr. Andreas Erhardt
External Expert: Prof. Dr. Daniel Cherix

1991–1997
University education

- Diploma in Biology I. Main subject: population biology (Prof. Dr. S. C. Stearns). Diploma thesis 'Effects of small-scale habitat fragmentation on ants'; supervised by Prof. Dr. B. Baur.

- Biology I, University of Basel, Switzerland, specialising on population biology, secondary subjects: herbivore biology, plant ecology, vertebrate biology, additional subject (Wahlfach): biochemistry

During my studies I attended lectures by:

Arber, W; Armbruster, GFJ; Bandle, C; Baroni Urbani, C; Baur, B; Boesch, C; Bruderer, B; Burckhardt, D; Burkhart, H; Doebeli, M; Duelli, P; Ebert, D; Flückiger, W; Freyvogel, T; Gabriel, W; Gering, W; J; Gisi, U; Haase, M; Hall, MN; Hauri, H-P; Im Hof, H-C; Jacomet, S; Keller, W; Kirchner, K; Körner, C; Küry, D; Leadley, P; Lüdin, E; Meier, U; Nagel, P; Nyffeler, M; Oelhafen, P; Rahier, M; Rahm, U; Rehmann-Sutter, C; Rowell, H; Rusterholz, H-P; Sanders, I; Schatz, C; Schmid, V; Schmidt, B; Schneider, H; Seelig, A; Senn, DG; Sigel, H; Spiess, M; Stearns, SC; Stöcklin, J; Tamm, C; Weber, D; Wiemken, A; Wiemken, V; Zschokke, S

1978–1991
Schools

- 28. June 1991	Matura Type C
- 1987 – 1991	Mathematisch Naturwissenschaftliches Gymnasium in Basel, Switzerland
- 1983 – 1987	Progymnasium Allschwil, Switzerland
- 1981 - 1983	Primary School Schönenbuch, Switzerland
- 1978 - 1981	Primary School Allschwil, Switzerland

Professional experience

Teaching experience

June 2003

- Teaching assistant in the 'Feldpraktikum Biodiversität' for undergraduate students. Course by Prof. Dr. B. Baur and PD Dr. A. Erhardt, University of Basel.

June 2002

- Biological expert and teacher for the school Project 'Biodiversitätsmonitoring im Pfeffingerwald' with students of the Gymnasium Kirschgarten, Basel, Switzerland.

Mai-June 2002

- Tutor in 'Grundlagen der Ethik für Studenten der Biologie und Pharmazie' for undergraduate students. Course by PD Dr. A. Seelig-Löffler and Prof. Dr. C. Rehmann-Sutter, University of Basel.

June 2000

- Teaching assistant in the 'Feldpraktikum Biodiversität' for advanced undergraduate students. Course by Prof. Dr. B. Baur and PD Dr. A. Erhardt, University of Basel.

1997-2002 winter semesters

- Teaching assistant in 'Modellbildung, Systemanalysen und Computersimulationen in der Ökologie'. Course by Prof. Dr. B. Baur and Dr. S. Zschokke and in two years Dr. E. Lüdin, University of Basel.

Short-term biology jobs at the University of Basel

1996

- Ant species determinations from pitfall traps. Project by Prof. B. Baur, University of Basel

1995-1997

- Field assistant in projects on snail activity rhythms and grassland snail diversity. Projects by P. Oggier and Prof. Dr. B. Baur, University of Basel.

Publications

Journal papers and book chapter
(includes articles based on the thesis that were published after the exam)

Braschler B. & Baur B. (2005) Experimental small-scale grassland fragmentation alters competitive interactions among ant species. *Oecologia* 143, 291-300.

Braschler B., Zschokke S., Dolt C., Thommen G. H., Oggier P. & Baur B. (2004) Grain-dependent relationships between plant productivity and invertebrate species richness and biomass in calcareous grasslands. *Basic and Applied Ecology* 5, 15-24.

Braschler B. & Baur B. (2003) Effects of experimental small-scale grassland fragmentation on spatial distribution, density, and persistence of ant nests. *Ecological Entomology* 28, 651-658.

Braschler B., Lampel G. & Baur B. (2003) Experimental small-scale grassland fragmentation alters aphid population dynamics. *Oikos* 100: 581-591.

Braschler B. (2003) Ameisen (Hymenoptera: Formicidae). In Burckhardt D., Baur B. & Studer. A. (eds) *Fauna und Flora auf dem Eisenbahngelände im Norden Basels* pp. 110-114.

Braschler B. (2002) Neue Aspekte zur Verbreitung von *Pyramica baudueri* (Emery, 1875) (Hymenoptera: Formicidae). *Mitteilungen der Entomologischen Gesellschaft Basel* 52: 139-142.

Zschokke S., Dolt C., Rusterholz H.-P., Oggier P., Braschler B., Thommen G. H., Lüdin E., Erhardt A. & Baur B. (2000) Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation. *Oecologia* 125: 559-572.

Project short note (unrefereed abstract)

Braschler B. (1998) Influence of habitat fragmentation on an ant community. *Biodiversity Newsletter* 12: 3.

Conference contributions

Braschler B., Zschokke S., Dolt C., Thommen G. H., Oggier P. & Baur B. (2003) Scale-dependent relationships between plant productivity and invertebrate species richness and biomass. Biology'03 in Zürich, Switzerland.

Braschler B. (2003) Interessante Ameisenfänge auf einer Eisenbahnbrücke in Basel. 9. Schweizerische Aculeaten-Tagung in Zürich, Switzerland.

Braschler B. & Baur B. (2002) Effects of experimental grassland fragmentation on aphid population dynamics. IX European Ecological Congress (Eureco‘02) in Lund, Sweden.

Braschler B. & Baur B. (2001) Effects of experimental grassland fragmentation on ant species composition. 31 Annual Conference of the Gesellschaft für Ökologie (GfÖ’01) in Basel, Switzerland. *Verhandlungen der Gesellschaft für Ökologie* 31: 341.

Conference contributions (continued)

Braschler B., Lampel G. & Baur B. (2001) Effects of experimental small-scale grassland fragmentation on the population dynamics of aphids. Zoologia et Botanica in Neuchâtel, Switzerland.

Braschler B. & Baur B. (2001) Effects of experimental small-scale habitat fragmentation on ant species composition in calcareous grasslands. Winter Meeting of the British Ecological Society in Birmingham, UK.

Braschler B. (2000) Effects of experimental small-scale grassland fragmentation on ants. Swiss Forum on Conservation Biology 2 in Winterthur, Switzerland.

Braschler B. (2000) Effects of experimental grassland fragmentation on ants. First Student Conference on Conservation Science in Cambridge, UK.

Braschler B. & Baur B. (1999) Effects of experimental grassland fragmentation on ant nest distribution and feeding behaviour. Winter Meeting of the British Ecological Society in Leeds, UK.

Braschler B. (1999) Einfluss kleinräumiger Habitatfragmentierung auf Ameisen. Internationale Entomologen-Tagung in Basel, Switzerland.

Braschler B. (1999) Influences of small-scale fragmentation on ants. Zoologia et Botanica 99 in Zürich, Switzerland. *Revue Suisse de Zoologie* 106: 755.

Braschler B. (1998) Ant nest dispersion patterns. Joint workshop Integrated Project Biodiversity (IPB) - Finnish Biodiversity Research Programme (FIBRE) in Basel, Switzerland.

Invited talks

Braschler B. (2003) Effects of small-scale grassland fragmentation on invertebrate populations. Institute of Environmental Sciences, University of Zürich, Switzerland.

Braschler B. (2003) Ameisen: Entdeckungsreise in ein faszinierendes Reich. Talk at the general assembly of the Reformierter Frauenverein Allschwil-Schönenbuch in Allschwil, Switzerland.

Braschler B. (2002) Ameisen in Haus und Garten: Interessant - harmlos - lästig. Public talk organized by the Freunde des Botanischen Gartens Brüglingen in Basel, Switzerland.

Excursions

Ryf M., Braschler B. & Lischer C. (2002) Excursion to the location of the planned Waldschulzimmer with demonstrations of field techniques for biodiversity monitoring for students of the Gymnasium Bäumlihof, Basel.

Baur B., Goverde M. & Braschler B. (1999) Excursion to the research site Nenzlingerweide with a presentation of ongoing projects for delegates of the Social Democratic Party of the Canton Baselland.

Baur B., Braschler B. & Dolt C. (1998) Excursion to the research site Nenzlingerweide with a presentation of ongoing projects for members of the Trockenwiesen und – weiden Inventar der Schweiz.