Hierarchical top-down control of biodiversity in agricultural landscapes across organisational levels and spatial scales

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“It is the little things that run the world”
Edward O. Wilson

Contents

1. Introduction

1.1. Biodiversity in agricultural landscapes

Biodiversity is one of the fundamental manifestations of life (Wilson & Peter 1988). Nevertheless, is has been increasingly threatened by anthropogenic activities (Wilson & Peter 1988). Land-use change is predicted to have the largest global impact on biodiversity by the year 2100 (Sala et al. 2000; Buckley & Roughgarden 2004). In European countries, land use is dominated by agriculture which shapes more than half of the land area (EUROSTAT 1998). In the 20th century, industrialisation supported major changes in agricultural land use, which led to significant declines in biodiversity (Krebs et al. 1999; Robinson & Sutherland 2002). These changes were driven by both the intensification of agricultural land management and a loss of area, connectivity and diversity of semi-natural habitats.

Agricultural land-use practices could be regarded as environmental stress factors due to frequent perturbations by fertiliser and pesticide applications as well as mechanical treatments. Mechanical crop management activities were shown to adversely affect arthropod diversity both directly by increasing mortality as well as indirectly by enhancing emigration due to habitat disruption (Thorbek & Bilde 2004). Increasing fertiliser input has both direct and indirect negative effects on biodiversity (Haddad, Haarstad, & Tilman 2000; Vickery et al. 2001). Pesticides actually target certain species and species groups but also affect non-target species (Helioevaara & Vaeisaenen 1993; Holland, Winder, & Perry 2000). Hence, intensively managed agricultural fields represent highly dynamic areas with a high level of environmental stress and discontinuity in resource supply.

In contrast, semi-natural habitats offer more stable conditions and promote biodiversity. They provide a variety of extra habitat, food, shelter, breeding sites or dispersal corridors, and are fundamental even for those species that are tolerant to intensive agrarian land use. However, the intensification of agricultural management led to changes in the landscape structure. A decrease in the area of semi-natural habitats is accompanied by a decrease in species richness according to the well known species-area relationship (see Rosenzweig 1995). This is most likely because of reducing habitat and resource diversity (Johnson & Simberloff 1974; Ricklefs & Lovette 1999; Morand 2000) while increasing potentially negative edge effects (Fahrig 2002). Reducing habitat area also reduces the effective population size and consequently decreases the probability of persistence of a particular species (Hedrik & Gilpin 1997; Fahrig 2003).

Additionally, increasing habitat fragmentation affects biodiversity due to a loss of connectivity. A huge amount of literature exists on this topic, discussing whether habitat loss or fragmentation *per se* is the main driver (Fahrig 2003). However, decreasing habitat connectivity adversely affects dispersal (Debinski & Holt 2000) and therefore the exchange of individuals and genetic material. This may expose the smaller sub-populations to a greater risk of local extinction and possibly disrupt genetic and evolutionary processes. In consequence, this might lead either to isolated populations or to a metapopulation structure, where regional persistence depends on a compensation of local extinction by recolonisation according to dispersal ability and the landscape structure (Hanski & Gilpin

1997). Hence, the spatial arrangement of the remaining habitat patches *per se* might negatively affect biodiversity (Kareiva & Wennergren 1995).

Biodiversity has also been accepted to have a more complex, spatial component according to habitat diversity within a landscape, the so called β-diversity (Whittaker 1972; Lande 1996). In contrast to α-diversity (local within-community diversity), β-diversity denotes the among-community diversity and contributes, together with α-diversity, to the total biodiversity within a landscape or region (γ-diversity; Veech et al. 2002). Hence, a reduction in habitat diversity has a negative effect on overall biodiversity by reducing β-diversity.

Since these multiple aspects of agrarian land-use change will affect not only species richness but all levels of biodiversity such as genes, individuals, populations, communities, landscapes and ecosystems in specific ways and act across different spatial scales, a detailed knowledge about the relative effects on particular dimensions of biodiversity is important for ecological theory and biodiversity research.

1.2. Objectives

The principal objective of this thesis is to explore the relative effects of scale and land-use changes on major organisational levels of biodiversity in European agricultural landscapes. Therefore, this thesis deals with three different aspects of biodiversity realised in the same landscapes: genetics, populations and communities.

The first part deals with the spatial genetic structure of the land snail *Cepaea nemoralis* (L.) in a medium fragmented landscape at the local and landscape scale. The second part focuses on habitat modelling relating occurrence patterns in populations of the butterfly *Pararge aegeria* (L.) to environmental variables. At the landscape scale, the variables included climate and land use and at the local scale they represented local habitat suitability. The third part analyses two aspects of communities. Firstly, we related the similarities among local plant and arthropod communities to land-use variables at the landscape scale while controlling for local effects. We used similarities (as an inverse measure of β-diversity) to consider species identities and abundances. Secondly, the relative effects of land-use factors at three spatial scales (region, landscape, local) on compositional and ecological aspects of local arthropod communities were investigated.

Genetics

The impact of land-use change on genetic diversity is critical, because genetic diversity is a fundamental precondition for evolutionary change, including adaptation and speciation. Hence, species diversity emerges from genetic diversity and affects all levels of biodiversity through evolutionary processes over corresponding time scales. Within ecological time scales, two opposite forces affecting the genetic variation are genetic drift and gene flow. Genetic drift decreases the genetic variation within but increases the genetic differentiation among local populations. Contrarily, gene flow increases the variation within but decreases the differentiation among local populations (Hutchison & Templeton 1999). A decrease in habitat patch size and connectivity most likely affects species with limited dispersal ability and therewith diminishes gene flow but enhances drift, which reduces genetic variation in local populations of these species. Population genetic theory and experiments predict that fragmentation events caused by human activities might facilitate local extinction possibly leading to metapopulation dynamics (Fahrig & Merriam 1994; Saccheri et al. 1998). In order to investigate the effects of such metapopulation dynamics on the spatial genetic structure of a species with limited dispersal ability, we used the land snail *Cepaea nemoralis* as a model organism and addressed the following questions (Chapter 3):

(1) Can spatial genetic structuring be observed on a local scale within a continuous population of *C. nemoralis*?
(2) Does *C. nemoralis* exhibit a metapopulation structure at a mesoscale in fragmented landscapes? Which landscape properties influence genetic structure and diversity?
(3) Can 'area effects' be observed? Are selectively neutral genetic and phenotypic properties related?

Populations

Population structure has been recognised to have a major influence on the maintenance and loss of genetic diversity (Hedrik & Gilpin 1997). The genetic diversity of a species might be reflected in the diversity of habitat needs and responses to other species. These species attributes in turn are the basis for biodiversity at the levels of communities and ecosystems. Consequently, the spatial distribution and habitat requirements (as well as species interactions) of single species contribute significantly to overall biodiversity. In Chapter 4, we focused on species distribution patterns and habitat requirements in relation to land-use factors acting on different spatial scales. We used the butterfly *Pararge aegeria* as a model organism occupying semi-natural habitats and investigated the following questions:

(1) Which environmental factors are appropriate for predicting the effects of land use on the distribution of *P. aegeria*?
(2) How important are factors operating on local scales compared to regional scale factors?
(3) Is this relation invariant?

Communities (similarity)

Chapter 5 addresses the spatial dimension of biodiversity at the level of communities. Measures of species turnover are usually based on species numbers or diversity indices (β-diversity). However, these measures ignore species specific information. Hence, approaches that incorporate species identity as well as abundance should be superior in calculating similarity between local communities. Similarity among local communities is increasingly recognised to be potentially related to ecosystem functioning (Fukami, Naeem, & Wardle 2001). The similarity hypothesis assumes that the degree of similarity in species composition increases as species richness increases. It predicts that this increased similarity supports ecosystem reliability by reducing the spatial variability in functional processes (Fukami, Naeem, & Wardle 2001). However, land-use change is not only expected to affect species richness in a landscape but also to influence spatial similarity by potentially disrupting the exchange of individuals and species between local communities (Mouquet & Loreau 2002). We analysed the effects of land-use factors on the similarity in local communities of plants and five arthropod groups (wild bees, true bugs, carabid beetles, hover flies and spiders) addressing the following hypothesis:

(1) Hypothesis 1: Community similarity is a function of landscape configuration: as connectivity among patches is reduced, dispersal is disrupted and communities may be mere random samples from the species pool, leading to a decrease in community similarity.
(2) Hypothesis 2: Community similarity is a function of landscape composition and land-use intensity: loss of semi-natural habitat as well as increasing land-use intensity threatens habitat specialists and rare species, while relatively benefiting generalist and common species, thereby increasing community similarity.

Communities (compositional and ecological aspects)

In addition to species identity and abundance, ecological aspects of local communities such as body size and trophic position contribute significantly to the diversity and functioning of ecosystems (Holt 1996; Tscharntke & Brandl 2004). Body size is a key to many life history traits such as reproduction and resource use and is positively related to foraging range and dispersal ability (Peters 1986; Brown & West 2000). Hence, local community structure is expected to reflect the effects of land-use change on functional processes. In Chapter 6, we focused on disentangling and quantifying the relative effects of particular land-use factors across three spatial scales on compositional and ecological aspects of local arthropod communities and investigated the following questions:

(1) What is the relative impact of scale to the effects of environmental factors on local arthropod community composition and structure?
(2) What is the relative influence of land-use intensity, landscape structure and habitat properties on local arthropod community composition?
(3) How are body size and trophic position affected by these factors?

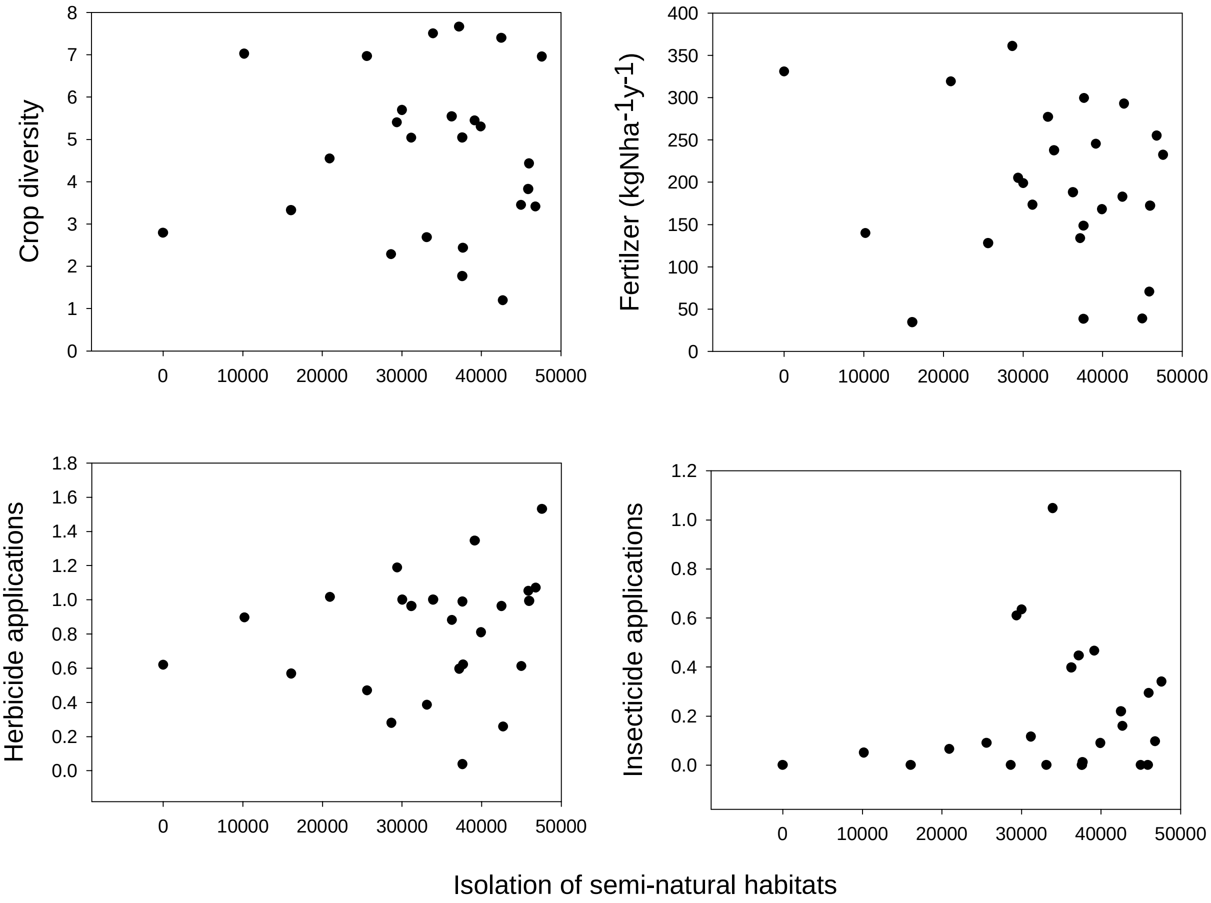

Fig. 1 Distribution of the 25 test sites according to land-use intensity and landscape structure. Neither crop diversity, measured as the number of crops in rotation (a) or the amount of fertilizer (b) nor the number of herbicide applications (c) or the number of pesticide applications (d) were significantly related to landscape structure (isolation of semi-natural habitats considering patch area and distance according to the mean proximity index).

1.3. Test sites

This thesis is based on data that were generated and compiled within the EU-project ‘GREENVEINS - Vulnerability of Biodiversity in the Agro-ecosystem as influenced by Green Veining and Land-use Intensity’ (contract number EVK2-CT-2000-00082), which aimed to establish large-scale relationships between biodiversity and the structure and management of agricultural landscapes for temperate Europe. 25 landscape test sites of 16 km^2 each were sampled within seven European countries: France (3 tests sites), Belgium (4), The Netherlands (4), Switzerland (3), Germany (4), Czech Republic (2) and Estonia (4). Together, these covered an independent gradient of both agrarian land-use intensity and landscape structure (Fig.1).

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2. Authors’ contribution to the research papers and manuscripts

The following chapters represent a compilation of research papers and manuscripts generated within the scope of the EU project ‘GREENVEINS’ in order to highlight the role of different organisational levels in biodiversity.

The authors’ contributions to the single chapters are as follows:

Chapter 3 *Genetics*:

Spatial genetic structure in a metapopulation of the land snail *Cepaea nemoralis* (Gastropoda: Helicidae)

O. Schweiger, M. Frenzel & W. Durka

Molecular Ecology (2004) **13**, 3645-3655

- Idea.
- Fieldwork and data collection; supervised by Walter Durka and Mark Frenzel.
- Data analysis; supervised by Walter Durka and Roland Brandl.
- Writing. Mark Frenzel, Walter Durka and Roland Brandl commented on the manuscript.

Chapter 4 *Populations*:

Occurrence pattern of *Pararge aegeria* (Lepidoptera: Nymphalidae) with respect to local habitat suitability, climate and landscape structure

O. Schweiger, C.F. Dormann, D. Bailey & Mark Frenzel

Manuscript submitted to *Conservation Biology*

- Idea in cooperation with Carsten Dormann.
- Fieldwork together with Mark Frenzel and other filed-workers within the GREENVEINS project. Sampling protocol by Rob Bugter.
- Data collection and unification (species coordinator within the project).
- Data analysis together with Carsten Dormann.
- Writing. Mark Frenzel, Carsten Dormann, Debra Bailey and Roland Brandl commented on the manuscript.

Chapter 5 *Communities*:

Effects of land use on similarity of plant and animal communities

Carsten F. Dormann, Oliver Schweiger, Isabel Augenstein, Regula Billeter, Mark Frenzel, Frederik Hendrickx, Torsten Schmidt, Walter van Wingerden

Manuscript submitted to *Journal of Applied Ecology*

- Idea in cooperation with Carsten Dormann.
- Fieldwork together with Mark Frenzel, Torsten Schmidt and other filed-workers within the GREENVEINS project. The author contributed significantly to the sampling protocol of arthropods.
- Identification of carabid beetles and wild bees for German test sites.
- Data collection and unification for all trapped arthropods; synonym check for all trapped carabid beetles, wild bees and hover flies.
- Data analysis together with Carsten Dormann.
- Writing together with Carsten Dormann. All co-authors and Roland Brandl commented on the manuscript.

Chapter 6 *Communities*:

Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organisational levels and spatial scales

O. Schweiger, J.P. Maelfait, W. van Wingerden, F. Hendrickx, R. Billeter, M. Speelmans, I. Augenstein, B. Aukema, S. Aviron, D. Bailey, R. Bukacek, F. Burel, T. Diekötter, J. Dirksen, M. Frenzel, F. Herzog, J. Liira, M. Roubalova & R. Bugter

Journal of Applied Ecology(2005) **in press**

- Idea
- Fieldwork together with other filed-workers within the GREENVEINS project. The author contributed significantly to the sampling protocol.
- Identification of carabid beetles and wild bees for German test sites.
- Data collection and unification; synonym check for all trapped carabid beetles, wild bees and hover flies.
- Data analysis; supervised by Roland Brandl.
- Writing. All co-authors and Roland Brandl commented on the manuscript.

3. *Genetics:* Spatial genetic structure in a metapopulation of the land snail *Cepaea nemoralis* (Gastropoda: Helicidae)

O. Schweiger, M. Frenzel & W. Durka

Molecular Ecology (2004) **13**, 3645-3655

3.1. Abstract

Habitat fragmentation is a major force affecting demography and genetic structure of wild populations, especially in agricultural landscapes. The land snail *Cepaea nemoralis* (L.) was selected to investigate the impact of habitat fragmentation on the spatial genetic structure of an organism with limited dispersal ability. Genetic and morphological patterns were investigated at a local scale of a 500 m transect and a mesoscale of 4 x 4 km in a fragmented agricultural landscape while accounting for variation in the landscape using least-cost models. Analysis of microsatellite loci using expected heterozygosity (H_E), pairwise genetic distance ($F_{ST}/(1-F_{ST})$) and spatial autocorrelograms (Moran´s I) as well as shell characteristics revealed spatial structuring at both scales and provided evidence for a metapopulation structure. Genetic diversity was related to morphological diversity regardless of landscape properties. This pointed to bottlenecks caused by founder effects after (re)colonisation. Our study suggests that metapopulation structure depended on both landscape features and the shape of the dispersal function. A range of genetic spatial autocorrelation up to 80 m at the local scale and up to 800 m at the mesoscale indicated leptokurtic dispersal patterns. The metapopulation dynamics of *C. nemoralis* resulted in a patchwork of interconnected, spatially structured subpopulations. They were shaped by gene flow, which was affected by landscape features, the dispersal function and an increasing role of genetic drift with distance.

Keywords: effective distance; gene flow; habitat fragmentation; isolation by distance; Moran´s *I*; stepping stone model.

3.2. Introduction

Habitat fragmentation is a major force affecting wild populations, especially in agricultural landscapes. Species inhabiting the mosaic of semi-natural habitats may experience population subdivision and reduced gene flow, which may contribute to local extinction (Fahrig & Merriam 1994, Saccheri et al. 1998, Reed & Bryant 2000). The metapopulation theory predicts regional persistence if local extinction is compensated by recolonisation (Hanski & Gilpin 1997). A metapopulation structure is accompanied by gene flow and may be reflected in the spatial genetic structure (Bohonak 1999, Hutchison & Templeton 1999). The effects of a metapopulation structure on genetic patterns mainly depend on dispersal ability and the landscape context. These effects might be most pronounced in species with low dispersal abilities that are living in highly fragmented landscapes. In this case, local extinction will result in empty patches and (re)colonisation might be accompanied by genetic bottlenecks if the number of founders is low and if they originate from only one or few source subpopulations (Wade & McCauley 1988). The resulting reduction in effective population size facilitates enhanced drift and reduces genetic diversity within recently founded subpopulations. Thus, repeated extinction and recolonisation events may enhance differentiation between distinct subpopulations compared with a continuous population (Harrison & Hastings 1996; Pannell & Charlesworth 2000). Furthermore, dispersal affects metapopulation genetics and may result in spatial structuring as a consequence of the opposite forces of gene flow and drift (Hutchison & Templeton 1999). In a spatially realistic metapopulation model, dispersal is a function of the landscape context (Hanski & Gilpin 1997). This underlines the importance of considering functional or effective distance measures for investigations of dispersal (Sork et al. 1999, Chardon et al. 2003, Adriaensen et al. 2003).

Land snails have been considered as ideal organisms for studies of ecological genetics over a wide range of spatial scales (see references in Davison 2002). They are characterized by low active dispersal ability, a high cost of locomotion (Denny 1980), an explicit homing behaviour (Taylor 1902, Edelstam & Palmer 1950, Rollo & Wellington 1981, Chelazzi 1990) and they reside in patchy habitats likely to promote geographical structuring.

We selected the land snail *Cepaea nemoralis* (L.) as a model organism of a species with limited dispersal (about 10 m per year; Lamotte 1951 in Cook 1998). *Cepaea nemoralis* can colonise a wide range of habitats such as deciduous woodlands, hedgerows or grasslands, almost all of which have been subject to massive alteration as a result of changes in anthropogenic land use. *Cepaea nemoralis* is not found on arable land (Cain & Currey 1963, Kerney et al. 1983) which will act as a barrier for dispersal and gene flow. However, a wide range of population sizes has been observed ranging from “a handful to a few thousand” individuals (Cook 1998). These conditions make it quite possible that *C. nemoralis* exhibits a metapopulation structure in a heterogeneous landscape dominated by arable land.

First studies about the population structure of *C. nemoralis* focused on the wide range of shell polymorphisms. The genetic control of the major forms is relatively simple (Lang 1904, Lamotte 1951 in Cook 1998, Cain et al. 1960, 1968). However, dominance of alleles and interacting loci rendered genotyping impossible in the field (Cook 1998). Cain & Sheppard (1950) showed that colour and banding pattern frequencies are influenced by the habitat and the corresponding selective pressure by visual predators, notably song thrushes (*Turdus philomelos).* In contrast, Cain and Currey (1963) reported on spatial patterns of shell polymorphism, so called area effects, where particular colour and banding types predominate in distinct areas regardless of both habitat and lack of selection by song thrushes. There is continuing discussion on whether selection or historical events explain the area effects (for a review of ideas see Cook 1998, Davison 2002). However, most studies supported historical reasons including random processes like founder effects during bottlenecks or the colonisation of new areas (e.g. Goodhart 1963, Davison & Clarke 2000, Bellido et al. 2002).

Combining phenotypic patterns of shell polymorphism with that of selectively neutral molecular markers analysed within and among subpopulations might provide valuable insights into processes of metapopulation structuring. Therefore, microsatellites represent ideal instruments, as they are highly polymorphic with high resolution at fine scales and they can cope with decreased genetic variability caused by population turnover (Jarne & Lagoda 1996, Gaggiotti 2004).

In the present study we investigated phenotypic and selectively neutral genetic patterns at two scales: (1) a local scale within a continuous local population and (2) a mesoscale among different local populations of the land snail *C. nemoralis* in a fragmented agricultural landscape. We assumed isolation by distance according to a stepping stone model of population structure (Kimura & Weiss 1964). This was applied at both spatial scales as Arnaud et al. (2001) observed small-scale genetic substructuring even within a continuous population of the land snail *Helix aspersa*. At the mesoscale, population subdivision was indicated by the fact that distinct habitat patches and subpopulations of *C. nemoralis* were separated by arable fields. Under the stepping stone model, gene flow is limited by dispersal and is most likely to occur between neighbouring sites. Consequently, more closely located populations are expected to be more similar, whereas remote populations should underlie the stochastic influence of drift.

We addressed the following questions: (1) Can spatial genetic structuring be observed on a local scale within a continuous population of *C. nemoralis*? (2) Does *C. nemoralis* exhibit a metapopulation structure at a mesoscale in fragmented landscapes? Which landscape properties influence the genetic structure and diversity? (3) Can area effects be observed? Are selectively neutral genetic and phenotypic properties related?

3.3 Materials and Methods

Study site and sampling design

Specimens of *Cepaea nemoralis* (L.) were collected at two spatial scales within a 4 x 4 km test site located in an agricultural landscape near the village of Friedeburg in Saxony-Anhalt, Germany (51°37′N, 11°42′E). At the local scale, 11 samples of a continuous local population within a hedgerow were taken at regular intervals of 50 m along a transect of 500 m. The hedgerow was adjacent to a field path and a cultivated field, respectively. Within the local population the samples are referred to as sites. At the mesoscale, 21 locations in distinct potential habitat patches within the test site were surveyed. *Cepaea nemoralis* was present in 9 locations. Empty shells indicated the former presence and hence possibly extinction events of *C. nemoralis* in at least four of the remaining 12 patches (Fig. 1).

To increase the number of samples to a total of 11, the first and last location of the transect were included in the mesoscale analysis. Since group discreteness depends upon limited mixing through dispersal and the minimum distance between the sample points (500 m) exceeded the average yearly movement of about 10 m by at least one order of magnitude, the specimens of each sample point were considered to represent single local populations of a metapopulation. Further on they are referred to as subpopulations. Genotypes were obtained from a total of 361 snails (transect, 213; test site, 184). Sample sizes ranged from 7 to 20 individuals. Snails were collected on a single day in September 2002 by searching the vegetation including the litter layer within a radius of 5 m. Specimens were stored at -40°C until DNA extraction.

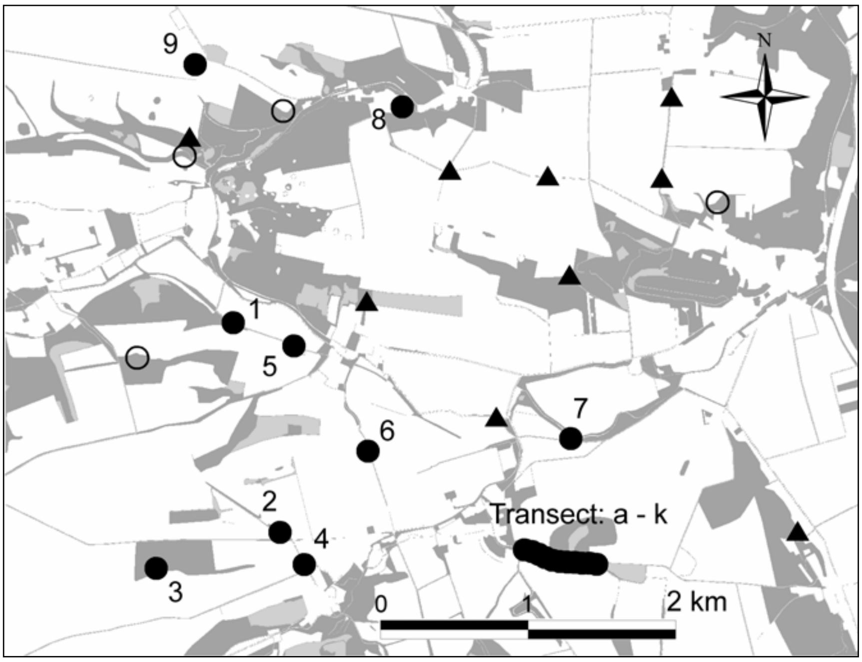

Fig. 1 Map of test site and sample sites. Dark grey, optimal habitat; light grey, suboptimal habitat; white, unsuitable habitat. Closed circles, *Cepaea nemoralis* was present; open circles, empty shells indicated local extinction; triangles, *C. nemoralis* was absent.

Microsatellite analysis

For genetic analyses, DNA was extracted from approximately 50 mg of tissue that was cut from the snail foot while still frozen. DNA was extracted using the DNeasy plant mini kit (Qiagen) according to manufacturers' instructions with the following modifications. The tissue was lysed for 3 h with 20 µL proteinase K (Qiagen) in 180 µL buffer AP1 (Qiagen) at 55°C, and the DNA was eluted with 100 µL of AE buffer (Qiagen). Polymerase chain reaction (PCR) was performed in a total volume of 8 µL with 2 µL of DNA solution diluted 1:10 and 2 pmol of each fluorescence labelled forward and unlabelled reverse primers using the Qiagen multiplex PCR kit and applying a hot-start thermocycling protocol. Four trinucleotide and one tetranucleotide microsatellite loci previously published were analysed (Davison 1999). The loci *Cne*1 (label: JOE), *Cne*11 (FAM), *Cne*15 (FAM) and *Cne6* (TAMRA) were developed in a multiplex PCR reaction at an annealing temperature of 57°C while locus *Cne*10 was run in a second PCR with a 65°C annealing temperature. PCR products were separated on an ABI 310 genetic analyzer (Applied Biosystems) with MapMarker 1000 (BioVentures Inc.) as internal size standard. Individuals were genotyped using GENOTYPER version 2.0 software (Applied Biosystems).

Genetic data analysis

The locus *Cne*10 did not produce any PCR product in more than 50% of the individuals and because of this abundant null allele, it was excluded from further analysis. To determine whether underlying assumptions for further statistical analysis of the remaining 4 loci were violated, deviations from Hardy-Weinberg equilibrium and genotypic linkage disequilibrium between loci were tested with GenePop (Raymond & Rousset 1995) with the Markov chain Monte Carlo method. Estimation of inbreeding coefficient (F_{IS}) followed the method of Weir & Cockerham 1984. *Cne*1 and *Cne*6 showed significant deviations from Hardy-Weinberg equilibrium in the majority of sites, whereas *Cne*11 and *Cne*15 did not. The heterozygote deficiency could have arisen if the sampling areas had exceeded those of Wrightian neighbourhoods ("Wahlund effect"), or because of rare null alleles. However, such inconsistent deviations from Hardy-Weinberg equilibrium among some of these loci were reported before (Davison & Clarke 2000). Since we also observed individuals that did not produce any PCR product (homozygous for null allele), we followed the assumption of Davison & Clarke (2000) that the sites were in Hardy-Weinberg equilibrium and that deviations in *Cne*1 and *Cne*6 were caused by null alleles. Null allele frequencies of both loci were estimated under the assumption of Hardy-Weinberg proportions according to Brookfield (1996) with the software MICRO-CHECKER (Van Oosterhout et al. 2004). Total allele frequencies were adjusted. The microsatellite loci are supposed to be selectively neutral except for *Cne*11, which showed evidence of linkage to shell banding (Davison 1999, Davison & Clarke 2000). As statistical prerequisites were satisfied, Fisher´s exact tests of population differentiation and estimators of Wright´s F-statistics following Weir and Cockerham (1984) were performed using GENEPOP. Genetic diversity corrected for sample size was computed as expected heterozygosity (H_E) (Nei 1973) with the software MSA (Dieringer & Schlötterer 2003).

Phenotypic data analysis

The specimens were scored for shell colour and banding, using slightly modified criteria of Cain and Sheppard (1950). The frequencies of white, yellow, pink, brown and the number of bands (0 - 5) were used to calculate the Shannon-Wiener index (Shannon 1948, Wiener 1948) for colour and banding patterns separately and combined as a measure of phenotypic diversity.

Spatial and environmental statistics

Landscape elements were digitized from orthophotos and mapped together with the sample points in a Geographic Information System (GIS) using ArcView software (ESRI 1996). Two different measures of distances between the sample points were used. The first one was simply the linear geographical distance. The underlying assumption is that snails disperse uniformly in any direction, regardless of landscape features. Although this is indeed suitable for the transect conditions, it is unrealistic in a heterogeneous landscape. Therefore, we used measures of functional or effective distance in order to account for differences in resistance of particular habitats to movement. The effective distances were computed using least-cost modelling (Adriaensen et al. 2003 and references therein) in a GIS. The habitats were classified as optimal, suboptimal and not suitable according to the habitat requirements of *C. nemoralis* (Cain & Currey 1963, Kerney et al. 1983). These classes were assigned to resistance values that determine the relative costs of *C. nemoralis* moving between patches. Since we had no detailed knowledge on the movement behaviour, three model scenarios were used that differed in the resistance of suboptimal and unsuitable habitats (Table 1). Cost values in optimal habitats were held constant at 1. The models yielded least-cost paths between the sampling points. The effective distances were obtained by moving along these paths and summing up the resistance values according to a grid of 1 x 1 m. Thus, they represent a product of distance and estimated resistance values. The effective distances were given in units of meter and are abbreviated "m*" to avoid confusion with geographical distance. The underlying assumption is that the dispersal of snails in an optimal habitat may be estimated by the linear geographical distance, whereas the probability of successfully crossing barriers decreases with distance according to the resistance of the barrier.

The degree of genetic population differentiation at the two scales was compared using global F_{ST} values across all loci and the corresponding 95% confidence intervals (CI), which were determined by jackknifing. To test for isolation by distance, pairwise (F_{ST}/(1-F_{ST}))-matrices were related to geographical distance as well as effective distances following Rousset (1997). Regressions were drawn for means of visualization only, as pairwise distance values are not independent. Mantel tests were used to test for significance (1000 permutations). A non linear (e.g. logarithmic) relationship between geographical or effective distance would reflect the differing roles of gene flow and genetic drift over different spatial scales as expected by the stepping stone model. Within short distances gene flow and drift were expected to be equal, whereas more distant subpopulations were expected to be relatively more influenced by drift (Hutchison & Templeton 1999).

Spatial autocorrelation of genetic variability was analysed with correlograms of Moran´s *I* statistics (Moran 1950, Sokal & Wartenberg 1983, Hardy & Vekemans 1999). Spatial autocorrelation techniques have the advantage that they allow inference of spatial genetic structure independent from the often violated assumptions of classic *F*-statistics,

Table 1 Habitat types, habitat suitability and the sets of resistance values for the different least-cost models (*r*1-*r*3)

Habitat types	Habitat suitability	Resistance value		
		*r*1	*r*2	*r*3
Mesic grasslands, grassy margins	Optimal	1	1	1
Tall forb habitats	Optimal	1	1	1
Woodland fringes and scrub habitats	Optimal	1	1	1
Deciduous woodlands and hedgerows	Optimal	1	1	1
Coniferous woodlands and hedgerows	Suboptimal	1	2	10
Pastures	Suboptimal	1	2	10
Dry grasslands	Suboptimal	1	2	10
Transport networks (soft-surfaced)	Suboptimal	1	2	10
Arable land, streets, urban areas, water bodies	Unsuitable	100	10	100

such as absence of selection and mutation or complete random migration of a constant number of individuals between the subpopulations (Whitlock & McCauley 1999). Distance classes of geographical and effective distances were created following Sturge´s rule (Legendre 1998), disregarding the last two classes because of too few replicates. As sampling was performed within a radius of 5 m, the first class represented a maximum distance between individuals of 10 m. The mean distance per distance class was used to draw correlograms. Moran´s *I* statistics of individual distance classes were tested for significance by a resampling procedure (1000 permutations). The global significance of the entire correlograms was evaluated using the progressive Bonferroni technique by dividing the significance level ($P = 0.05$) according to the rank of each subsequent distance class (Hewitt et al. 1997). If at least one distance class remained significant the entire correlogram is deemed to be globally significant (Legendre 1998). If global significance was shown, the range of genetic autocorrelation was estimated by the first *x*-intercept of the correlogram (Sokal & Wartenberg 1983, Sokal et al. 1997, Escudero et al. 2003). The *x*-intercept gives the average distance at which the similarity of any two sites is equal to the region-wide similarity expected by chance alone. This was termed “genetic patch size” by Sokal and Wartenberg (1983). The *x*-intercept was shown to be positively related to parent vagility and neighbourhood size and therefore to average distance of gene flow per generation (Epperson 1993, Epperson & Li 1997, Sokal et al. 1997). To obtain an impression of the variability of individual pairwise Moran´s *I* coefficients and the *x*-intercept we calculated 95% confidence intervals by bootstrapping 10 000 times within each distance class. All spatial autocorrelograms were calculated with the software SPAGEDI (Hardy & Vekemans 2002).

The analysis of phenotypic data was similar to the genetic analysis for means of comparison. The shell morphology is known to be determined by an allelic series, with darker colours being dominant over paler ones and unbanded dominant over banded (Lang 1904, Lamotte 1951 in Cook 1998, Cain et al. 1960, 1968). However, dominance of alleles and interacting loci rendered genotyping impossible in the field (Cook 1998). Therefore, we relied on phenotypic data that were treated as two artificial loci (colour and banding) with four alleles (white, yellow, pink, brown) and six alleles (0 - 5 bands), respectively. Pairwise phenotypic distances were calculated as χ^2 distance. Population differentiation at both scales was compared by the average values of the pairwise χ^2 distances. Their 95% confidence intervals were retrieved by bootstrapping 10 000 times. The analysis of isolation by distance was performed in the same way as for microsatellites but using χ^2 distance. Spatial structuring was analysed with autocorrelograms of Moran´s *I*.

To investigate the role of landscape structure at the mesoscale, circular areas were defined around each sample site. Within the circular areas the following landscape variables were calculated: local patch size, number of habitat types, number of patches, sum of patch size, average patch size, area of single habitat types and area of habitats aggregated into optimal, suboptimal and unsuitable habitat classes. To account for scale-dependent differences in landscape structure, we calculated areas of two diameters around each sample site. The diameters were derived from the *x*-intercept of the autocorrelation analyses at both spatial scales. The *x*-intercept is an approximation of the genetically homogenous surface (Sokal & Wartenberg 1983, Epperson 1993, Arnaud et al. 2001). Hence, it reflected the range of genetic influence at a smaller and a larger scale.

Selective pressure due to visual predation by song thrushes (*T. philomelos)* contributes to spatial structuring in snails. To account for this, we determined bird density using the point-stop-method (Bibby 2000). At 20 points on a grid of 500 m laid over the test site the birds were recorded during a stop of 10 min on 3 monthly visits from April to June 2001.

3.4. Results

Genetic diversity and global population differentiation

All microsatellite loci were polymorphic, having between 2 and 13 alleles per sample site. Mean expected heterozygosity (H_E) per sample site ranged from 0.73 to 0.80 at the local scale and from 0.56 to 0.80 at the mesoscale (Table 2). No significant genetic linkage disequilibrium between loci was detected. Tests of population differentiation showed significant heterogeneity for all loci among sites of the entire test site ($P < 0.001$) and the transect ($P < 0.049$), indicating spatial structuring at both scales.

Scale	**Site**	**Sample size**	**No. alleles**	**Mean alleles**	H_E
Mesoscale	1	20	28	7.0	0.74
	2	14	27	6.8	0.80
	3	7	12	3.0	0.63
	4	18	21	5.3	0.56
	5	20	34	8.5	0.78
	6	20	24	6.0	0.76
	7	20	29	7.3	0.79
	8	10	24	6.0	0.71
	9	19	30	7.5	0.73
Local scale	a	17	26	6.5	0.75
	b	20	29	7.3	0.79
	c	20	29	7.3	0.79
	d	20	26	6.5	0.79
	e	19	28	7.0	0.77
	f	20	24	6.0	0.73
	g	20	27	6.8	0.79
	h	19	30	7.5	0.80
	i	17	25	6.3	0.76
	j	20	33	8.3	0.76
	k	18	35	8.8	0.79

Table 2 Sample size, number of alleles and expected heterozygosity at the sample sites. No. alleles, total number of alleles over all four microsatellite loci; mean alleles, mean number of alleles per locus; H_E, mean expected heterozygosity over all loci after adjustment for null alleles under assumption of Hardy-Weinberg equilibrium.

Local scale: genetic differentiation within a continuous subpopulation

The field survey showed that the subpopulation of the transect along the hedgerow could be regarded as continuous as no major gap between single individuals was observed. Nevertheless, a minor but significant level of differentiation occurred at the local scale (global $F_{ST} = 0.012$, 95% CI 0.0010 – 0.0228). A positive correlation between genetic (F_{ST} /(1- F_{ST})) and geographical distance evidenced isolation by distance within the 500 m of the transect ($R^2 = 0.052$, $P = 0.015$, Mantel test). The correlogram of the average Moran´s *I* statistics over all loci indicated positive autocorrelation that ended between 50 and 100 m (Fig. 2a).

Mesoscale: genetic differentiation among distinct subpopulations

At the mesoscale, the subpopulations of the entire test site exhibited a significantly greater amount of differentiation (global $F_{ST} = 0.076$, 95% CI, 0.053 – 0.100) than the sites at the local scale, as both confidence intervals did not overlap. Significant pairwise F_{ST} values between neighbouring sample sites indicated discrete subpopulations. However, no significant correlation between genetic (F_{ST} /(1- F_{ST})) and geographical distance (untransformed or logarithmic) was detected with the Mantel test, while correlograms revealed significant spatial structuring. Average Moran´s *I* statistics over all loci indicated positive autocorrelation that ended between 416 and 854 m (mean distance per distance class; Fig. 2a). This was significantly larger than at the local scale and pointed to different modes of dispersal at both scales.

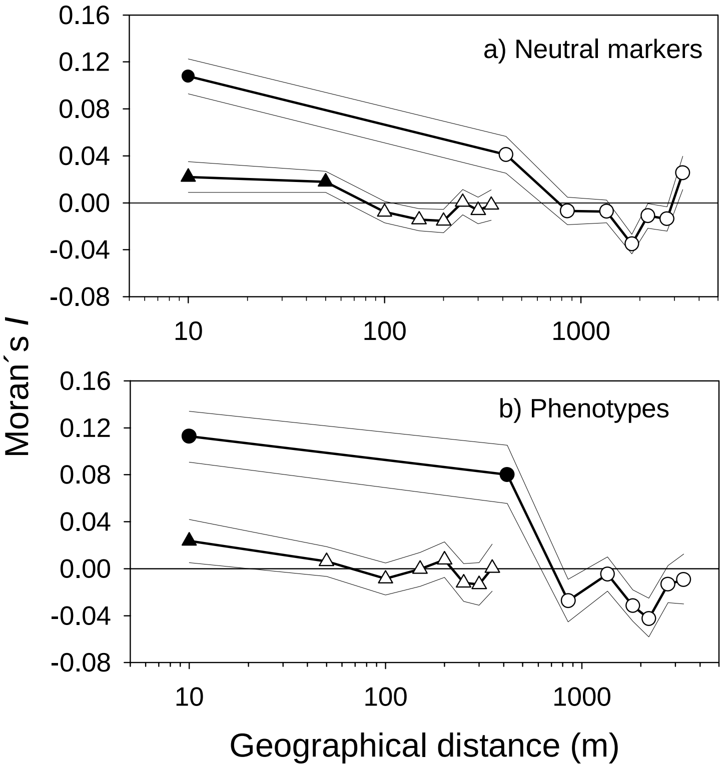

Fig. 2 Spatial autocorrelograms based on average Moran´s *I* coefficients for all microsatellite loci (a) and phenotypic data (b). All correlograms were globally significant. Closed symbols indicate significant individual autocorrelation coefficients after progressive Bonferroni correction. The range of autocorrelation can be assessed by the *x*-intercept. Triangles, autocorrelation at the local scale; eight continuous distance classes of 50 m along the transect of 500 m were used. Circles, autocorrelation at the mesoscale; eight continuous distance classes of 500 m for the subpopulations of the test site were used (average distance within a class given). Thin lines, 95% confidence intervals of individual pairwise Moran´s *I* coefficients per class.

In addition to geographical distance we considered landscape properties and evaluated the effective distances among the sampling points with three alternative models (Table 1). The correlation between genetic distance (F_{ST} /(1- F_{ST})) and the logarithm of effective distance was only significant in models *r*1 and *r*3. The explained variance of r1 was quite similar ($R^2 = 0.14$) to *r*3 ($R^2 = 0.13$). We chose to use *r*1 because of higher R^2 and the fact that fewer assumptions were made about the resistance values (see Crawley 2002). Correlations between genetic distance and untransformed effective distances were not significant, whereas significant results were obtained using the logarithm of effective distances ($R^2 = 0.14$, $P = 0.007$, Mantel test; Fig. 3a). Spatial autocorrelation analysis in terms of effective distance revealed significant autocorrelation up to the distance class with a mean of 2358 m* and an upper class border of 3500 m* effective distance. Below this effective distance of 3500 m* gene flow and drift were in equilibrium as the linear regression of (F_{ST} /(1- F_{ST})) on effective distance was significant ($R^2 = 0.47$, $P = 0.001$, Mantel test). Above this threshold, drift was dominating as no significant correlation was shown.

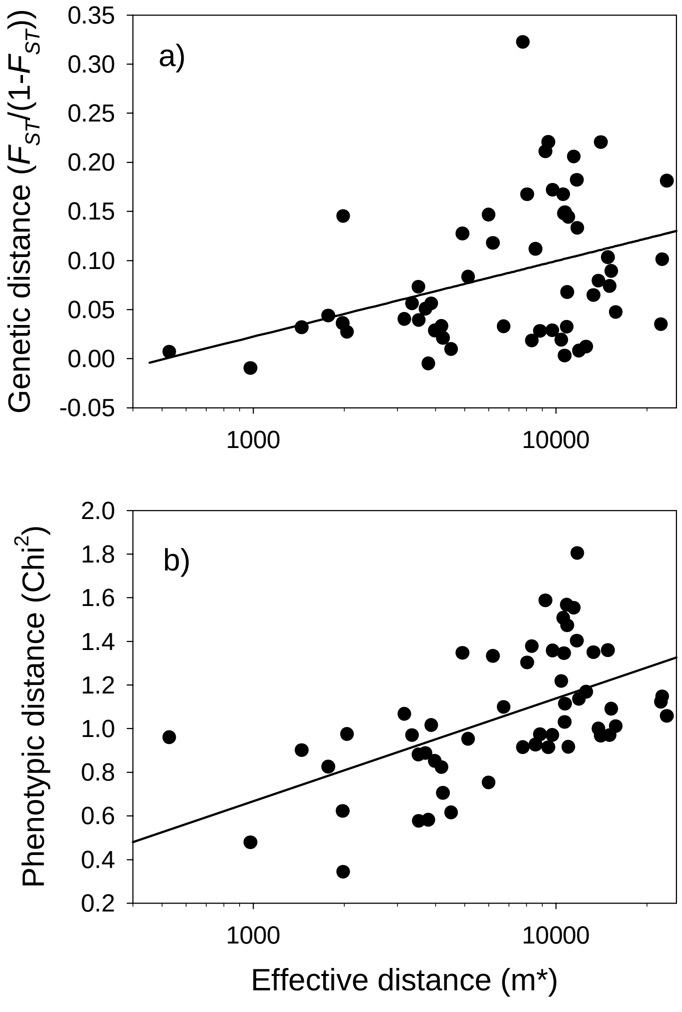

Fig. 3 Isolation by distance at the mesoscale. Effective distance (m*) was calculated according to least-cost modelling and represents a product of distance (m) and an estimated resistance value of the particular habitat class. (a) Pairwise genetic distance (F_{ST} /(1- F_{ST})) showed a logarithmic relation to pairwise effective distance over the entire test site ($R^2 = 0.14$, $P = 0.007$, Mantel test). (b) Pairwise phenotypic distance (χ^2) exhibited a similar distance dependence ($R^2 = 0.31$, $P < 0.001$, Mantel test).

Mesoscale: Genetic and phenotypic diversity within subpopulations

The diversity of colour and banding patterns (Shannon-Wiener index) was highly correlated ($R^2 = 0.51$; $P < 0.001$). This indicated that forces affecting their diversity did not differ significantly between both characteristics. Therefore both characteristics were combined as morphological diversity. Bird surveys showed that the density of song thrushes was negligibly low within the test site and zero around all sample points. Hence, the absence of selection by predation on phenotypic patterns was assumed.

No significant relationship between genetic (H_E) and morphological diversity (Shannon-Wiener index) was encountered at the local scale of the transect, whereas the correlation was significant at the mesoscale of the test site ($R^2 = 0.44$, $P = 0.001$; Fig. 4). However, the correlation was influenced by two sites with both reduced morphological and genetic diversity, so was not significant when these two points were omitted from the analysis ($R^2 = 0.16$, $P = 0.102$).

To analyse the effect of landscape structure on genetic diversity within the subpopulations of the mesoscale we related the landscape structure variables to H_E. For a small scale analysis a radius of 80 m was chosen according to the local range of genetic autocorrelation (x-intercept in Fig. 2a). In a stepwise multiple regression including all landscape variables, only the area of field paths significantly enhanced genetic diversity ($R^2 = 0.41$, $P = 0.002$). Neither local patch size nor other local variables had significant effects on genetic diversity. For a larger scale analysis, a radius of 500 m was chosen from the correlogram of the test site (Fig. 2a), but there was no significant correlation between H_E and any of the landscape variables.

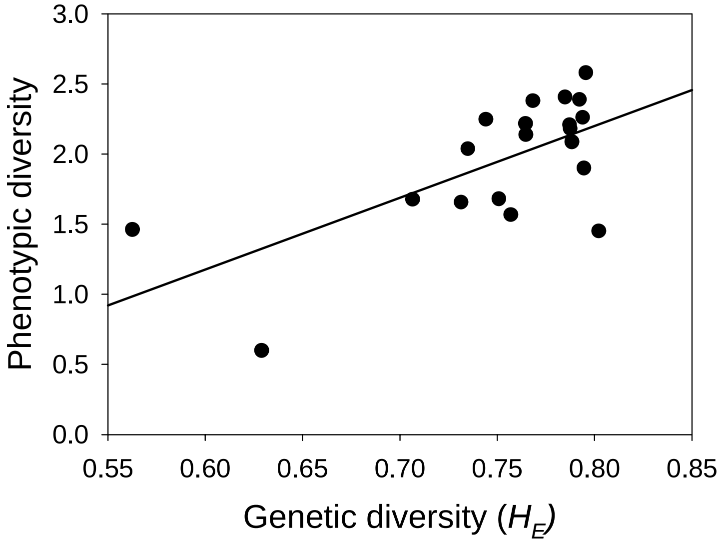

Fig. 4 Genetic (H_E) and phenotypic diversity (Shannon-Wiener index) were positively correlated ($R^2 = 0.44$, $P = 0.001$). The two outliers to the left are supposed to have recently undergone severe demographic bottlenecks (see text).

Genetic related to phenotypic differentiation, area effects

The analysis of the phenotypic data yielded results similar to the genetic data. The subpopulations exhibited a greater amount of differentiation at the mesoscale (mean χ^2 distance = 1.06, 95% CI 0.98 - 1.14) compared to the local scale (mean χ^2 distance = 0.72, 95% CI 0.68 - 0.76).

Local scale. In contrast to the genetic analysis the pairwise phenotypic distances (χ^2) were not correlated with geographical distance (Mantel test). However, average Moran´s *I* correlograms for colour and banding indicated a globally significant spatial autocorrelation (Fig. 2b). The *x*-intercept was between 50 m and 100 m, but 95% CIs indicated a potential restriction of spatial autocorrelation to the first distance class, which is in fact the diameter of the sample sites.

Mesoscale. The spatial analyses were consistent with results obtained from the microsatellites. No correlation between phenotypic (χ^2) and geographical distance was detected (Mantel test). However, spatial structuring was indicated by significant Moran´s *I* correlograms for colour and banding separately with *x*-intercepts between 416 m and 854 m. The average correlogram of both characteristics combined corresponded to that of the genetic analysis and indicated positive autocorrelation that ended between 416 m and 854 m (Fig. 2b). When landscape properties were considered, correlations were significant between the logarithm of effective distance and pairwise phenotypic distances (χ^2) of colour ($R^2 = 0.16$, $P = 0.009$) and banding ($R^2 = 0.21$, $P = 0.013$) as well as for both characteristics combined ($R^2 = 0.31$, $P < 0.001$, Mantel test; Fig. 3b).

The spatial structuring of colour and banding patterns revealed by Mantel tests and correlograms indicated area effects (Cain & Currey 1963), as closer subpopulations were morphologically more similar than distant ones (Figs 2b and 3b). However, the spatial arrangement of these patterns differed between colour, banding and genetics since the respective pairwise distances were not significantly related to one another (Mantel test).

3.5. Discussion

Local scale genetic structure within a continuous subpopulation

Cepaea nemoralis exhibited spatial structuring at both scales of the investigation. Even within a continuous subpopulation and in absence of barriers genetic patterns revealed a deme-like structure that was panmictic internally, but isolated from adjacent demes to some extent. This reflected the marked homing behaviour and limited dispersal abilities. The monotonic increase of pairwise genetic distance ($F_{ST}/(1-F_{ST})$) evidenced isolation by distance over at least 500 m. The average Moran´s *I* correlogram indicated a range of genetic autocorrelation that ended between 50 m and 100 m (Fig. 2a). This corresponded well to previous studies of the land snail *H. aspersa*, where the length of a panmictic unit was found to range between 50 m and 80 m by indirect (Arnaud et al. 1999) and direct methods (Madec 1989 in Arnaud et al. 1999).

Mesoscale metapopulation structure

In our study we found evidence for a metapopulation structure of *C. nemoralis* in a fragmented landscape. A first hint was that suitable habitat patches were not colonised and empty shells indicated local extinction in some of them (Fig. 1). The two major forces shaping metapopulation structure are demographic processes and dispersal. Demography can be affected by a drastic reduction in population size owing to a reduction in patch size or colonisation by a low number of migrants. Depending on dispersal ability and landscape properties empty habitat patches may be (re)colonised. However, both reduction in population size and colonisation can cause severe bottleneck effects. In consequence of random drift, bottlenecks are characterized by a drastic reduction in genetic diversity. This should affect both diversity of selectively neutral markers as well as phenotypic diversity regardless of possible differences in selection, mutation or drift. In the present study, recent bottlenecks were indicated by Fig. 4 at the mesoscale. As the proportion of subpopulations that have undergone recent bottlenecks might be low, the two points to the left in Fig. 4 should not be regarded as outliers, but as an indication of recent drastic bottlenecks. This is corroborated by the fact that in these two sample points both shell colour and banding diversity were reduced. As the bottlenecks were unlikely caused by selective predation, we assumed that they were caused by common, namely demographic processes.

To investigate whether the demographic processes reflected a metapopulation structure that was created by local extinction and (re)colonisation or if the observed patterns merely reflected the influence of landscape patterns on a more or less static population, we related the genetic diversity to landscape and patch characteristics. We found that genetic diversity at the mesoscale was not related to landscape or patch characteristics. This was consistent with previous studies of the land snail *Pomatias elegans* (Pfenninger 2002). Here it was reported that the density of the individuals rather than patch size contributed significantly to genetic diversity. As neither reduction of patch size nor connectivity reduced genetic diversity, we assumed that the population bottlenecks were a consequence of founder effects after colonisation of empty patches indicating a metapopulation structure. Multiple regression revealed that the presence of field paths increased the genetic diversity of a particular subpopulation. This could be either due to migration along the grassy margins of field paths or by passive displacement by animals or even agricultural implements (e.g. Dorge et al. 1999).

The consequences of a metapopulation structure on genetic structure may depend on the dispersal function. *Cepaea nemoralis* is known do display a leptokurtic dispersal distribution (Davison 2000), where most individuals disperse over short distances and only a few disperse over intermediate and long distances (Ibrahim et al. 1996). This was reflected in our study by the patterns of genetic and phenotypic variability across the scales. The higher number of short-distance dispersers was indicated by a comparably low degree of genetic differentiation ($F_{ST} = 0.012$) and a low range of spatial autocorrelation at the local scale (50-100 m; Fig. 2). Consequently, a small number of long-distance dispersers was evidenced by a higher degree of genetic differentiation ($F_{ST} = 0.076$) and a higher range of spatial autocorrelation (416-854 m) at the mesoscale. This was in accordance with expectations from the leptokurtic dispersal function and suggested different structuring processes at both spatial scales. Davison (2000) reported that the ability of even a small number of individuals to disperse over long distances makes *C. nemoralis* an efficient coloniser of vacant habitats. Thus, within a fragmented anthropogenous landscape, *C. nemoralis* may be able to establish a metapopulation with an equilibrium of local extinction and colonisation.

The range of positive spatial autocorrelation corresponded well with previous studies of the land snail *Pomatias elegans* in moderately fragmented landscapes, where spatial genetic autocorrelation ended at distances greater than 500 m (Pfenninger 2002). As active migration of land snails in general is restricted to a few meters per year (Pfenninger et al. 1996, Arnaud et al. 1999), passive displacement by abiotic, biotic and anthropogenic vectors is the most likely mechanism for long-distance dispersal and appears to be more common than previously thought (Dorge et al. 1999).

Despite the importance of passive displacement, gene flow between subpopulations of land snails is significantly affected by landscape features. Arndaud (2003) found evidence that *H. aspersa* uses functional migration pathways such as canal embankments, road verges and hedgerows. In the present study we considered resistance values of particular habitat classes in order to evaluate functional aspects of the landscape context. Thereby we revealed a positive correlation between genetic and effective distance over the range of the whole test site, whereas the linear geographical distance failed. Effective distances mostly increased by the influence of barriers, while they were less affected by the resistance values of optimal and suboptimal habitats like woodlands or grassy margins. Such sites may have served as habitat for *C. nemoralis* in the past or as active or more likely as passive migration pathway. Gene flow and drift were shown to be in equilibrium at the mesoscale but the importance of genetic drift increased with effective distance (Fig. 3a). However, the logarithmic relation indicated a shift in the importance from gene flow to drift. Furthermore, the *x*-intercept of a Moran´s *I* correlogram (not shown) provided evidence for a threshold. Below this threshold of an effective distance of 3500 m* the regression of genetic distance on effective distance was linear and significant. This indicated an equilibrium between gene flow and drift up to this effective distance (Hutchison & Templeton 1999). Above the threshold the regression was not significant, indicating the increased importance of drift. Thus, with least-cost modelling and adequate setting of resistance values, a more realistic landscape model was developed.

Area effects

The spatial structuring of shell colour and banding morphs revealed significant area effects at the mesoscale (Figs 2b and 3b). The observed patterns were unlikely to be caused by selection of visual predators or by habitat features. However, equal ranges of phenotypic and genetic spatial autocorrelation supported common structuring processes such as dispersal (Fig. 2).

Assuming a metapopulation structure and leptokurtic dispersal, the pronounced spatial structuring is most likely the consequence of bottlenecks. These bottlenecks produced three sets of area effects, one in genetic population structure and two in shell morphology (banding and colour). This was also suggested by Davison and Clarke (2000) for *C. nemoralis* studied in the Marlborough Downs in Wiltshire, UK. They reported that the differences in the spatial patterns of genetic and morphological structure were only marginal. In the present study these differences were more pronounced, although the observed spatial autocorrelation was similar. This is most likely due to the fact that gene flow and phenotypic exchange are driven by the same dispersal function. The observed decoupling of the spatial genetic and phenotypic patterns might be a consequence of metapopulation dynamics in fragmented landscapes and the stochastic nature of colonisation and drift. Low numbers of founders colonising empty patches establish unique allele frequencies. Subsequently neighbouring patches are colonised or become genetically mixed, thereby establishing area effects. In the absence of visual predators colour and banding morphs may develop independent spatial patterns similar to neutral genetic markers.

Conclusions

Taking *C. nemoralis* as an example of an organism with limited dispersal capabilities, our study suggests that the metapopulation structure of such species in fragmented landscapes depends on both the landscape features and the shape of the dispersal function. *Cepaea nemoralis* exhibited spatial structuring at two scales. At the local scale a deme-structured subdivision of a continuous subpopulation corresponded to the limited active dispersal ability. At the mesoscale rare dispersal events, most likely driven by passive displacement, are suggested to lead to metapopulation persistence in a fragmented landscape. Under absence of visual predators the observed area effects of shell morphs may reflect the historical events structuring the metapopulation. The stochastic nature of drift and colonisation in fragmented landscapes is suggested to cause a decoupling of genetic and phenotypic spatial patterns.

Further research may focus on expectations of metapopulation theory concerning genetic patterns over a broad range of landscapes. Comparative investigations including continuous, subdivided and highly isolated populations may provide detection, understanding and discrimination of metapopulation effects on population genetics.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/MEC/MEC2357/MEC2357sm.htm

Appendix S1. Sample coordinates (X, Y, in Gauss-Krüger coordinate system) and allele frequencies at four microsatellite loci for nine sample sites at the mesoscale and 11 sample sites at the local scale. Frequencies were adjusted for estimated null allele frequencies (Null)

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4. *Populations*: Occurrence pattern of *Pararge aegeria* (Lepidoptera: Nymphalidae) with respect to local habitat suitability, climate and landscape structure

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4.1. Abstract

Distribution patterns of wild species are often adversely affected by human activities. Climate, land use and habitat quality are acting simultaneously at different scales. Knowing the relative importance of particular factors and scales on population response is of great importance for theoretical and applied ecology. We selected the speckled wood *Pararge aegeria* (L.) as a model organism occupying natural and semi-natural habitats. Its distribution was recorded at 23 test sites of 5 x 5 km in agricultural landscapes across seven European countries. Environmental predictors were mapped at a local (250 m) and a regional scale (5 x 5 km). We developed logistic regression models for two environmental scenarios. (1) The "High abundance scenario" was characterized by beneficial environmental and weather conditions coinciding with high local abundance of *P. aegeria*. (2) The "Low abundance scenario" reflected environmental stress and adverse weather conditions during larval development coinciding with low local abundance. The high abundance scenario revealed a low but equal effect of local and regional factors. Hence, *P. aegeria* was predicted to occur nearly anywhere under beneficial conditions. The low abundance scenario revealed totally different patterns. The effects of local and regional factors were high but climate dominated. *P. aegeria* was restricted to high quality patches and landscapes under adverse conditions. As both scenarios resulted in entirely different models, our study showed that the sensitivity of *P. aegeria* to local and landscape features might change, and alleged less important factors could turn into limiting factors. This stressed the importance of high quality landscape conditions at both scales even for species that appear to be relatively tolerant, and sounds a note of caution when predicting population response for management purposes based on just a single (or a few) year(s) of observation.

Keywords: butterfly; distribution; fragmentation; habitat quality; logistic regression; occurrence probability; predictive habitat model.

4.2. Introduction

Biodiversity is adversely affected by human induced changes in land use that operate over a broad range of spatial scales (Tilman & Kareiva 1997; Opdam, Verboom, & Pouwels 2003). Several factors are acting simultaneously at different scales in determining the local occurrence of species (Cushman & McGarigal 2002; Jeanneret, Schupbach, & Luka 2003). It is a major issue in both theoretical and applied ecology to understand the effects and interactions of the environmental factors on the distribution of organisms (Lawton 1996;

Hanski & Gilpin 1997; Gaston & Blackburn 1999; Rushton, Ormerod & Kerby 2004). Therefore, statistical modelling techniques such as generalized linear models (GLM) provide powerful tools (Guisan & Zimmermann 2000). These models also offer valuable ecological insights as they may guide conservation management in order to select the most important scales or factors.

Habitat quality corresponding to the requirements of a particular species is expected to be of major importance at the local scale (Duelli 1997). However, information on such high resolution is costly to obtain and update. At larger scales, climatic factors (Pollard, Rothery, & Yates 1996; Hill, Thomas, & Huntley 1999; Warren et al. 2001) as well as landscape structure (Thomas & Kunin 1999; Hanski 1999) affect the persistence of natural populations. Two aspects of landscape structure can be distinguished. Landscape composition (i.e. amount of habitat) was shown to be one of the key factors (e.g. Wagner, Wildi, & Ewald 2000), but also the configuration (i.e. spatial arrangement) of habitats has a strong impact on local populations (Hanski & Gilpin 1997). Environmental predictors like climate data and landscape structure are currently easy to obtain thanks to the increasing development of Geographical Information Systems (GIS) and digital cartography. However, these data are often focused on land use and may provide only coarse habitat classification that might not reflect the precise requirements of a particular species. Investigating the relative importance of site- and species-specific local habitat quality, climate and landscape structure at coarse resolution at larger scales is of great interest not only in theoretical ecology covering population dynamics but also in applied ecology and conservation management.

Butterflies have turned out to be excellent model organisms for investigations of (meta-) population response to habitat quality (Wettstein & Schmid 1999), landscape composition (Summerville & Crist 2001), landscape configuration (Hanski & Gilpin 1997; Baguette et al. 2003) and matrix properties (Chardon, Adriaensen, & Matthysen 2003; Jeanneret, Schupbach, & Luka 2003). We selected the speckled wood *Pararge aegeria* (L.) as a model organism occupying natural and semi-natural habitats which have been subject to massive alteration as a result of changes in anthropogenic land use. *P. aegeria* is essentially a species of woodlands and their margins. Larvae feed on a variety of grass species and overwintering can be either as larvae or pupae (Hesselbarth, Van Oorschot, & Wagener 1995). *P. aegeria* can persist as two or three generations per year. The flight periods of different generations overlap but two distinct peaks in phenology occur around May and August (Ebert & Rennwald 1991). *Pararge aegeria* is currently expanding its range corresponding to a northwards shift of climatic isotherms due to climate warming in Europe (Parmesan et al. 1999). A higher percentage cover of woodland was shown to increase the rate of expansion (Hill et al. 2001) and it prefers moving along woody features like tree rows or hedgerows between woodland patches (Chardon, Adriaensen, & Matthysen 2003).

In the present study we focus on the impacts of climate, local habitat quality and landscape structure in agricultural landscapes on the distribution of *Pararge aegeria*. For this reason we did not develop our model for specific habitat requirements of *P. aegeria* at the landscape level but focused on a coarse classification of landscape elements into arable fields, woodlike elements and herbaceous elements. In contrast, we considered habitat requirements of *P. aegeria* at the local scale when evaluating local habitat quality. We addressed the following questions: (1) Which environmental factors are appropriate for describing the effects of land use on the distribution of *Pararge aegeria*? (2) How important are factors operating on local scales compared to regional scale factors? (3) Is this relation invariant?

4.3. Methods

Study sites and environmental variables

Pararge aegeria was investigated at 23 test sites of 5 x 5 km in arable landscapes. The test sites were distributed across seven European countries: France, Belgium, The Netherlands, Switzerland, Germany, Czech Republic and Estonia (Fig. 1).

We recorded environmental data about land-use intensity of arable fields, landscape structure (focusing on natural and semi-natural elements) and climatic factors plus weather conditions during the sample years. The landscape structure was evaluated from digitized habitat maps. These maps emerged from orthophotos in a GIS using ArcGIS software (ESRI 2003). The habitats were mapped according to EUNIS classification system (available at http://mrw.wallonie.be/dgrne/sibw/EUNIS/home.html). We aggregated the

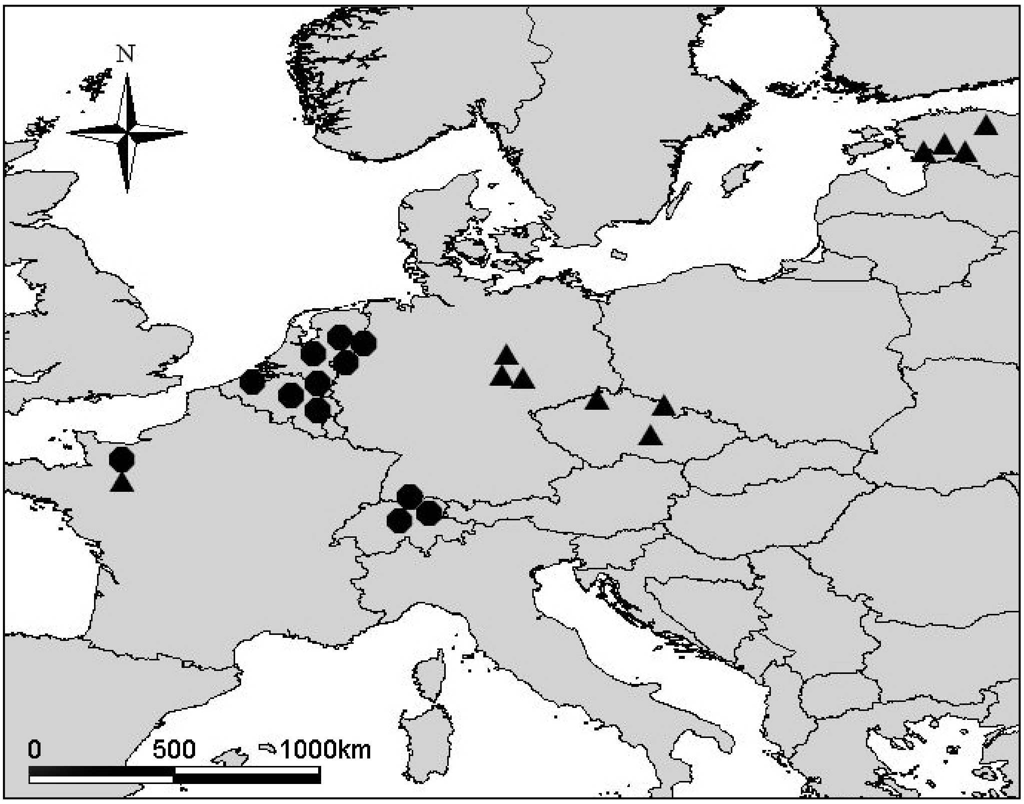

Fig. 1 Geographical distribution of test sites. Circles, sampled in 2002; Triangles, sampled in 2003.

Table 1 Habitat classification. Habitat class, focusing on the landscape; *P. aegeria,* focusing on the species.

Habitat	Habitat class	*P. aegeria*
Scrubby woodland edges	Woody	optimal
Broadleaved hedgerows	Woody	optimal
Woodland fringes, tall forb habitats	Woody	optimal
Mixed deciduous and coniferous hedgerows	Woody	suboptimal
Temperate scrub habitats	Woody	suboptimal
Temperate scrub heathlands	Woody	suboptimal
Broadleaved deciduous woodlands	Woody	suboptimal
Fruit and nut orchards	Woody	suboptimal
Mixed deciduous and coniferous woodlands	Woody	suboptimal
Grassy margins	Herbaceous	not suitable
Coniferous hedgerows	Woody	not suitable
Line of trees	Woody	not suitable
Mires, bogs, fens	Herbaceous	not suitable
Grasslands, tall forb habitats	Herbaceous	not suitable
Coniferous woodlands	Woody	not suitable
Arable land, urban areas, water bodies	Not suitable	not suitable

habitats into woody or herbaceous elements (Table 1) and together as natural and semi-natural habitat to contrast the unsuitable elements of arable land and urban areas. In order to consider specific habitat requirements of *P. aegeria* we additionally recoded the maps into optimal, suboptimal and unsuitable habitats (Table 1). Variables describing landscape composition were calculated as the percentage cover of semi-natural, woody and herbaceous patches as well as optimal, suboptimal and arable patches. In order to describe landscape configuration the landscape structure metrics Mean Patch Size, Number of Patches, Largest Patch Index, Edge Density, Proximity Index, Euclidean Nearest Neighbor Distance, Cohesion and Split were computed for woody and herbaceous elements and for the aggregated natural and semi-natural habitats using FRAGSTATS analysis (McGarigal & Marks 1995).

To account for the geographical gradient covering our study we considered longitude, latitude and corresponding climatic variables at test site level (temperature, precipitation and humidity at monthly resolution over the last 25 years) which were provided by interpolated climate data at a resolution of 0.5 degrees (available at http://climate.geog.udel.edu/~climate). Weather conditions during the sample years (temperature and precipitation) were recorded and analyzed at monthly resolution. But no interpolation was available and the test sites (in some cases several at once) were assigned to the nearest weather station.

Field surveys for occurrence of Pararge aegeria

A stratified random sampling design (Hirzel & Guisan 2002) was applied. Up to10 high quality, 10 medium quality and 10 low quality sample points were selected from digitized habitat maps. The quality of the sample points was assessed according to habitat suitability (as defined in Table 1) within a radius of 100 m. The number of points depended on the amount and distribution of potential habitat and ranged between 10 and 30 spots per test site. Single points were spaced at least 500 m apart to avoid double counting. The presence or absence of *P. aegeria* within a radius of 50 m around each point was mapped by visiting each test site once. Additionally the number of individuals present was roughly estimated. Surveys were carried out at the phenological peak of the second generation between July and August 2002 (12 test sites) and 2003 (remaining 11 test sites; Fig. 1).

Statistical analysis

Pre-analysis for scale of local influence and spatial autocorrelation

We recorded the environmental variables at two spatial scales: the regional level of the test site (5 x 5 km) and the local level of the sample point. To assess the scale of local influence we calculated the proportions of optimal and suboptimal habitat (as defined in Table 1) within areas of varying size around each sample point using diameters of 50, 125 and 250 m. No larger areas were considered to avoid substantial overlap and a resulting interdependency of local environmental predictors. Logistic regression models on presence-absence data of *P. aegeria* revealed that the radius of 250 m performed best according to deviance ratio. Hence, it was used for further analyses.

Linear model statistics are confounded by spatial autocorrelation, as it contradicts the assumption of independence among samples replicated through space. Therefore we checked whether the butterfly data were autocorrelated. Semivariograms showed no overall trend for an increase or decrease in dissimilarity among sample points. Hence, no spatial autocorrelation was evident.

Occurrence pattern analysis

Since the estimation of abundance data came from numerous filed-workers across Europe, we relied on the more robust presence-absence data for model building. The presence-absence data were analyzed using a nested binomial generalized linear model (GLM) where the sample point data were considered nested within test sites. These models were implemented in the glmmPQL-routine in the statistical software package R (R Development Core Team 2004). The environmental variables were standardized to avoid problems of collinearity between lower order and interaction terms and to make the coefficient estimates more interpretable (Quinn & Keough 2002). To allow for curvilinear relationships between each environmental variable and presence-absence data we incorporated linear and quadratic terms of the environmental variables. The models were simplified manually stepwise minimizing Akaike´s information criterion (AIC; Sakamoto

Table 2 Differences in test sites sampled in 2002 and 2003. Climate data are based on monthly resolution over the last 25 years. Woody patches, number of woodlike patches (woodlands, scrubs and hedgerows); suitable local habitat, frequency of optimal and suboptimal habitat within a circle of 250 m radius around a sampling point; Euclidean nearest neighbor, mean Euclidean nearest neighbor distance between the semi-natural elements of a test site. Bold, significant factors (t-test).

Factor	**Variable**	**2002**	**2003**	***P***
Geographical position	LAT	50.4	53.5	**0.027**
	LONG	5.9	16.6	< **0.001**
Climate	Mean annual temperature (°C)	9.3	7.2	**0.002**
	Mean monthly precipitation (mm)	72.2	53.7	< **0.001**
	Mean precipitation 6., 7., 8. (mm)	82.6	68.1	**0.007**
Weather in sample year	Mean precipitation 6., 7., 8. (mm)	85.5	41.5	< **0.001**
Landscape structure	Woody patches	747	382	< **0.001**
Abundance *P. aegeria*	Abundance per sample point	3.7	1.4	< **0.001**
Climate	Mean temperature 6., 7., 8. (°C)	16.4	16.3	n.s.
Local quality	Suitable local habitat (%)	23	15	n.s.
Landscape composition	Semi-natural elements (%)	25	30	n.s.
	Woody elements (%)	12	17	n.s.
Landscape structure	Euclidean nearest neighbor (m)	13	18	n.s.

et al. 1986; Rushton, Ormerod and Kerby 2004) and to contain only effects significant at the 5% level.

Several statistical methods have been developed to evaluate model performance (Fielding & Bell 1997; Manel, Williams, & Ormerod 2001). Since no external data set was available for testing model robustness, we used the area under the curve (AUC) of a receiver operating characteristic (ROC) plot for internal validation. This is a powerful, threshold-independent measure of overall fit that varies between 0.5 (for a chance performance) to 1.0 for a perfect fit (Fielding & Bell 1997; Cumming 2000; Manel, Williams & Ormerod 2001; Gibson et al. 2004). We calculated the AUC using SPSS software. The results are reported as AUC ± its standard error retrieved by bootstrapping.

The occurrence of *P. aegeria* was analyzed at both spatial scales simultaneously: the local level of the sample points and the regional level of the test sites. The analysis of optimal and suboptimal habitat patches at the local scale by means of a logistic regression model based on binary occurrence showed that the combination of optimal and suboptimal habitat contributed most significantly to an explanation of *P. aegeria* occurrence. Thus, "suitable local habitat" was the only factor from the local scale retained in further nested models and was used to describe local habitat quality.

In the initial model only the factors "sample year", "mean precipitation" and their interaction remained significant in addition to "suitable local habitat". As different sites were sampled in 2002 and 2003, they differed significantly in various aspects (Table 2). The test sites sampled in 2003 were located more east- and northwards with corresponding differences in climate (i.e. lower mean annual temperature and precipitation). Additionally, the test sites sampled in 2003 were characterized by a lower number of woody patches. However, no differences were detected in the landscape composition (percentage of woody, herbaceous and all semi-natural habitats) or local level factors (i.e. percentage of suitable local habitat). Moreover, weather conditions during the larval development of *P. aegeria* in the summer differed dramatically between test sites sampled in 2002 and 2003. Such differences are most likely influencing the appearance of the second generation. The summer in test sites sampled in 2002 was relatively humid with an average monthly precipitation of 85.5 mm in June, July and August, which differed not significantly from long-term mean (82.6 mm). Such humid conditions are regarded as optimal for *P. aegeria* (Hesselbarth, Van Oorschot, & Wagener 1995). In contrast, the same period in summer of test sites sampled in 2003 was significantly dryer (41.5 mm) compared to both long-term mean (68.1 mm) and test sites sampled in 2002 (both $P < 0.001$, t-test; Table 2). These arid conditions are unfavorable for the development of *P. aegeria* (Hesselbarth, Van Oorschot, & Wagener 1995). Drought is thought to have a direct influence on egg mortality (Wiklund & Persson 1983) and an indirect influence over desiccation of food plants (Pollard 1988; Roy et al. 2001). The consequences for the occurrence of imagos can be illustrated by the (unquantified) observation of *P. aegeria* individuals in two German test sites (with adequate composition of habitats) in 2002, but none in 2003. Another striking discrepancy concerned the mean abundance of *P. aegeria* per occupied sample point. The density of *P. aegeria* was significantly lower in test sites sampled in 2003 (Table 2). This huge discrepancy between the two survey “regimes” required for a separate analysis of the two years.

4.4. Results

Two scenarios

The two survey regimes revealed fundamental differences. The test sites sampled in 2002 were characterized by advantageous conditions like humid climate, high number of woody patches and humid weather conditions during larval development in the sample year. These beneficial conditions coincided with a high abundance of *P. aegeria* in occupied patches. Therefore the survey regime of 2002 was referred to as a “high abundance scenario”. In contrast, the survey regime of 2003 reflected environmental stress: the long-term mean annual precipitation was low, as well as the number of woody patches, and the weather during the larval development in the summer of the sample year was remarkably dry (Table 2). These adverse conditions coincided with a low abundance of *P. aegeria*. Consequently, the survey regime of 2003 was referred to as a “low abundance scenario”. The pronounced differences between both scenarios were reflected by the differences in the two final best models (Table 3). High model accuracy was indicated for both models by AUC values of 0.84 (± 0.024) for the high abundance scenario and 0.93 (± 0.024) for the low abundance scenario, respectively.

Table 3 Generalized linear mixed model of *Pararge aegeria* occurrence for two different scenarios. The environmental variables are ranked by their relative importance according to the standardized regression coefficients (Std.Coeff.). Std.Error, standard error; DF, numerator degrees of freedom; 2002: N total = 291 sample points in 12 test sites; 2003: N total = 194 sample points in 11 test sites. Euclidean nearest neighbor, mean Euclidean nearest neighbor distance between semi-natural habitat patches; suitable local habitat, percentage of optimal and suboptimal habitat within a radius of 250 m; Woody patches, number of woody patches; Woody patches:Local habitat, interaction term of the number of woody patches and suitable local habitat.

Variable	**Std.Coeff.**	**Std.Error**	**DF**	**t-value**	***P***
High abundance scenario:					
Intercept	0.58	0.30	278	1.950	0.052
Euclidean nearest neighbor	0.97	0.29	10	3.393	0.007
Suitable local habitat	0.94	0.22	278	4.284	< 0.001
Low abundance scenario:					
Intercept	-3.39	0.50	181	-6.829	< 0.001
Mean monthly precipitation	1.62	0.38	8	4.301	0.003
Woody patches:Local habitat	0.94	0.33	181	2.872	0.005
Woody patches	0.91	0.25	8	3.586	0.007
Suitable local habitat	0.47	0.30	181	1.557	0.121

High abundance scenario

When local abundance of *P. aegeria* was high (mean abundance = 3.7 individuals per occupied sample point, 95% CI: 3.1 – 4.3), local and regional factors were of similar but low importance in predicting the occurrence probability of *P. aegeria*. This was indicated by similar standardized coefficients of the model (Table 3) and can be assessed from Fig. 2. It shows the probability of occurrence as a function of the local factor “Suitable local habitat” around a sample point and the regional factor “mean Euclidean nearest neighbor” distance of semi-natural elements within a test site. A low effect of both factors was indicated by a generally high probability of occurrence. Surprisingly, the effect of the mean Euclidean nearest neighbor distance of semi-natural habitats was positive: even at low levels of local habitat availability occurrence probabilities of about 0.8 were predicted for test sites with larger mean distances between semi-natural habitats.

Low abundance scenario

In 2003, on average 1.8 individuals were recorded per occupied sample point (95% CI: 1.4 – 2.1). We observed a positive effect of three factors: “Suitable local habitat”, “Long-term mean monthly precipitation” and the number of “Woody patches” (Table 3). For means of convenience long-term mean monthly precipitation will be simply referred to as “precipitation”. The regional factors precipitation and number of woody patches per test site seemed to be of particular importance, since they were generally significantly lower

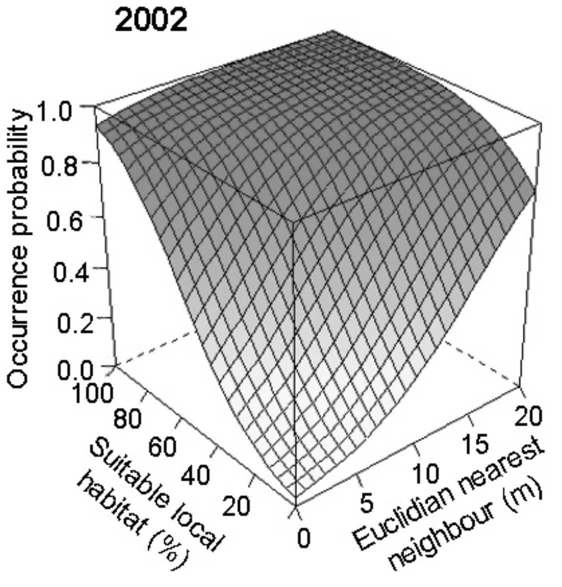

Fig. 2 High abundance scenario: Occurrence probability of *Pararge aegeria* as a function of the local factor availability of suitable local habitat and the regional factor mean Euclidean nearest neighbor distance of semi-natural habitats. The surface was calculated on the basis of the logistic model presented in Table 3.

compared to the high abundance scenario (both $P < 0.001$; Table 2). Standardized coefficient estimates indicated that the effect of precipitation on the occurrence of *P. aegeria* was most important, followed by the number of woody patches and the interaction between the number of woody patches and suitable local habitat. In the low abundance scenario the dependence of occurrence probability on environmental factors was rather high, as a predicted probability of one was only achieved when all three factors were near their maximum values (Fig. 3).

The significant interaction between suitable local habitat and woody patches illustrated a change in the relative importance of local habitat availability as a function of the number of woody patches (Table 3; Fig. 3a).

Relative importance of local habitat under the low abundance scenario

Plotting the occurrence probability of *P. aegeria* as a function of the number of woody patches and precipitation revealed a strong positive effect of both factors in the low abundance scenario (Fig. 4a). To illustrate the relationship of all variables (occurrence probability, suitable local habitat, woody patches and mean precipitation) in a 3d-plot, we had to keep one variable constant (in this case suitable local habitat). In Fig. 4a we chose to set the value of the proportion of suitable local habitat to its mean across all test sites (15%) to illustrate the occurrence probability for average local conditions. Indicated by the positive interaction between local habitat availability and the number of woody patches (Table 3), the shape of the probability surface of occurrence differed among different values of suitable local habitat. Analyzing the difference between the predictions for minimum (0%) and maximum (83%) amount of local habitat revealed the relative importance of local habitat availability as a function of the number of woody patches and precipitation (Fig. 4b). A relative importance of one indicated an occurrence probability of zero for patches with a minimum amount of suitable local habitat but of one for patches

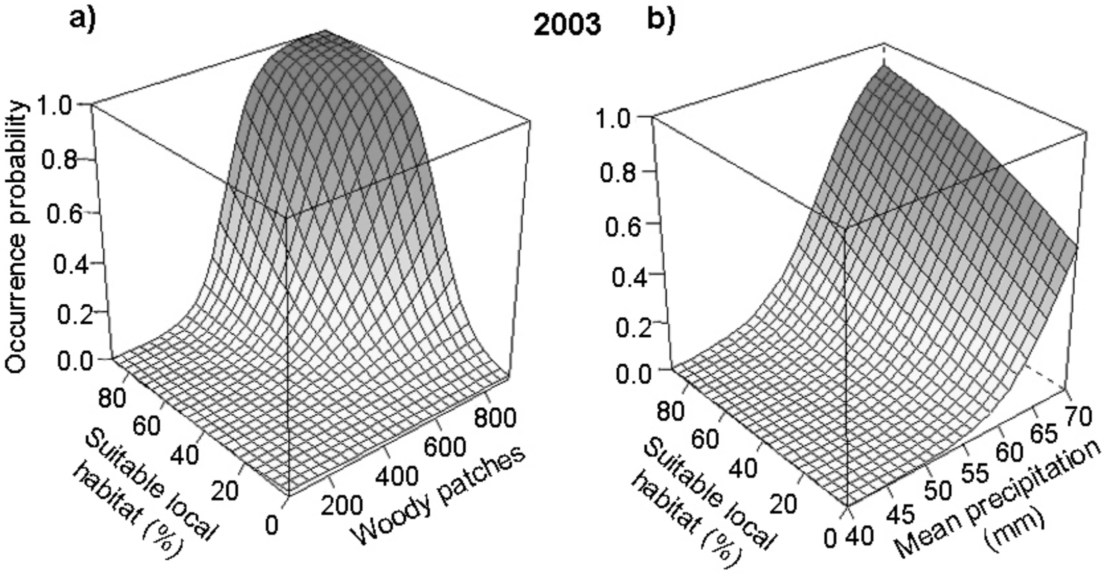

Fig. 3 Low abundance scenario: Occurrence probability of *Pararge aegeria*. Surfaces were calculated on the basis of the logistic model presented in Table 3. **a)** Dependence on the local factor availability of suitable local habitat and the regional factor number of woody patches. The value of mean monthly precipitation was set to its mean across all test sites (54 mm). **b)** Dependence on the local factor availability of suitable local habitat and the regional factor long-term mean monthly precipitation. The value of woody patches was set to its mean across all test sites (382).

with a maximum amount. Relative importance values of zero indicated no difference in the predictions for the minimum and maximum amount of suitable local habitat.

The response surface of the relative importance of suitable local habitat exhibited two peaks: One in test sites with a high number of woody patches and low precipitation, and the second in test sites with a low number of woody patches and high precipitation. Local habitat was of no importance in test sites with both a low number of woody patches and low precipitation and of minor importance in test sites with both a high number of woody patches and high precipitation.

4.5. Discussion

Since the data for our analysis were obtained from two different regions in Europe that were sampled in two different years and environmental factors differed in various ways, it was not possible to identify single environmental factors that caused the observed differences between both models of occurrence probability. However, some general patterns were obvious with respect to local and regional abundance. The high abundance scenario was characterized by beneficial conditions such as climate, weather during larval development, large scale habitat structure and an average high local abundance of *Pararge aegeria* (Table 2). Under such conditions *P. aegeria* was predicted to occur nearly everywhere, exhibiting equally low dependence on habitat quality at the local scale

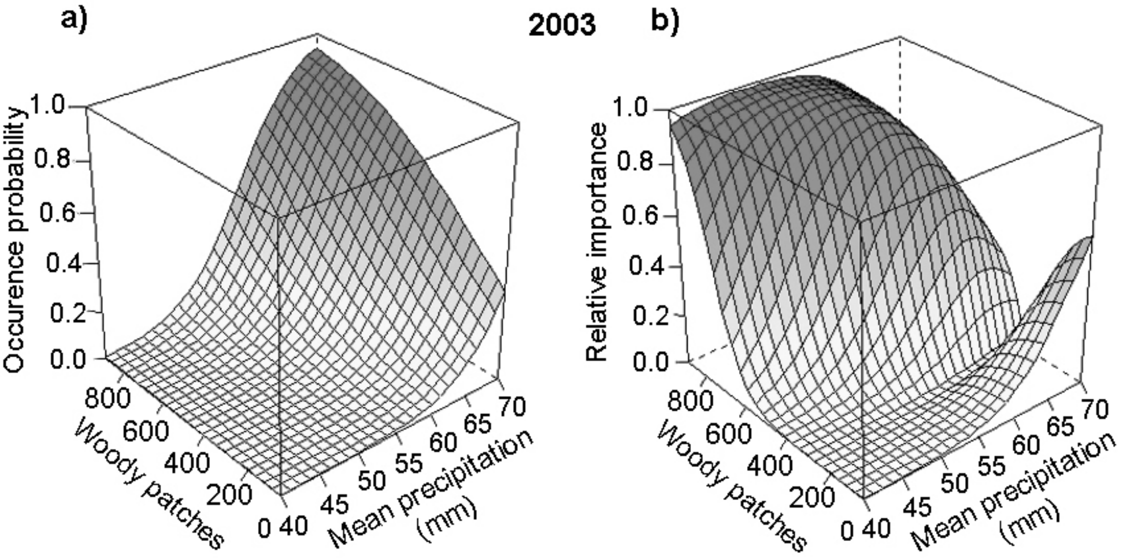

Fig. 4 Low abundance scenario **a)** Occurrence probability of *Pararge aegeria* depending on the number of woody patches and long-term mean monthly precipitation. The surface was calculated on the basis of the logistic model presented in Table 3. The value of suitable local habitat was set to its mean across all test sites (15%). **b)** Relative importance of local habitat availability depending on the number of woody patches and long-term mean monthly precipitation. The relative importance was calculated as the difference in predicted occurrence probability for the minimum and maximum amount of local habitat.

(measured as the availability of suitable habitat within a radius of 250 m) and the mean Euclidean nearest neighbor distance of semi-natural elements at the regional scale of the test sites (Fig. 2). Nevertheless, the positive relation between predicted occurrence probability and the mean Euclidean nearest neighbor distance of semi-natural habitats seemed curious. We could see no reason why *P. aegeria* should benefit from larger distances between the semi-natural habitats. However, as statistical model fitting does not overcome problems with collinearity among explanatory variables, causality must be inferred with caution (MacNally 2000). Therefore, we analyzed correlations between the Euclidean nearest neighbor distance of semi-natural habitats and the other environmental variables. Latitude was correlated most strongly with Euclidean nearest neighbor distance (r = 0.86), followed by landscape metrics that are related to Euclidean nearest neighbor distance (proximity index of semi-natural habitats, r = 0.80; proximity of herbaceous habitats, r = 0.66; Euclidean nearest neighbor distance of herbaceous habitats, r = 0.65). Thus, the predicted increase of occurrence probability with Euclidean nearest neighbor distance of semi-natural habitats might be in fact a function of latitude and the corresponding changes in climate (increasing humidity) from continental to Atlantic conditions, instead (see Fig. 1).

Dependence on local as well as regional factors was generally low under the high abundance scenario. This could be a consequence of general advantageous environmental conditions leading to high local abundance and density dependent dispersal which has been previously demonstrated for other butterfly species (Kuussaari, Nieminen, & Hanski 1996;

Brunzel 2002; Mennechez et al. 2004). The males of *P. aegeria* are also known to exhibit territorial behaviour (Davies 1978, Shreeve 1984). Petit et al. (2001) reported a positive relationship between male movements and population size of the butterfly *Proclossiana eunomia*. If this also applies to *P. aegeria*, it is likely that males dispersed from high quality patches with high densities of butterflies to lower quality patches. Hence, beneficial environmental conditions and corresponding high local abundances were assumed to cause a decoupling of *P. aegeria* occurrence from the local and regional factors under study due to density dependent dispersal supported by territoriality. Under such conditions *P. aegeria* is expected to occur even in patches with only a minimum amount of its favored habitats, namely scrubby woodland edges and hedgerows regardless of the regional landscape structure.

However, totally different patterns were revealed by the analysis of the low abundance scenario. This was characterized by environmental stress due to climate, weather during larval development and large scale habitat structure (Table 2). We interpreted the observed low average local abundance of *P. aegeria* to be a consequence of these adverse conditions. In contrast to the high abundance scenario the effects of regional and local factors on the occurrence of *P. aegeria* were high and restricted the butterfly to high quality patches as well as high quality landscapes (Fig. 3). As the long-term mean monthly precipitation and the number of woody patches were generally low and *P. aegeria* showed a strong dependence on these two factors in particular, they suggest to represent limiting factors, at least under critical weather conditions. Mean monthly precipitation (i.e. during the larval development in summer) might affect the general potential of population growth, whereas the number of woody patches represented the amount and spatial structure of suitable habitat patches (i.e. woodland edges and hedgerows) and therefore the specific capacity of the landscape (Hanski & Ovaskainen 2000).

Under unfavorable conditions, standardized coefficient estimates indicated an increased importance of regional factors dominating over local habitat quality in general (Table 3). Even patches with highest local quality were predicted to be empty when the number of woody patches or the long-term mean monthly precipitation was low (Fig. 3). Many patches that were comparable to that of the high abundance scenario were not occupied. This led us to the assumption that local extinction might have occurred due to the critical weather conditions during larval development in combination with disadvantageous climatic and landscape preconditions.

The relative importance of local and regional factors on the occurrence probability of *P. aegeria* changed according to their composition (Fig. 4b). In test sites where only one regional factor was high (number of woody habitats or long-term mean monthly precipitation) and the other was low, local habitat quality was of major importance increasing local occurrence probability. High local habitat quality compensated either a regional low number of woody patches or a dry climate. Hence, a consequence for management activities could be to invest in quality at the local scale. In test sites with both regional factors being low, local habitat quality had obviously no effect as *P. aegeria* was totally absent from such test sites due to adverse landscape and climate prerequisites. In such a case a consequence for management activities would be to invest in quality at the regional scale. Finally, in test sites with both regional factors being high, local habitat quality was also of minor importance as the occurrence probability was generally high (Fig. 4a). Here, high values of both regional factors compensated for low local habitat quality. A consequence here for management activities could be to keep the state of the art.

Based on our statistical analysis, we would predict *Pararge aegeria* to show a high colonizing potential even in low quality patches under beneficial conditions, but should be restricted to high quality patches and landscapes under adverse conditions. This may be indicative of metapopulation patterns. Most butterfly species, which, like *P. aegeria*, live in landscapes subject to massive alteration due to changes in anthropogenic land use form metapopulations (reviews in Thomas & Hanski 1997; Cowley et al. 2000). Metapopulations are regarded as spatially structured populations consisting of distinct subpopulations that are separated by unhabitable space or barriers and connected by dispersal. Their persistence at larger scales depends on a compensation of local extinction by recolonisation. In a spatially realistic metapopulation model, dispersal is a function of the landscape context (Hanski & Gilpin 1997). Our study stresses the importance of high quality landscape conditions at both scales even for species that appear to be tolerant to low quality landscape structure. The alleged less important landscape quality could even turn into a limiting factor if other environmental factors like climate or incisive singular events like drought affect *P. aegeria*. When events occur that affect population demography drastically, such as extreme weather conditions in summer, butterfly species such as *P. aegeria* are expected to respond more sensitive to landscape structure. Such extreme events will occur more frequently and pronounced at the margins of the species range. Hence, an increased sensitivity to landscape features might explain the observed pronounced differences in the rate of range expansion in landscapes that differed only slightly but significantly in the percentage cover of suitable habitat (3.6% and 2.7% of woodland; Hill et al. 2001).

The marked differences between the high abundance and low abundance models sound a note of caution when predicting population response for management purposes on a basis of single (or few) year observations. As our study showed, single environmental events affecting the demography of species might change their sensitivity and thus the population response to landscape features dramatically. Hence, generalizations to areas at the distribution margins or recommendations about thresholds might be in a majority of cases over-optimistic.

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5. *Communities:* Effects of land use on similarity of plant and animal communities

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5.1. Abstract

Landscape structure and land-use intensity may affect the exchange of species between local communities. We measured the similarity of plant, bird, wild bee, true bug, carabid beetle, hover fly and spider communities sampled in a pan-European transect along gradients in landscape composition (e.g. total availability of semi-natural habitat), landscape configuration (e.g. fragmentation) and land-use intensity (e.g. pesticide loads). Total availability of semi-natural habitats had little effect on community similarity, except for bird communities, which were in better exchange in more natural landscapes. Bee communities were less similar in landscapes with higher percentage of semi-natural habitats. Landscape fragmentation decreased similarity of true bug communities, while plant communities showed a non-linear response. More intense land use (i.e. increasing pesticide index) led to a homogenisation of bee, bug and spider communities within sites. In these cases habitat fragmentation interacted with pesticide load. Hover fly and carabid beetle community similarity was differentially affected by higher pesticide levels: for carabid beetles similarity decreased, while for hover flies it was an inverse hump-shaped relationship. Our study demonstrates effects of landscape composition and configuration and land-use intensity on the similarity of species communities. It indicates reduced exchange of communities in landscapes dominated by agricultural activities. Groups differed in their responses to environmental drivers and using but one group as an indicator for “biodiversity” as such would thus not be feasible.

Keywords: community similarity; dispersal; diversity; fragmentation; landscape ecology; land-use management; pesticide.

5.2. Introduction

In Europe, natural and semi-natural habitats are located in a man-made, agriculture dominated, cultural landscape. To prevent species restricted to these natural and semi-natural habitats from going extinct (Robinson & Sutherland, 2002), we need a better understanding of the effects of landscape structure and land-use management on species community composition (Brose, 2003; Piorr, 2003; Waldhardt, 2003). Many studies have examined the effects of landscape structure on individual species or groups of species at a small scale (e.g. Atauri & de Lucio, 2001; Baudry et al., 2000; Bergman et al., 2004; Bruun, 2000; Burel et al., 1998; Weibull, Ostman & Granqvist, 2003), but only very recently also larger scales came into focus (Billeter et al., 2005): In the latter study, species diversity increased with increasing area of semi-natural landscape elements and decreased with increasing land-use intensity.

In some studies, communities are compared over large geographic distances (e.g. Cleary & Genner, 2004; Cleary et al., 2004), requiring information on species pools for the different locations. In this study, we are interested in the similarity among local communities at the spatial scale of landscapes (i.e. 16 km^2) and how it is affected by agricultural land-use management and landscape structure (see methods for definitions). We assessed which of these features impact on species composition and how they affect community assembly processes. We chose community similarity (as defined below) as our community descriptor, rather than species richness or diversity, because it not solely tallies species in a given site. Instead, it allows us to compare different communities within a site with respect to how many species they have in common weighted by their abundance. This way, our assessment considers species identities within local communities, while it is independent of differences in species pools.

The degree to which two communities are alike each other is called community similarity. It is conceptually equivalent to 1 – □-diversity (which is used in different meanings) and can be interpreted ecologically as the turnover of species between communities. As pointed out by Crawley (1997, p. 488), there are many potential determinants for species richness and equally many conceptual pitfalls (Gotelli & Colwell, 2001). In comparison with species richness (□-diversity), community similarity is better suited to compare trends in composition of different communities (Cleary et al., 2004; Su et al., 2004) for two reasons: Firstly, regional species pools will differ in size, □-diversity might thus depict climatic or historic influences on species pool size rather than the factor of interest (here landscape structure and land-use intensity). Secondly, land use and landscape configuration may impact on the exchange of local communities, which has consequences for community similarity, although local species richness may stay the same; this means that community similarity is more sensitive than species richness, as has been shown for pond communities (Chase, 2003; Forbes & Chase, 2002). However, when analysing community similarity, we have to correct for two processes confounding the results: (1) local species richness (because more rare species lead to lower similarity) and (2) similarity of plots within a site (as communities will be less similar when sampled habitats differ greatly).

Different processes affect the spatial exchange of organisms and hence community similarity: landscape structure (e.g. the distance between adjacent habitat patches, the presence of dispersal barriers etc.) interacts with dispersal traits (flying abilities, seed weight, foraging range, etc), and these interactions are likely to be species-specific. On the other hand do ecological preferences for nesting or food as well as trophic interactions drive distribution pattern of organisms. Here, we deal primarily with the landscape component of factors affecting community similarity, while the organism traits are represented by the seven different groups of organisms we studied: vascular plants, birds, spiders (Araneae) and four groups of insects: wild bees (Apoidea), true bugs (Heteroptera), carabid beetles (Carabidae) and hover flies (Syrphidae).

Using species composition data from a nested, multi-site, pan-European study compiled in a standardised approach, we assess how similar communities are within a site and how this local similarity is affected by regional variation in land use and landscape structure.

Specifically, we focus on two hypotheses:

> *Hypothesis 1*: Community similarity is a function of landscape configuration: as connectivity among patches is reduced, dispersal is disrupted and communities may be mere spatially independent random samples from the species pool, leading to a decrease in community similarity.
>
> *Hypothesis 2*: Community similarity is a function of landscape composition and land-use intensity: loss of semi-natural habitat as well as increasing land-use intensity threatens habitat specialists and rare species, while relatively benefiting generalist and common species, thereby increasing community similarity.

5.3. Methods

Our study is based on data generated and compiled in the EU research project GREENVEINS. The analysis of species numbers at the site level (i.e. γ-diversity) is subject of a different paper (Billeter et al., 2005) and will only be considered here as far as it is necessary to conceive our results.

Study sites and environmental variables

Vascular plants, birds and five arthropod taxa (wild bees, true bugs, carabid beetles, hover flies and spiders) were sampled in 25 landscape test sites of 4 × 4 km in agricultural landscapes. The test sites were distributed over seven European countries: France (3 tests sites), Belgium (4), The Netherlands (4), Switzerland (3), Germany (4), Czech Republic (3; in one site only plant and bird data were collected) and Estonia (4). Together, they covered a wide range of both agrarian land-use intensity and landscape structure.

We recorded environmental data about land-use intensity of arable fields and landscape structure (focusing on semi-natural elements). The intensity of agrarian land use was evaluated at test site level by standardised interviews with farmers about management practices on arable fields (Herzog et al., 2005). The number of crops in rotation, pesticide applications (insecticides, herbicides, fungicides) and the amount of nitrogen fertilizer applied per hectare and year were recorded and transformed to the respective index by ranging them from 0 to 100 (Legendre & Legendre, 1998).

The landscape structure was evaluated from digitized habitat maps (see also Bailey et al., in prep). The habitats were mapped using ortho-rectified aerial photographs with spatial resolutions better than 1 x 1 m and ArcGIS software (ESRI, 2003). The classification of the habitats was based on the European Nature Information System (EUNIS) habitat classification (available at http://mrw.wallonie.be/dgrne/sibw/EUNIS/home.html) which was adapted to the requirements of the project. We aggregated the habitats into woody or herbaceous elements and together as semi-natural habitat (‘green veining’) to contrast them to the highly anthropogenic elements of arable land and built-up areas. Two indices describing landscape composition and configuration were retrieved from FRAGSTATS analyses (McGarigal et al., 2002). *Proximity* is an ecologically intuitive measure describing the size-weighted distance between habitat patches: the larger and closer patches of the same type are to each other, the larger is the proximity value for this habitat type. However, proximity, like most landscape metrics commonly employed, has very poor mathematical properties, which led to the development of the *splitting index* (Jäger, 2000). The number given by the splitting index equals the number of equal-sized habitat patches needed to produce the same degree of landscape division as is found in the landscape under consideration (Jäger, 2000). It can also be interpreted as the 'effective mesh number' of a network of habitat patches. The higher the value of the splitting index, the more fragmented a landscape is. Both indices had to be log-transformed to derive an even spacing.

Plant survey

Depending on the structure of the sample sites, floristic surveys were based on 100-300 vegetation plots per site. A stratified random sampling was ensured by ranking the total area of all available habitat types and a respective distribution of maximum 300 sample plots according to habitat area. The resulting number of plots per habitat type was then randomly distributed using a GIS routine. Within 2 x 2 m plots for herbaceous vegetation and 20 x 20 m plots for tree and shrub layer vegetation, all vascular plant species were recorded and their abundances were estimated according to the Braun-Blanquet scale. Mosses and lichens were not considered.

Bird survey

For bird surveys and arthropod sampling, the test sites were divided into 16 grid cells of 1 km^2. Birds were recorded by 20 point counts in five central grid-cells selected in a checkerboard pattern. Within each of these five cells, four observation points were selected and at each point sightings and hearings of birds were counted for five minutes. This was repeated three times, in April, May and June 2001, half an hour before until two hours after sunrise. Only presence of a species at a visit was considered for further analysis.

Arthropod sampling

Spiders and carabid beetles were captured with pitfall traps, whereas wild bees, true bugs and hover flies were sampled with combined flight traps (a combination of window and yellow pan trap, see Duelli, Obrist & Schmatz, 1999). In every grid cell a trap set was placed at a randomly chosen ecotone between a semi-natural habitat and agricultural field. Each trap set consisted of two trap units, which were spaced at least 25 m and maximally 50 m apart from each other. A trap unit was composed of one pitfall and one combined flight trap. In consequence, a total of 16 trap sets comprised 32 pitfall traps and 32 combined flight traps per test site. The sampling was carried out according to Duelli (1997). In order to minimize the sampling effort while maximizing the efficiency, we restricted the sampling to two periods of maximum activity and density of the species at 7 weeks in autumn 2001 and 5 weeks in early summer 2002. To correct for climatic and consequently phenological differences between the countries, we used full bloom of *Taraxacum officinale* Wiggers as a trigger for the beginning of sampling. The traps were emptied weekly. To account for differences in weather conditions between the test sites during the sampling periods, we considered only the most abundant samples for the analysis (in total 4 weeks from autumn 2001 and 3 weeks from early summer 2002). The samples were pooled over each trap set and the specimens were identified to the species level.

Statistical analysis

Response variables

Each test site has a slightly different set of species for biogeographical and climatic reasons. Thus, in a first step we calculated similarity between sample points within each test site: We used the same distance measure for all groups, although for arthropods and plants distance was calculated based on log-transformed abundances, while for birds it was done on presence/absence data. The distance algorithm used was the Horn-Morisita index (Krebs, 1989), which is able to handle any type of abundance data and is robust with respect to sample sizes (Oksanen, 2004). Distances between all samples from one test site were calculated and averaged. The resulting value for each test site expresses the average distance between local communities in that test site. Similarity is simply calculated as 1 minus distance.

Explanatory variables

We corrected for local species richness (see Introduction for reasoning) by calculating the mean number of species in each sample (trap set or relevé, i.e. at the within-site level) and using this as covariate. Similarly, we corrected for the fact that different habitats were sampled. A buffer of 50 m (200 m for birds) was placed around every sampling location in a GIS and the cover of all habitat types (according to EUNIS classification) was determined. The similarity of sampling point buffers was calculated (again using the Horn-Morisita index) and averaged. The resulting similarity was used as covariate in the further analysis.

Our list of pre-selected explanatory variables thus comprised 11 variables: local species richness, local habitat similarity, log-transformed proximity and splitting indices for the three habitat types *herb, woody* and *green veining* (GV), percentage GV and pesticide and nitrogen application indices.

MANOVA

A multivariate analysis of variance (MANOVA) was carried out on the similarity data of all groups as dependent variable, and the pre-selected set of landscape structure and land-use explanatory variables.

ANCOVA

To relate community similarity values to our explanatory factors, we carried out a best subset regression analysis (Neter, Wasserman & Kutner, 1985). We investigated for non-linear effects of the explanatory variables by incorporating second-order terms of all remaining nine variables into the full model. Additionally, we incorporated the interaction of all proximity and splitting indices with pesticide (a first analysis had shown that percentage greenveins and nitrogen application did not interact with landscape metrics). Next, we determined all subsets of the full model in terms of adjusted R^2 (Lumley, 2004). We then compared the best models of increasing complexity with each other, starting with the most simple. We accepted a more complex model if the increase in model fit was significant according to F-test statistics (Burnham & Anderson, 2002; Johnson & Omland, 2004). To simplify the model further, we similarly deleted non-significant terms, if dropping them from the model did not cause a significant (F-test) reduction in model performance. As landscape configuration indices for the three habitat types were sometimes correlated, we allowed only uncorrelated terms to be in the final model, by deleting the less important of two correlated terms and simplifying the model further. All explanatory variables were scaled to mean 0 and standard deviation of 1 prior to analysis to reduce correlation between the different interaction terms (Quinn & Keough, 2002). Final model structure was identical for scaled and unscaled models, and thus the latter are presented here.

All analyses were carried out using the free software R (R Development Core Team, 2004).

5.4. Results

Community similarity values were lowest for plants (0.14; Table 1), but markedly higher for all other groups (0.39 - 0.54). Community similarities of species groups were entirely uncorrelated (Table 2). This means that each group seems to respond differently to landscape structure and land use. Accordingly, similarity of all groups combined was significantly related only to splitting index for herbaceous habitat (Pillai's $F_{1, 22} = 4.58$, $P < 0.01$; higher splitting index values correlated with lower community similarity). Interestingly, this variable was not included in any of the final univariate models (see below).

Sample size, which for plants exceeded that for animal communities by a factor of 10, was appropriately large for all groups, as coefficients of variance were similar (CV for plants = 21%; birds = 24%; bees = 19%; bugs = 33%; carabids = 22%; spiders = 16% and hover flies = 30%). This suggests that even far more samples per site would not have decreased the coefficients of variance for community similarity much further.

Table 1. Mean local species richness (± 1 standard deviation) and community similarity for the seven investigated groups. Sample sizes (numbers of samples within sites and number of sites) differ between groups.

	N (samples | sites)	**local species richness**	**community similarity**
Plants	100-300 | 25	11.3 ± 2.72	0.14 ± 0.03
Birds	20 | 25	16.0 ± 4.06	0.49 ± 0.12
Bees	16 | 24	14.1 ± 10.0	0.52 ± 0.10
Bugs	16 | 24	11.0 ± 5.99	0.39 ± 0.13
Carabids	16 | 24	22.1 ± 6.84	0.54 ± 0.12
Syrphids	16 | 24	6.5 ± 2.32	0.48 ± 0.14
Spiders	16 | 24	20.9 ± 4.55	0.51 ± 0.08

Table 2. Correlation matrix of community similarities for the different groups. Values are Pearson's r, critical value for $P = 0.05$ is $r = \pm 0.520$ (printed in bold).

	Birds	Plants	Bees	Bugs	Carabids	Syrphids	Spiders
Birds	1						
Plants	0.11	1					
Bees	0.01	0.06	1				
Bugs	-0.01	0.25	-0.08	1			
Carabids	-0.45	-0.24	0.04	-0.29	1		
Syrphids	-0.20	-0.10	0.03	0.15	0.04	1	
Spiders	-0.50	-0.40	-0.02	0.01	0.50	**0.58**	1

In most cases was the correction for local species richness and/or local environmental similarity important (Table 3). Local species richness was the most important variable in true bug, carabid beetle and hover fly communities, while local environmental similarity was most important for birds and spiders. These final models differed greatly in their complexity (i.e. number of model parameters), with simple models for hover flies containing only the correction for local species richness and the quadratic regression on pesticides, while for true bugs the model contained both local corrections and six parameters. Adjusted R^2-values ranged from 0.42 to 0.76 and were uncorrelated with model complexity. Final models are given in Appendix A.

Plant similarity values were the lowest, indicating the least exchange of species between communities (Table 1). Similarity of sampled environments explained only 8% of the variation in plant community similarity in terms of ANOVA F-values (Table 3). This is not very surprising, since the classification of habitats used is far less differentiated than the plant communities. Community similarity values showed an inverse hump-shaped relationship with the splitting index for green veining (Fig. 1), indicating that homogenous habitats on one side, and highly fragmented landscapes on the other, lead to highest similarity among local plant communities. Although the data point with the highest splitting index looks like an outlier, the model does not change much after its deletion (for which there is no methodological or other reason): the non-linearity is still apparent.

Table 3. R^2-values for the final model fitted to community similarity data. Partial R^2s do not add up to adjusted R^2 in the last column, as this corrects for the number of parameters in the model and as the intercept of the model also carries some (trivial) explained variance. Note that model selection was not based on the significance level of the effect in the model, but on the comparison of models with and without the respective effect (F-test). R^2-values are based on “type III sum of squares” (Fox 2004). See Appendix A for models.

Group	local species richness	local environment	pesticide index	pesticide^2	% GV	%GV^2	log(proximity_gv)	log(proximity_wood)	log(proximity_herb)	log(split_gv)	log(split_gv)^2	log(split_wood)	pesticide x log(proximity_gv)	pesticide x log(split_gv)	pesticide x log(split_wood)	Total model
Plants	0.11**	0.08*								0.15**	0.16**					0.43**
Birds	--	0.32**			0.21**											0.42**
Bees	0.08**	0.11**	0.12**			0.04*	0.05*					0.10**			0.17**	0.72**
Bugs	0.19**	0.05*	0.16**					0.16**	0.05*	0.05*		0.07**		0.17**		0.74**
Carabids	0.52**	0.10**	0.06*													0.76**
Syrphids	0.36**	--	0.07*	0.16**												0.68**
Spiders	0.11*	0.18*	0.10†				0.09†						0.10†			0.48**

†, * and ** refer to significance values of the model term (in the final model) of $P < 0.1$, < 0.05 and < 0.01, respectively.

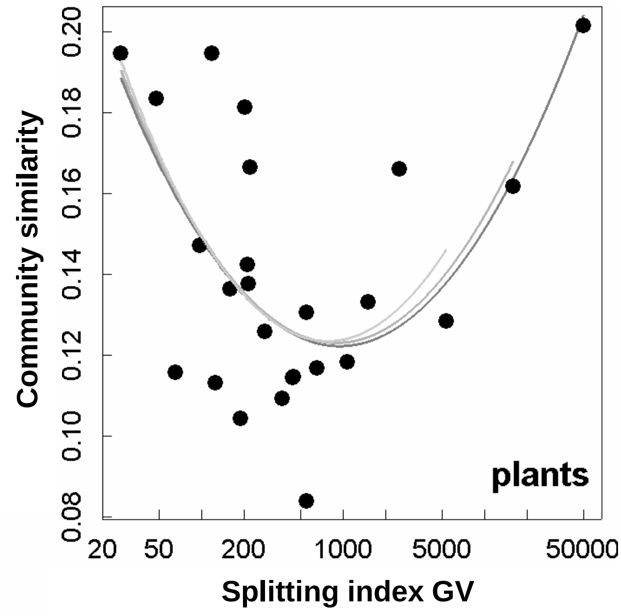

Fig. 1. Response of plant community similarity to landscape configuration, as represented by the splitting index for green veining habitats. Regression lines are based on the parameters of the final model. Deleting the (two) point(s) with the highest splitting index value(s) still yields a (marginally) significant quadratic relationship (indicated by the lines in lighter grey.

Bird community similarity was positively related to the similarity of habitats sampled (Table 3). Local environments sampled were more alike each other than for the other groups (similarity values > 0.59), due to a larger buffer around the observation points (which in turn takes account of the greater activity range of this group). As could be expected, sample patches more similar to each other also harboured bird communities that were more alike. Bird community similarity furthermore corresponded with the coarse measure of how much semi-natural habitat was available, explaining 21% of all variation (Fig. 2a; Table 3). Low percentage of green veining habitats led to low avian community similarity.

The similarity of wild bee communities was affected by local species richness (explaining 8% of the variation), by the similarity of the local environment (11%), and most of all by pesticide burden, landscape structure and their interaction (Table 3). Similar to birds, bee communities were impacted by the percentage of green veining. They responded, however, in the opposite way (Fig. 2b): a lower cover of semi-natural habitats increased bee community similarity. The effect of landscape fragmentation of woody elements (i.e. splitting index) depended on the intensity of pesticide applications. At low levels of pesticide load, community similarity decreased with habitat fragmentation, while at high pesticide levels, community similarity increased with habitat fragmentation (Fig. 3). Thus, community similarity was highest under optimal conditions (i.e. low splitting index and low pesticide level) as well as under worst conditions (i.e. high splitting index and high pesticide level). This means that fragmentation and pesticides in concert result in an inverse hump-shaped response curve that is comparable to that of plants in dependence of fragmentation alone. Figure 3 illustrates that pesticides are a more important determinant of similarity among local bee communities in highly fragmented landscapes than in those with a low level of fragmentation (contour lines are slightly denser at higher levels of the splitting index).

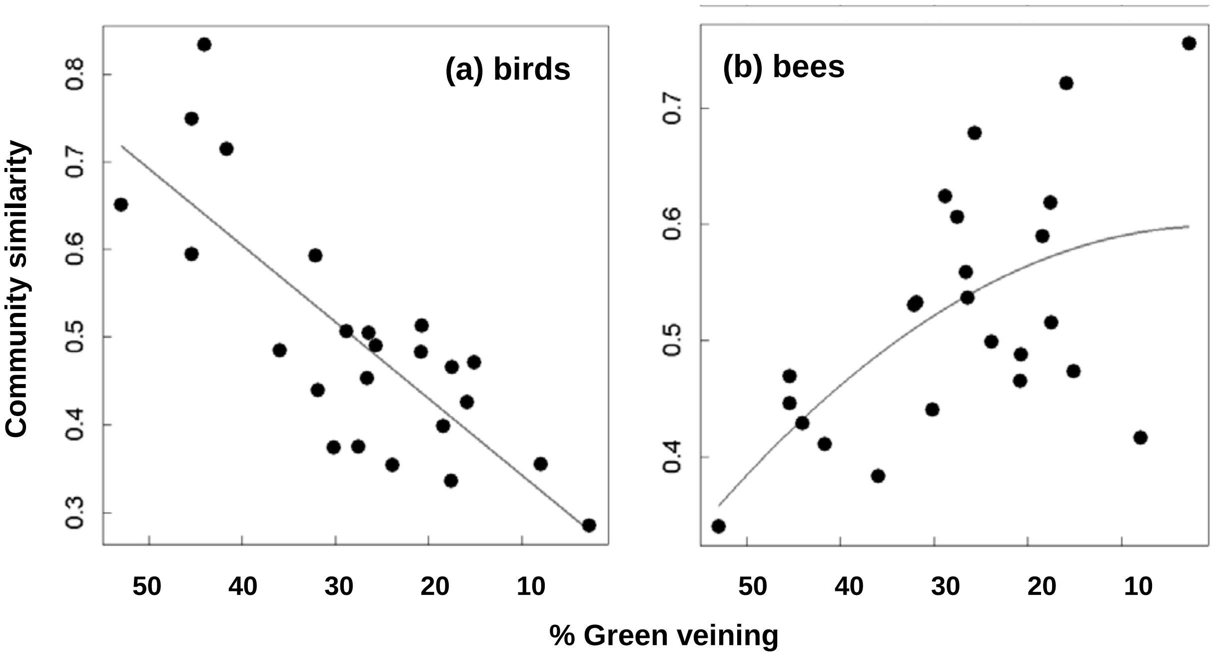

Fig. 2. Response of bird (a) and bee (b) community similarities to landscape structure, as represented by the percentage of green veining habitats. For consistency with other figures the x-axis is inversed to have lower quality landscapes to the right of the graph.

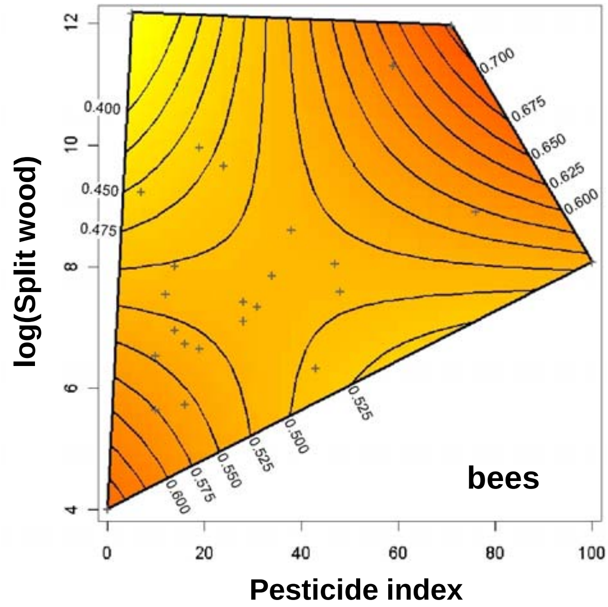

Fig. 3. Bee community similarity as a function of pesticide burden and fragmentation of woody habitats. The polygon delimits the sample space, i.e. those parameter combinations assessed in our study. Grey crosses indicate the actual parameter values for the 24 sample sites. Contour lines indicate same level of community similarity (in steps of 0.025 units) and darker shading corresponds with higher similarity.

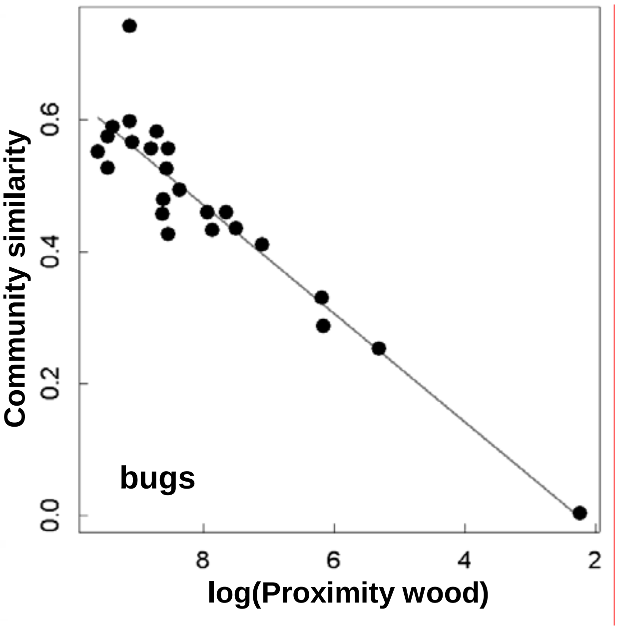

Fig. 4. Response of true bug community similarity to landscape structure as represented by the proximity index for woody habitats. For consistency with other figures the x-axis is inversed to have lower quality landscapes to the right of the graph.

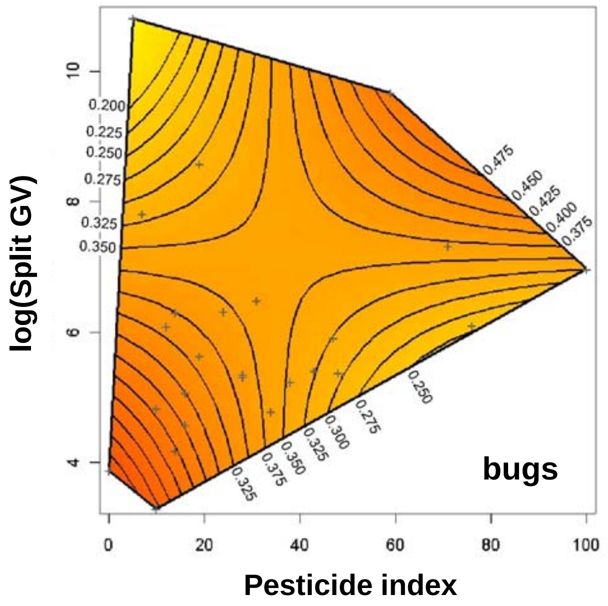

Fig. 5. Bug community similarity as a function of pesticide burden and fragmentation of semi-natural habitats. See caption Fig. 3 for details.

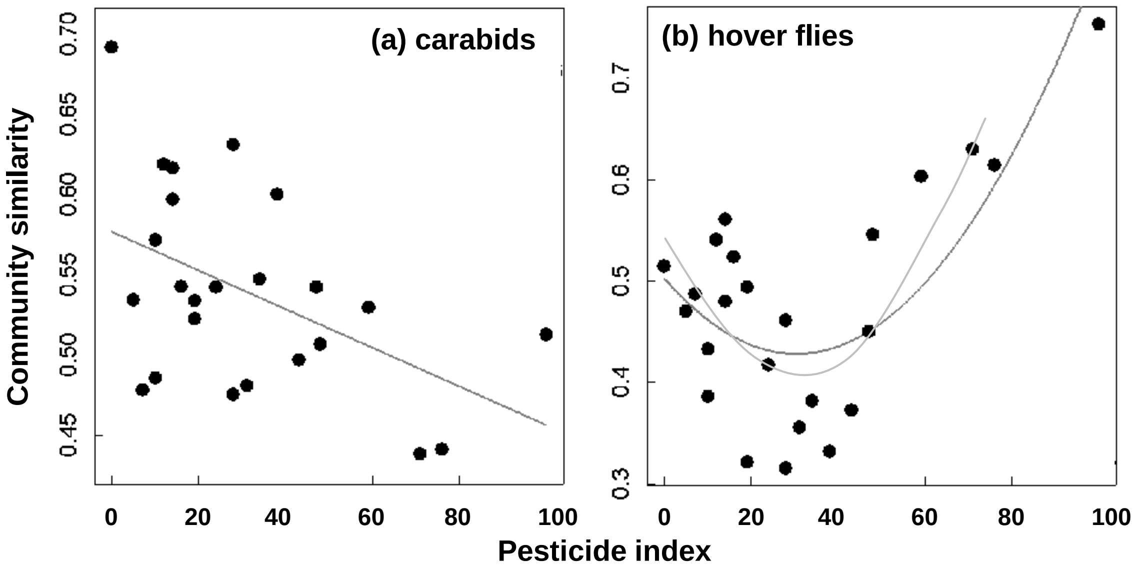

Fig. 6. Response of carabid (a) and hover fly (b) community similarities to land-use intensity as represented by the pesticide index. The quadratic model for hover flies is robust to the deletion of the highest pesticide data point: the lighter grey line indicates the model without the rightmost data point (quadratic term is still highly significant).

True bugs exhibited a similar pattern to bees. Instead of percentage green veining (bees), similarity of local bug communities was impacted by the proximity of woody habitats. Low proximity (i.e. small, distant patches) led to lower similarity in bug communities (Fig. 4). The interaction of pesticides with fragmentation of green veining elements (splitting index) was essentially the same as for bees. At low levels of pesticide load, community similarity decreased with habitat fragmentation, while at high pesticide levels, community similarity tended to increase (Fig. 5). Thus, community similarity was highest under best conditions (i.e. low splitting index and low pesticide level) as well as

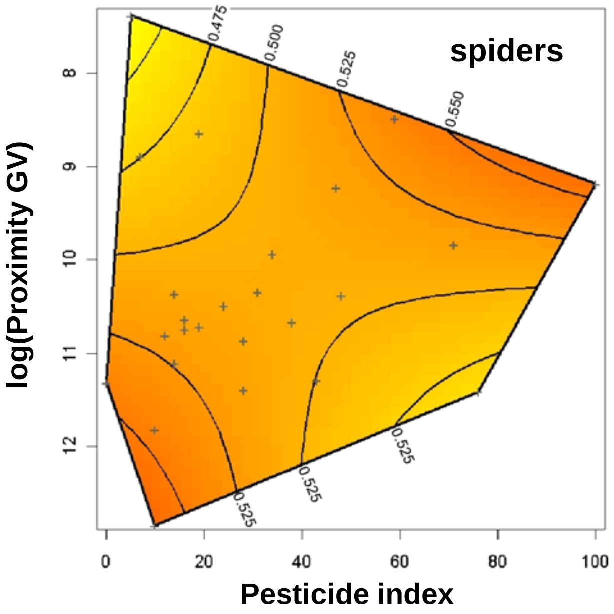

Fig. 7. Spider community similarity as a function of pesticide burden and fragmentation (i.e. proximity index) of green veining habitats. Note that scaling of the y-axis is inverted to make it comparable to bees and bugs, where the y-axis displays decreasing habitat quality.

under the worst conditions (i.e. high splitting index and high pesticide level), which is exactly the pattern found for bees as well.

Carabid beetle communities responded only to one variable at the regional scale (Table 3), namely pesticide burden. Higher amounts of pesticides reduced carabid community similarity (Fig. 6a), although this effect was not very strong (6% explained variance). Most important determinant of community similarity was in this case the local species richness (52% variance explained). Carabids had, on average, most species per trap (Table 1), as well as the highest similarity values of all groups. For all other groups, except birds, community similarity increased with increasing local species richness: sampling of a larger proportion of the total species pool per trap will necessarily lead to higher similarity of samples.

Hover fly community similarity was determined mainly by local species richness and, to a lesser extend, pesticide index, together explaining approx. 68% of the variance (Table 3). As for plant community responses to fragmentation, hover fly community similarity was related to pesticide burden by an inverse hump-shaped function (Fig. 6b; this pattern was only slightly altered after deletion of the highest pesticide data point). Data show a wide scatter of similarity values until a threshold of pesticide dose is reached (at approx. 40 units), after which similarity strongly increases with pesticide values. Although the quadratic regression does not quite capture the exact shape of the relationship, which is more acute, it indicates its non-linearity. Hover flies were the species-poorest group (Table 1) in our data set, and community similarity reflects the fact that only common generalists form the hover fly community at high pesticide doses.

Spider communities were mainly determined by local species richness and the similarity of habitats sampled (Table 3). These two correction factors explained most of the observed variance in community similarity, and the interaction of pesticide burden and proximity of woody habitat was only marginally significant. Figure 7 shows that the pattern for spiders is comparable to that for wild bees and true bugs, although the effects are considerably weaker (i.e. the contour lines are spaced further apart).

5.5. Discussion

Landscape structure and land-use intensity did affect the similarity of plant, bird and arthropod communities. Across all groups only fragmentation of herbaceous habitats had explanatory power for community similarities (as indicated by MANOVA results). However, the univariate analyses showed that species groups responded differently to different features of land use.

Hypothesis 1: Landscape fragmentation decreases community similarity

Our first hypothesis received substantial support by the data (Figs 1, 3, 4, 5 and 7, Table 3). The effects were strongest for plant and true bug communities, where splitting and proximity indices, respectively, were as main factors significantly related to community similarity. For wild bees and spiders landscape configuration interacted with land-use intensity (see below). Only bird, carabids and hover fly communities were seemingly unaffected by landscape configuration (as represented in the proximity and splitting index). Landscape structure affects dispersal, especially at low levels of habitat connectedness (King & With, 2002), which could explain the pattern found: birds and hover flies are very potent dispersers due to their high mobility. However, this explanation does not hold for ground beetles.

Hypothesis 2: Loss of habitat and increasing land-use intensity increase community similarity

The second hypothesis comes in two parts: the effects of habitat loss and that of land-use intensity. Only birds responded solely to the amount of semi-natural habitat, which is partly due to their mobility and partly caused by a correlation of the percentage semi-natural habitat with its fragmentation (as measure by the splitting index for green veining: $r = -0.766$ or by the proximity index: $r = 0.660$). Hence groups responding to fragmentation will not show a response to the percentage green veining (i.e. plants, true bugs and spiders), as this is partly coded for in the statistical model already. It should be noted that fragmentation (e.g. as described by the proximity or splitting indices) is highly correlated with the percentage of semi-natural habitat, both in our data set and in cultural landscapes generally (Fahrig, 2003). However, only for bees were indices of landscape configuration *and* percentage of semi-natural habitat in the final model. This may be seen as evidence that mostly configuration *or* composition, but rarely both, drive community similarity.

All arthropod groups responded to land-use intensity (i.e. pesticide burden; although we incorporated the dose of nitrogen application in the list of explanatory variables, it was eliminated from all models during model simplification). The pesticide index is a summary measure for insecticides, herbicides and fungicides, which are all highly correlated (Herzog et al., 2005). The fact that insecticide applications on agricultural land have an impact on all arthropod communities is not surprising. However, groups responded differently to pesticide burden: some only in interaction with landscape structure (wild bees, true bugs and spiders, see below), others (carabids and hover flies) showed direct, but idiosyncratic responses (Fig. 6). In most of these cases, our hypothesis of pesticide burden *increasing* community similarity could *not* be confirmed. Most often (Figs 3, 5, 6b, 7) we noted a non-linear relationship between pesticides and community similarity, with maximum values at both ends of the pesticide gradient.

Interactions of land-use intensity and landscape structure

For three groups we detected an interaction between land-use intensity and landscape configuration in their effect on community similarity: wild bees, true bugs and spiders (Figs 3, 5 and 7). Despite differences in the importance of specific indices describing landscape structure, these three groups share the same response pattern. We interpret this pattern as an interaction of the two different processes affecting community similarity in our study: dispersal (hypothesis 1) and selection of generalists (hypothesis 2). Both processes are potentially affected by land-use and structure. We illustrate their interaction, and the consequences for community similarity, in Figure 8. We consider two factors as most important for the degree of similarity of two communities: dispersal processes, i.e. the exchange of species between the communities; and restriction of community members to generalist species in the community. (In a sense this is the "fragmentation version" of the "intermediate disturbance hypothesis", which also conceptually rests on the relative proportions of r- and K-strategists along a disturbance gradient, Connell, 1977). Both processes lead to a homogenisation of the community (see, e.g., Loreau, 2000), i.e. higher similarity, but they are differentially affected by landscape structure and land-use intensity (Fig. 8). While increasing fragmentation impedes the effectiveness of dispersal and thereby reduces community similarity, habitat loss or high pesticide load increases the percentage of generalist species, and therewith community similarity. How community similarity relates to landscape structure and usage now depends on the shape (and slopes) of these functions. Any relationship, from monotonic increasing and decreasing to hump-shaped and its inverse is possible, and may even be expected. If this concept is realistic, the type of response we see in the data may reveal something about the way landscape impacts on relative effects of dispersal and restriction to generalists.

As an example, we found the splitting index for green veining to be related to plant community similarity in an inverse hump-shaped fashion. According to Figure 8, we conclude that probably dispersal efficiency is rapidly reduced as fragmentation is increased. At the same time, the percentage of generalist species in the community only gradually increases, until, at very high degrees of fragmentation, generalists dominate.

Thus plants in agricultural landscapes would represent "generalists/bad dispersers", which is certainly true compared to the flying groups in our sample.

The interactive effect of pesticides and habitat fragmentation on similarity patterns of bee, bug and spider communities showed that our hypothesis 2 was only supported under high levels of habitat fragmentation (Figs 3, 5 and 7). Here, community similarity increased with increasing pesticide applications, possibly because of a dominance of relatively pesticide-tolerant species, the "selection of generalists"-process. However, a low response to pesticide application was predicted for bee communities in little fragmented

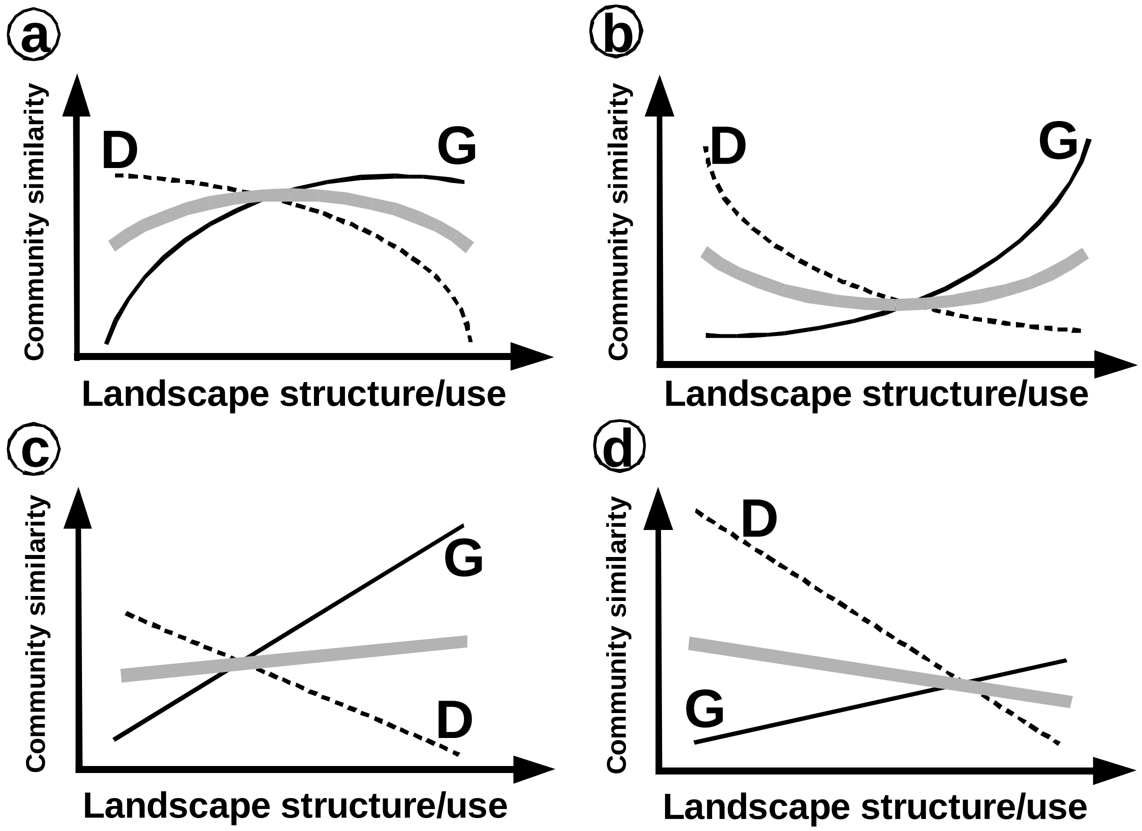

Fig. 8. The importance of dispersal (D) or the percentage generalist species (G) for community similarity depends on the way these two factors are affected by landscape structure/use. Landscape quality (structure or use) decreases towards the right. Grey lines are net outcome of both processes. The scenario a) depicts communities of "specialists/good dispersers": a rapid increase in the percentage of generalists in the community, i.e. a rapid loss of specialists. At the same time most species still disperse effectively until the environment declines to a low quality. The scenario b) is the opposite, i.e. "generalist/bad dispersers": the importance of dispersal is quickly reduced as landscape quality erodes, while most species are able to tolerate this environment until eventually all species disappear in fast sequence. The two lower scenarios are illustrating the effect of different slopes on net community similarity. Panel c) depicts groups where dispersal is less affected by landscape than the selection of generalists, while for panel d) it is the opposite.

landscapes. In such landscapes, habitat connectivity may be sufficient to support the exchange of individuals and species which overcome the effects of frequent perturbations and poisoning by pesticide applications. This indicates that dispersal processes may dominate over generalist selection. Bug communities showed this effect even at intermediate levels of landscape fragmentation. The decrease of community similarity with increasing pesticide levels at *low* levels of fragmentation is more difficult to understand. At high landscape integrity and low pesticide applications these two factors were correlated (see crosses in the lower left corner of Figs 3, 5 and 7). Thus, we cannot differentiate between a landscape structure and a land-use intensity effect at this benign section of our sample space. It may well be that we see community similarity decreasing with pesticide applications because this takes place along a gradient of increasing fragmentation and bee, bug and spider communities are already hindered in their exchange of species.

We could expect organism groups that differ greatly in their dispersal ability to produce different similarity pattern. Comparing, e.g., birds and bees, we would find that Figure 8d best describes the pattern for birds. We deduce that effective bird mobility is strongly reduced by more green veining, while the level of generalisation is little affected. Indeed it has been often observed that territories of songbirds are considerably smaller in more suitable habitats (e.g. Bezzel, 1982; e.g. Smith & Shugart, 1987); thus, as green veining increases, so does bird species density, and hence community similarity. For bees we found the opposite trend, indicating that the percentage of generalists in a community increases with a reduction in percentage green veining.

Community similarity and the agricultural landscape

Earlier studies have shown that pesticide applications are a major component of land-use intensity that affected organisms in agricultural landscapes (Heliovaara & Vaisanen, 1993; Holland, Winder & Perry, 2000). In our analysis, nitrogen fertilisation input was included in the set of explanatory variables, but was not retained in any of the final models. Pesticide applications, on the other hand, seem to affect the community similarity of carabid beetles and hover flies, as well as bees and bugs and, to a lesser extend, spiders through the interaction with habitat fragmentation, contrary to our hypothesis 2. Increasing pesticide loads led to a decrease in community similarity in carabid beetles. As the hover fly data indicate (Fig. 6), the pattern may be non-linear, with initially more randomly recruited communities, until the high pesticide burden selects for the few pesticide-tolerant species. This does confirm hypothesis 2 for hover flies, and it may be that carabids are overall less sensitive (Holland, Winder & Perry, 2000; Walters et al., 1998) and hence the selection effect of pesticide does not come into force within this land-use intensity gradient. Insecticides were the most common form of pesticides used in our study areas, with fungicides and herbicides being less common (Herzog et al., 2005).

The percentage of green veining habitats as such was only significant for bird and bee community similarity (Table 3, Fig. 2). Highly mobile organisms such as birds interact with their environment at far larger scales than arthropods; the levels of fragmentation described e.g. by the splitting index within our 16 km^2 test sites may thus be too small. Percentage green veining in this case was a better assessor of overall landscape structure, explaining 21% of the variation in bird community similarity (Fig. 2a). Bee community similarity increased with lower percentage of green veining habitats (Fig. 2b). We ascribe this to the 'selection for generalists'-effect (Fig. 8). Interestingly, Tockner et al. (1999) also report on a similar, non-linear relationship between landscape structure and community similarity (or rather β-diversity) for macrophytes and dragonflies. They, however, argue that niche breadth rather than dispersal causes this pattern.

Comparing community similarity responses across groups

Overall, groups responded idiosyncratically to landscape structure and usage. Even for groups using comparable resources and sharing similar movement patterns (bees and hover flies; carabid beetles and spiders) or that are trophically linked (plants and bees), community similarities were unrelated (Table 2). Using only one of these seven groups as an indicator for the response of the others to landscape structure and management seems thus not possible.

Community similarity has been used to compare communities between years, sites and environmental variables (e.g. for butterflies: Cleary & Genner, 2004). In most such studies community similarity was highly correlated between different groups (birds,

amphibians, reptiles and lepidopterans: Atauri & de Lucio 2001; butterflies and birds: Fleishman et al. 2003; butterflies and dragonflies: Cleary et al. 2004; birds, butterflies and plants: Su et al. 2004), even if α-diversity was not (Su et al., 2004). This was not the case in our study (Table 2). Our analysis indicates that groups respond differently to landscape structure and land-use intensity. Although land-use intensity generally increased and fragmentation decreased similarity of communities, the responses of the groups were best described by different variables: for bugs the emerging pattern was similar to what one would expect on the basis of meta-population theory (Hanski, 1990): larger patches and closer distance made communities more similar (Fig. 4). Similarly, community similarity of plants, bees, bugs and spiders was negatively correlated with descriptors of habitat fragmentation (e.g. splitting index). No such relationship could be detected for birds, carabids and hover flies. While birds and hover flies are highly mobile and may integrate landscape structure at a larger spatial scale, this argument would also apply to bees, and it does not explain the lack of response for carabid communities. The apparent lack of response of the bird community to landscape configuration (but response to percentage green veining) supports the findings of other studies on bird community similarity in relation to habitat structure (Clergeau, Jokimäki & Savard, 2001; Jokimäki & Kaisanlahti-Jokimäki, 2003).

Our different organism groups respond differently and have the potential to be used as indicators for different features of the landscape and its usage. The plant community was most responsive to fragmentation of green veining habitat. The total percentage of green veining was best tracked by the similarity of bird and, less well, by bee communities (Table 3). Hover fly community similarity responded most sensitively to pesticide burden. However, their non-linear response makes them of little use as an indicator group for pesticide burden in our systems. Although bees and bugs were similarly responsive, pesticide effects were dependent on landscape configuration and hence it would be more difficult to use these groups as indicators for pesticide burden alone. Carabids, which are commonly used as indicators in environmental impact assessments (Doring et al., 2003; Huusela-Vesitola, 1996; Kromp, 1999; Luff, 1996; Niemela, 2001), are *as a community* no good indicators of landscape structure or use. Carabid similarity was only little affected by pesticides (Table 3). Spider community similarity also seems to be unsuitable to describe landscape changes.

What drives community similarity: local species richness and habitat similarity or regional landscape structure and land-use intensity?

Harrison et al. (1992) reported on the importance of □-diversity and environmental similarity for community similarity (or rather their measure of β-diversity, which is conceptually equivalent to 1 – community similarity, Fukami, Naeem & Wardle, 2001). Because both were highly correlated in their study, they could not differentiate between these two effects. Our predictor variables are different: local species richness values are averages of several plots per site, and there is no ecological reason why average species richness should increase or decrease with the diversity of sampled habitats (i.e. the environmental similarity of plots): starting from an "average" habitat, any new habitat is equally likely to contain more or less species. We would, however, expect a positive effect of environmental similarity on community similarity. As Table 3 shows, it was either species richness or environmental similarity that affected community similarity at the local scale.

In our study we tried to elucidate the effect of regional landscape structure and management together with patch-level (i.e. local) landscape composition. Several spatial levels may contribute to the finally observed diversity patterns (Wagner, Wildi & Ewald, 2000). Local environmental similarity significantly contributed to community similarity in all groups except the hover flies (Table 3). When ranking factors of influence, we find local species richness to explain most of the variation in community similarity, followed by landscape structure and land-use intensity and finally local environmental similarity, although considerable variation around this trend exists (Table 3).

Conclusion

This study showed that the way we utilise landscapes affects the structure of communities at the local scale. In turn we can assess the ecological quality of a landscape by quantifying its effect on communities. Different species will reveal different impacts and tailoring the indicator system to the impact is hence crucial but difficult. Although community similarity is a less intuitive diversity measure than species richness, it repeatedly proved a more sensitive measure of the ecological quality of a system and it has been claimed as a measure of ecosystem reliability (Fukami, Naeem & Wardle, 2001).

Acknowledgements

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Appendix A: model details for all groups

PLANTS

Variable	**Coefficient**	**Std. Error**	**t value**	***P***
Intercept	0.334432	0.071014	4.709	< 0.001
Local speceis richness	0.006465	0.002128	3.038	0.006
Local environment	-0.081403	0.031655	-2.572	0.018
log(split_gv)	-0.071356	0.019839	-3.597	0.0018
log(split_gv)^2	0.005204	0.00144	3.614	0.0017

Anova Table (Type III tests)

Variable	**Sum Sq**	**Df**	**F value**	***P***
Local speceis richness	0.0064209	1	9.2298	0.006
Local environment	0.0046004	1	6.6129	0.018
log(split_gv)	0.0089995	1	12.9366	0.002
log(split_gv)^2	0.0090846	1	13.0588	0.002
Residuals	0.0139133	20		

BIRDS

Variable	**Coefficient**	**Std. Error**	**t value**	***P***
Intercept	-0.484652	0.242774	-1.996	0.058
Local environment	0.950403	0.237988	3.993	< 0.001
%GV	0.007408	0.002951	3.301	0.003

Anova Table (Type III tests)

Variable	**Sum Sq**	**Df**	**F value**	***P***
Intercept	0.036194	1	3.9853	0.058
Local environment	0.144839	1	15.9480	< 0.001
%GV	0.098973	1	10.8978	0.003
Residuals	0.199803	22		

BEES

Variable	**Coefficient**	**Std. Error**	**t value**	***P***
Intercept	1.56E+00	3.03E-01	5.149	< 0.001
Local speceis richness	4.35E-03	1.30E-03	3.357	0.004
Local environment	-3.64E-01	9.45E-02	-3.854	0.001
%GV^2	-4.93E-05	2.31E-05	-2.129	0.049
log(proximity_gv)	-4.74E-02	1.78E-02	-2.665	0.017
Pesticide	-9.94E-03	2.55E-03	-3.889	0.001
log(split_wood)	-4.42E-02	1.26E-02	-3.515	0.003
Pesticide:log(split_wood)	1.28E-03	2.76E-04	4.656	< 0.001

Anova Table (Type III tests)

Variable	**Sum Sq**	**Df**	**F value**	***P***
Intercept	0.074509	1	26.5154	< 0.001
Local speceis richness	0.031669	1	11.2698	0.004
Local environment	0.041746	1	14.8561	0.001
%GV^2	0.012732	1	4.531	0.049
log(proximity_gv)	0.01996	1	7.1032	0.017
Pesticide	0.042507	1	15.1267	0.001
log(split_wood)	0.034719	1	12.3553	0.003
Pesticide:log(split_wood)	0.06091	1	21.676	< 0.001
Residuals	0.044961	16		

BUGS

Variable	**Coefficient**	**Std. Error**	**t value**	***P***
Intercept	0.1692156	0.2458919	0.688	0.501
Local speceis richness	0.0143077	0.0027202	5.26	< 0.001
Local environment	-0.3010791	0.1164517	-2.585	0.020
log(proximity_herb)	-0.0481953	0.0172592	-2.792	0.013
log(split_wood)	0.064994	0.020492	3.172	0.006
Pesticide	-0.0188552	0.0038404	-4.91	< 0.001
log(proximity_wood)	0.0822277	0.0170721	4.817	< 0.001
log(split_gv)	-0.0735527	0.0259347	-2.836	0.012
Pesticide:log(split_gv)	0.002687	0.0005431	4.947	< 0.001

Anova Table (Type III tests)

Variable	**Sum Sq**	**Df**	**F value**	***P***
Intercept	0.00194	1	0.4736	0.501
Local speceis richness	0.113316	1	27.6648	< 0.001
Local environment	0.02738	1	6.6845	0.020
log(proximity_herb)	0.03194	1	7.7977	0.013
log(split_wood)	0.041204	1	10.0595	0.006
Pesticide	0.098735	1	24.1051	< 0.001
log(proximity_wood)	0.095023	1	23.1987	< 0.001
log(split_gv)	0.032946	1	8.0433	0.012
Pesticide:log(split_gv)	0.100262	1	24.4777	< 0.001
Residuals	0.06144	15		

CARABIDS

Variable	**Coefficient**	**Std. Error**	**t value**	***P***
Intercept	0.1597779	0.0529608	3.017	0.007
Local speceis richness	0.0130674	0.0018917	6.908	< 0.001
Local environment	0.1942214	0.0656467	2.959	0.008
Pesticide	-0.0012027	0.0004936	-2.436	0.024

Anova Table (Type III tests)

Variable	**Sum Sq**	**Df**	**F value**	***P***
Intercept	0.031318	1	9.1017	0.006
Local speceis richness	0.164187	1	47.7163	< 0.001
Local environment	0.030119	1	8.7532	0.008
Pesticide	0.020427	1	5.9364	0.024
Residuals	0.068818	20		

HOVER FLIES

Variable	**Coefficient**	**Std. Error**	**t value**	***P***
Intercept	2.47E-01	6.39E-02	3.859	< 0.001
Local speceis richness	3.91E-02	7.08E-03	5.528	< 0.001
Pesticide	-4.88E-03	2.07E-03	-2.351	0.029
Pesticide^2	8.01E-05	2.18E-05	3.677	0.001

Anova Table (Type III tests)

Variable	**Sum Sq**	**Df**	**F value**	***P***
Intercept	0.087274	1	14.8904	< 0.001
Local speceis richness	0.17913	1	30.5624	< 0.001
Pesticide	0.032399	1	5.5279	0.029
Pesticide^2	0.079223	1	13.5167	0.001
Residuals	0.117222	20		

SPIDERS

Variable	**Coefficient**	**Std. Error**	**t value**	***P***
Intercept	-0.0951682	0.1849771	-0.514	0.613
Local speceis richness	0.0064839	0.0029994	2.162	0.044
Local environment	0.2321944	0.0841423	2.76	0.012
log(proximity_gv)	0.0307439	0.0158766	1.936	0.068
Pesticide	0.008613	0.0041741	2.063	0.053
log(proximity_gv):Pesticide	-0.0008476	0.0004201	-2.017	0.058

Anova Table (Type III tests)

Variable	**Sum Sq**	**Df**	**F value**	***P***
Intercept	0.000887	1	0.2647	0.613
Local speceis richness	0.015653	1	4.673	0.044
Local environment	0.025507	1	7.6151	0.012
log(proximity_gv)	0.01256	1	3.7498	0.068
Pesticide	0.014261	1	4.2577	0.053
log(proximity_gv):Pesticide	0.013633	1	4.0703	0.058
Residuals	0.060292	18		

6. *Communities:* Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organisational levels and spatial scales

O. Schweiger, J.P. Maelfait, W. van Wingerden, F. Hendrickx, R. Billeter, M. Speelmans, I. Augenstein, B. Aukema, S. Aviron, D. Bailey, R. Bukacek, F. Burel, T. Diekötter, J. Dirksen, M. Frenzel, F. Herzog, J. Liira, M. Roubalova & R. Bugter

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6.1. Summary

1. In landscapes where biodiversity is threatened by anthropogenic activities like in intensive agricultural areas, detailed knowledge about the impact and hierarchical structure of environmental factors on the composition, structure and function of local communities is of major importance for development and maintenance of biodiversity.

2. We analysed five arthropod taxa covering a broad range of functional aspects (wild bees, true bugs, carabid beetles, hover flies and spiders). They were sampled at 24 landscape test sites (4x4km) across seven European countries along an independent gradient of both agrarian land-use intensity and landscape structure. We examined species-environment relationships in a hierarchical design of four main sets of environmental factors (country, land-use intensity, landscape structure, local habitat properties) that covered three spatial scales (region, landscape, local) by means of hierarchical variability partitioning using partial CCA´s.

3. This approach revealed an increasing importance of scale from local to landscape to region, possibly reflecting general patterns in assembling local communities. After correcting for regional effects, factors at the landscape scale dominated over local habitat factors. Land-use intensity explained most of the variability in species data, whereas landscape characteristics (especially connectivity) accounted for most of the variability in body size and trophic guilds.

4. *Synthesis and application.* Our results indicated relatively independent effects of agricultural management and landscape structure on local arthropod communities pointing to great scope for conservation management. Changes in each of the environmental factors will result in specific effects on local communities most likely according to dispersal ability and the resource use of species.

Keywords: biodiversity; community structure; functional groups; landscape structure; partial canonical correspondence analysis; variation partitioning.

6.2. Introduction

In the 20th century agricultural intensification and changes in landscape structure started to threaten overall biodiversity seriously (Robinson & Sutherland 2002). Besides analysis of species richness (e.g. α–, β–, γ–diversity), investigations considering local species identity and abundance, which are essential components of biodiversity, provide valuable insights into the relation of biodiversity and environmental factors altered by anthropogenic activities. However, the effects of the environmental factors on local communities differ between organisational levels and spatial scales (Steffan-Dewenter et al. 2002; Cushman & McGarigal 2002; Grand & Cushman 2003). When local communities are assembled from the regional species pool they have to pass a series of filters (Zobel 1997; Lawton 1999). These filters may act on a regional scale (e.g. history of climate and environment, evolution), a landscape scale (e.g. dispersal in the landscape context) and on a local scale (e.g. food, competition and predation, disturbance, habitat properties). The relative strength and synergistic effects of these environmental filters will not only determine species composition, but also their functional structure according to ecological characteristics.

These ecological characteristics tend to be related to body size and trophic guild (Holt 1996; Tscharntke & Brandl 2004). Allometric scaling laws indicate that body size is a key to many life history traits such as reproduction and resource use and is positively related to foraging range and dispersal ability (Peters 1986; Brown & West 2000; Gathmann & Tscharntke 2002). Hence, local community structure according to body size and trophic guild is expected to reflect the effects of scale and environmental factors on functional processes.

In landscapes where biodiversity is threatened by anthropogenic activities like in intensively managed agricultural areas, detailed knowledge about the hierarchical structure and relative impact of relevant environmental factors affecting community composition, structure and functioning is of major importance for the development and conservation of biodiversity.

Results from the recently completed EU research project 'GREENVEINS' demonstrated robust relationships between species richness of plants, birds and arthropods and both landscape structure and agricultural land-use intensity that apply across temperate Europe (Billeter et al., submitted). In order to analyse these relationships in detail, the present study aimed to quantify the relative impact of these environmental factors on local arthropod communities across three organisational levels (taxon, size class, trophic guild). We focused on arthropod species as they make up about 65% of all organisms (Groombridge 1992) with a significant impact on ecosystem processes and they represent good correlates for species diversity (Duelli & Obrist 1998). To cover a broad range of functional aspects, we analysed five arthropod taxa (wild bees, true bugs, carabid beetles, hover flies and spiders).

We examined species-environment relationships in a hierarchical design of four main sets of environmental variables that covered three spatial scales. At the regional scale, we accounted for the effects of regional species pools and other historical influences. At the landscape scale, we analysed several aspects of land-use intensity on arable fields and the landscape structure of semi-natural elements. At the local scale, we evaluated aspects of local habitat properties. To cope with the nested, multi-scale structure of communities as well as environmental data, we used a hierarchical variability decomposition approach based on partial canonical correspondence analysis (partial CCA; Borcard, Legendre, and Drapeau 1992; Legendre 1998). This method provides a powerful tool to quantify the relative importance, independent effects and confounding of the factors affecting communities (Cushman & McGarigal 2002; Cottenie et al. 2003; Jeanneret, Schupbach & Luka 2003).

We addressed the following questions: (1) What is the relative impact of scale to the effects of environmental factors on local arthropod community composition and structure? (2) What is the relative influence of land-use intensity, landscape structure and habitat properties on local arthropod community composition? (3) How are body size and trophic position affected by these factors?

6.3. Methods

Study sites and environmental variables

Five arthropod taxa, wild bees (Apoidea), true bugs (Heteroptera), carabid beetles (Carabidae), hover flies (Syrphidae) and spiders (Araneae), were sampled at 24 landscape test sites of 4 x 4 km in agricultural landscapes. The test sites were distributed over seven European countries (Fig. 1): France (3 tests sites), Belgium (4), The Netherlands (4), Switzerland (3), Germany (4), Czech Republic (2) and Estonia (4). Together, these covered an independent gradient of both agrarian land-use intensity and landscape structure.

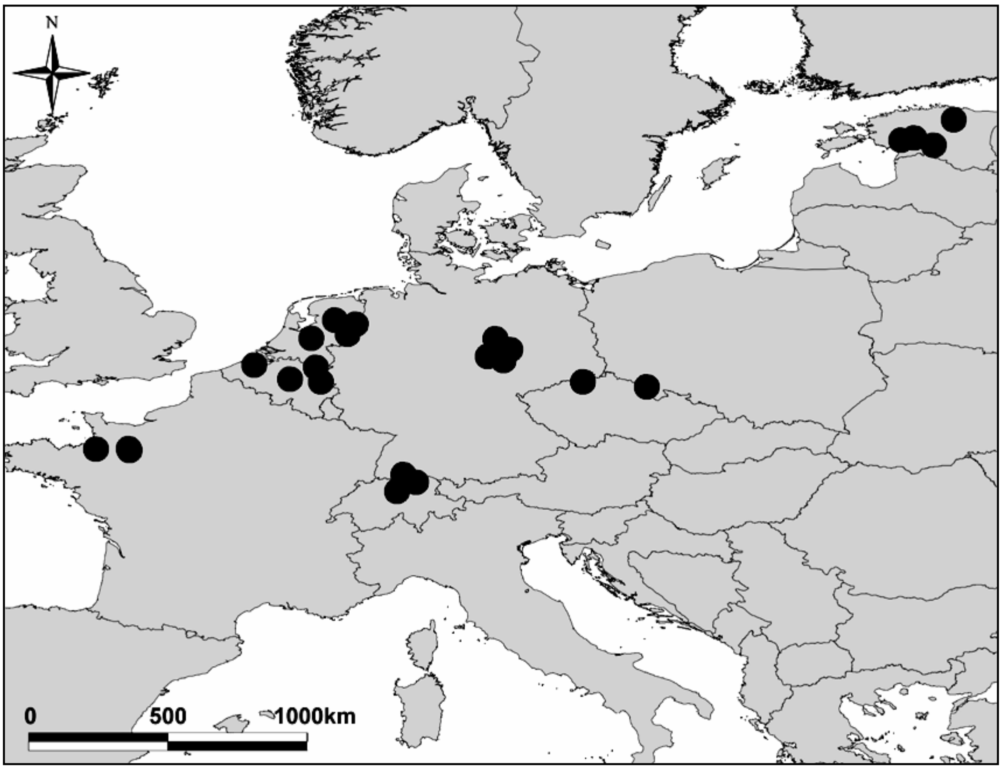


Fig. 1 Geographical distribution of the 24 test sites.

Table 1 Nested structure of environmental variables. LUI, land-use intensity; GV, green veining.

Scale	Main set	Subset	Variable
Region	Country	Country	7 dummy variables
Landscape (4 x 4 km)	LUI	Stress	Number of pesticide application per year
			Nitrogen fertilizer applied per hectare and year
		Spatial	Crop diversity
			Intensely fertilised area
	GV	Composition	Proportion of green veining
		Configuration	Area weighted proximity index of green veining
		Diversity	Number of habitat types
Local (50 m)	Habitat	Composition	Proportion of green veining
		Diversity	Number of habitat types

We recorded environmental variables in a nested, hierarchical design of four main sets and eight subsets that covered three spatial scales (Table 1). At the regional scale, we considered ‘country’ (coded as a dummy variable) as a main set to account for the biogeographical gradient covering our study and the possible influences of country-specific historical or cultural effects on regional species pools.

At the landscape scale, two main sets were distinguished. For the first main set, average land-use intensity was evaluated per test site by standardised interviews from farmers about management practices on arable fields (Herzog et al., submitted). This main set of variables will be denoted by the acronym ‘LUI’ (Land-Use Intensity) further on. We recorded two subsets of LUI. The first subset consisted of two variables representing environmental stress factors of LUI (‘stress’): (a) Number of pesticide applications to major crops per year, (b) amount of nitrogen fertilizer applied per hectare and year. The second subset of variables represented spatio-temporal patterns of LUI (‘spatial’): (c) Crop diversity (number of crops in the rotation), (d) proportion of intensely fertilized area (> $150 \text{kgNha}^{-1}\text{y}^{-1}$).

The second main set of environmental variables represented landscape structure. Here, we focused on semi-natural elements (e.g. woodlands, hedgerows, ditches, grasslands), so called ‘green veining’ at the landscape scale, as these elements predominantly contribute to biodiversity. Environmental variables were evaluated from digitized habitat maps using orthorectified aerial photographs with spatial resolutions better than 1 x 1 m and ArcGIS software (ESRI 2003). The classification of the habitats was based on the European Nature Information System (EUNIS) habitat classification (available at http://mrw.wallonie.be/dgrne/sibw/EUNIS/home.html). We aggregated the semi-natural habitats as green veining to contrast the highly dynamic anthropogenic elements of arable land and built-up areas. To avoid confusion, further on we will speak of ‘green veining’ when general aspects of semi-natural habitats are referred to and of ‘GV’ (Green Veining) when we are referring to this particular main set of variables. To describe the structure of green veining at the landscape scale and to separate the impacts of species-area relationships, landscape connectivity and landscape diversity, we recorded three subsets of landscape variables per test site: (1) Landscape composition was calculated as the proportion of green veining ('composition'). (2) Landscape configuration was assessed by several landscape structure metrics retrieved from FRAGSTATS analyses based on the aggregated green veining habitats ('configuration'; McGarigal et al. 2002). (3) Landscape diversity was measured as the number of green veining habitat types based on EUNIS classification ('diversity'). As for reliable comparisons an equal number of variables within each environmental subset is required, the landscape configuration metrics retrieved from FRAGSTATS (Number of Patches, Edge Density, Proximity Index, Euclidean Nearest Neighbour Distance, Patch Cohesion Index, Splitting Index, Clumpiness Index) were subjected to a forward selection procedure in a canonical correspondence analysis (CCA) with all arthropod species and the species of single taxa as the dependent matrices, respectively. We used CCA, because preliminary analyses based on detrended canonical correspondence analysis (DCA) indicated unimodal response patterns at least for some of the arthropod taxa. Although, the results differed somewhat between the five arthropod taxa and several metrics accounted significantly for the explanation of community variability, we selected only one configuration metric to keep consistency with landscape composition and landscape diversity. The area weighted mean proximity index of the aggregated green veining elements explained the pooled arthropod data as well as most of the single taxonomic groups best and was significant in all cases. Therefore, this metric was used for further analyses. The proximity index considers both local patch size and distance and will be interpreted as a measure of connectivity.

The fourth main set of environmental variables described properties of green veining at the local scale. This main set will be referred to as 'habitat' further on. The variables in this set were calculated for circular areas with a radius of 50 m around the arthropod sampling points. The 50 m radius was a compromise regarding differences in average home ranges of ground dwelling and flying species. We recorded two subsets of local variables within the circular areas: (1) Local habitat composition included the proportions of single and aggregated green veining habitat types ('composition'). (2) Local habitat diversity was measured as the number of green veining habitat types ('diversity'). The local habitat composition variables were subjected to a forward selection procedure in a CCA and resulted in the selection of the proportion of aggregated green veining elements for further analyses. This led to a total of 16 explanatory variables, nested within eight subsets, which are in turn nested within four main sets (Table 1).

Arthropod sampling

Spiders and carabid beetles were captured with pitfall traps, whereas wild bees, true bugs and hover flies were sampled with combined flight traps (a combination of window and yellow pan trap; see Duelli, Obrist, and Schmatz 1999). The test sites were divided into 16 grid cells of 1 km^2. In every grid cell a trap set was placed at a randomly chosen ecotone between a green veining habitat and agricultural field. Each trap set consisted of two trap units, which were spaced between 25 m and 50 m apart from each other. A trap unit was composed of one pitfall and one combined flight trap. Consequently, a total of 16 trap sets comprised 32 pitfall traps and 32 combined flight traps per test site. The circular areas for local scale analysis were created around the centre point between both trap units of a trap set. Sampling was carried out according to Duelli (1997). In order to minimize the sampling effort while maximizing efficiency, we restricted the sampling to two periods of maximum activity and density of the species to 7 weeks in the autumn of 2001 and to 5 weeks in the early summer of 2002. To correct for climatic and consequently phenological differences between the countries, we used the blossoming of *Taraxacum officinale* Wiggers as an indicator to start sampling. The traps were emptied weekly. To account for differences in weather conditions between the test sites during the sampling periods, we considered only the most abundant samples for the analysis (4 weeks from the autumn period, 3 weeks from the early summer period). The samples were pooled for each trap set and the specimens were identified to the species level.

Classification of arthropods

The analysis was performed on different sets of taxonomic and ecological groups. In a first step we analysed community composition based on the logarithms of abundance data from all arthropod species together regardless of their taxonomic or ecological grouping. We removed species captured in less than 5 trap sets from the data set resulting in a total number of 628 species represented by 170,105 individuals (Appendix A). To test the general trend of this analysis we repeated it for each of the five arthropod taxa. Next, we classified the arthropod species into ecological groups according to body size and trophic guild. In order to account for general differences in size between the arthropod taxa, we created four size classes for each of the five taxa (Appendix A).

Additionally, the arthropod species were assigned to four trophic guilds: omnivores, herbivores, predators and saprophages. Contributions to the single trophic guilds differed between the taxa (Appendix B). Wild bees, true bugs, carabid beetles and spiders were classified according to the feeding habits of the adults, whereas for hover flies the larvae were decisive. The ecological information was obtained from the literature (references in Appendix A).

Hierarchical partitioning of community variation

To quantify the species-environment relationships in detail we hierarchically partitioned the variability in the community data that was subsequently explained by specific sets of environmental data. We performed this analysis for the arthropod community as a whole based on either taxonomic (species) or ecological units (size classes, trophic guilds) and replicated this analysis for each of the five arthropod taxa by means of a partial CCA. We used the same set of explanatory variables for all multivariate analyses to allow reliable comparisons between taxonomic and ecological groups (Okland 1999).

The partial CCA explicitly separated the effects of the particular environmental subsets at a given hierarchical level and quantified their relative contribution in explaining the variability in the arthropod community. Hence, it allowed the comparison of environmental factors across organisational levels as well as spatial scales. This was achieved by a series of partial CCA´s calculating the ‘marginal’ and ‘conditional’ effects of the environmental main sets and subsets. Marginal effects denoted the variability explained by a given set of environmental variables without considering other environmental factors, whereas conditional effects denoted the variability explained by a given environmental set after removing the confounding effect of one or more other environmental variables (covariables). Marginal and conditional effects were tested for significance with Monte Carlo permutation tests by 999 permutations within the particular hierarchical level.

Due to differences in the lack-of-fit of data to the response models for different multivariate data sets, the unexplained variation and hence the ‘total variability explained’ by all environmental factors is generally inappropriate for comparisons of different data sets (Okland 1999). To overcome this problem, we followed Okland (1999) and focused on the explainable variability only, using the ‘proportions of total variability explained’ by the particular sets of environmental variables instead. Hence, we analysed the relative importance of single sets of environmental variables, not their absolute impact.

Differences between the proportions of variability explained by the sets of environmental variables were tested for significance by replications over the single taxa by means of a one-way ANOVA.

To interpret the responses of taxonomic and ecological units, we produced biplots of the respective partial CCA´s in order to illustrate the relationships between environmental variables and species or ecological groups at a specific hierarchical level. The analysis was performed with CANOCO (Ter Braak & Smilauer 2002) and the statistical software package R (R Development Core Team 2004).

6.4. Results

Arthropod species

Pooled taxa. When all arthropod species were pooled, the total variability explained by the set of 16 independent variables (country and environment) was 28%. Of these 28%, the environmental factors accounted for 60% (that is the proportion of total variability explained). However, country-specific characteristics explained 78%. This led to an overlap and consequently to a redundancy of 38% in the explanation by country and environment. Thus, more than half of the total variability explained by environmental factors was confounded by country-specific properties. Hence, we focused on the conditional effect of the environment (country as covariable) further on, which accounted for 22% of the total variability explained.

Environmental factors at the landscape scale explained more variation than local scale factors (Fig. 2). The main set of LUI variables explained most of the variability with spatial factors dominating slightly over stress factors. The variability explained by GV was slightly lower than that of LUI. The effect of GV was clearly dominated by configurational aspects (i.e. mean proximity index of green veining elements). Local habitat factors were of minor importance. All marginal and conditional effects were significant (all $P < 0.05$). The low level of confounding between the main sets and between the GV and LUI subsets

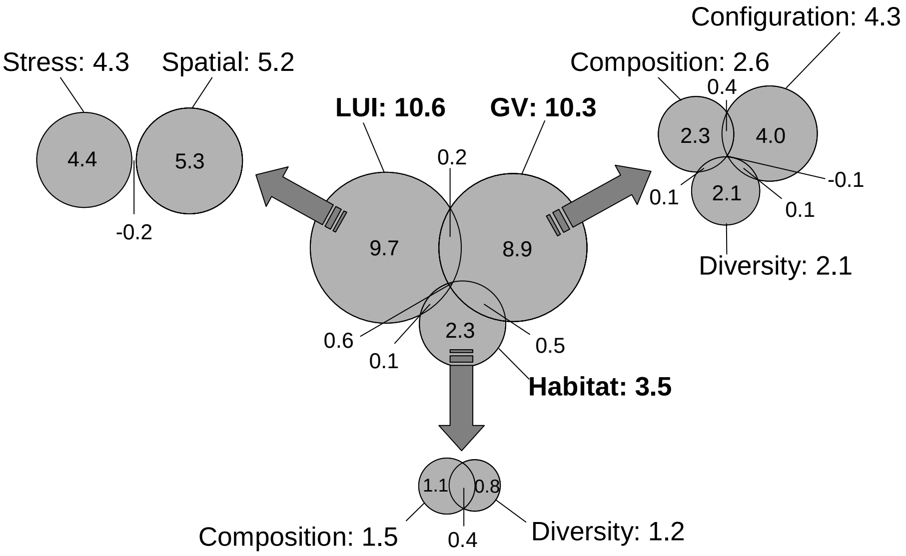


Fig. 2 Hierarchical variability partitioning (%) of the influence of land-use intensity (LUI), green veining (GV) and local habitat factors (Habitat) on the pooled arthropod community. The area of the circles is proportional to the fraction of total variability explained. Values outside the circles, marginal effects; values inside the circles, conditional effects (see text). All effects were significant.

indicated their relative independence of each other. In contrast, the confounding between the local habitat subsets composition and diversity was high (27% of variability explained by composition).

The biplot of the partial CCA (not shown) including all conditional environmental variables (country as covariable) revealed two major gradients. The gradient along the first canonical axis explained 20% of the species variation and reflected a GV – LUI gradient. It ranged from high connectivity (i.e. proximity index; correlation coefficient: -0.72) and proportion of green veining (correlation coefficient: -0.65) to high land-use intensity (correlation coefficients between 0.46 and 0.54). The second axis explained 17% of the species data and represented a pure GV gradient from high connectivity (i.e. proximity index; correlation coefficient: -0.43) to high landscape diversity (i.e. number of habitat types; correlation coefficient: 0.31).

Separate taxa. In separate analyses of the five arthropod taxa, the total variability explained by all independent variables was rather similar (minimum 22% for bugs to maximum 31% for carabid beetles). After removing the confounding effect of country, the environmental variables accounted for minimum 20% (carabid beetles) to maximum 25% (hover flies) of the total variability explained, which corresponded to the results of the pooled taxa.

Despite the fundamental ecological differences between the five arthropod taxa, they were quite similar in their dependence on the environmental factors and confirmed the general trend of the pooled arthropod community (Fig. 3). At the level of the main sets of environmental variables, the observed differences in the effects of LUI, GV and local habitat factors were significant (*P* < 0.001, ANOVA; Fig. 3a). Post hoc tests indicated that

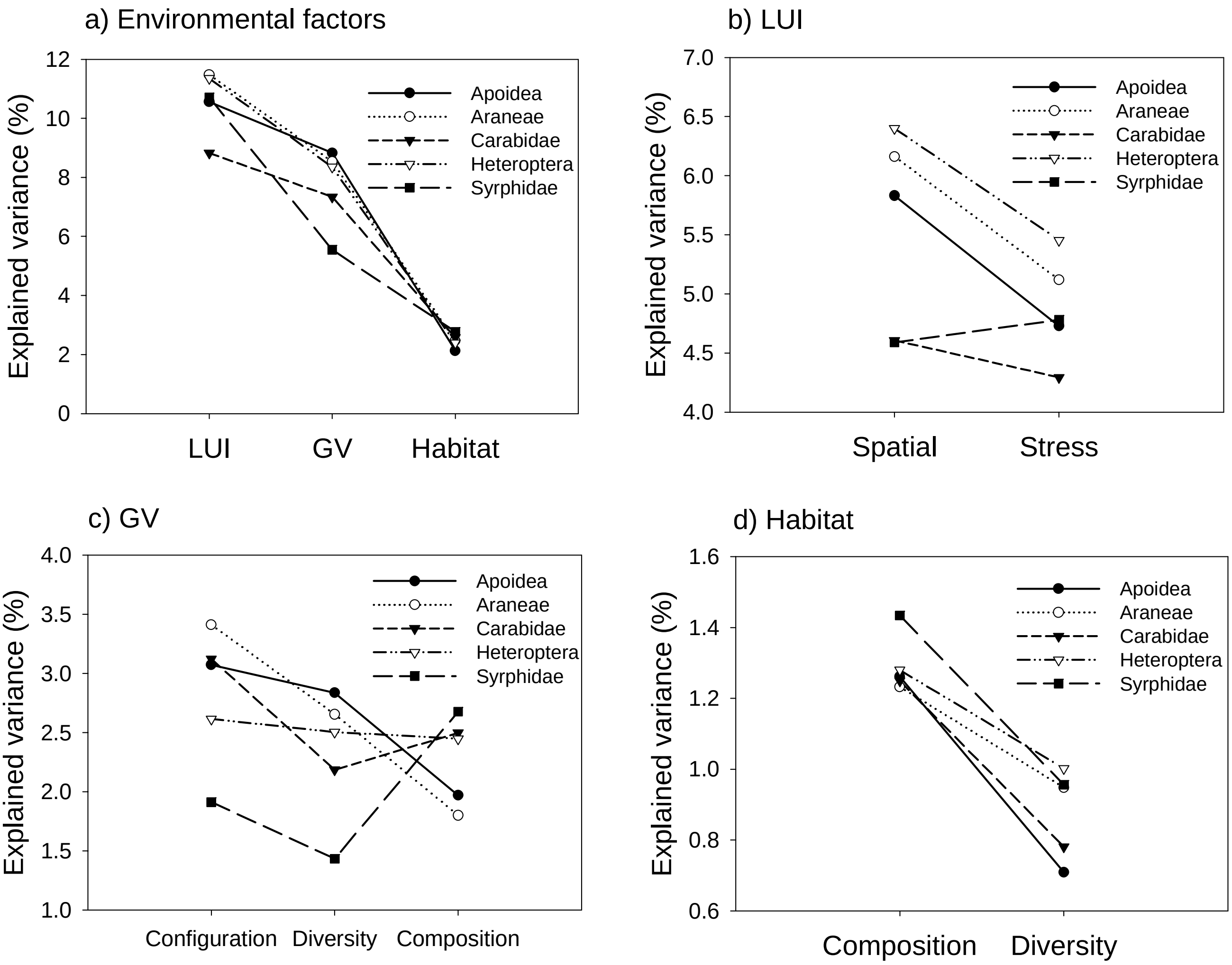


Fig. 3 Proportion of total variability explained by conditional effects of land-use intensity (LUI), green veining (GV) and local habitat factors (Habitat) for five arthropod taxa. (a) Main sets of environmental factors. (b) Subsets of LUI. (c) Subsets of GV. (d) Subsets of Habitat.

the proportion of total variability explained by LUI was greater than that of GV and that the effect of GV was greater than that of local habitat features. Visual inspections of Fig. 3a revealed no substantial differences between the arthropod taxa.

Analyses of the LUI subsets at the landscape scale confirmed the dominance of spatial factors over stress factors (*P* = 0.022, ANOVA; Fig. 3b). It was also indicated that the strength of the effect of LUI depended on the taxonomic group. Spatial as well as stress factors contributed most to the explanation of variability in bug communities, followed by spiders and wild bees. The effect of LUI was lowest in hover fly and carabid communities.

Within the main set of GV variables at the landscape scale, the response of the five arthropod taxa was comparatively heterogeneous (Fig. 3c). The proportions of variability explained by the three subsets was significantly different (*P* = 0.048, ANOVA), but post hoc tests revealed that the effect of landscape configuration was only marginally significantly higher than that of landscape diversity or composition (both *P* = 0.076). However, it was highest in all arthropod taxa except for hover flies. Visual inspections of

Fig. 3c indicated taxon-specific response patterns. Wild bees, spiders and true bugs showed a decrease in the proportion of total variability explained mainly by configuration followed by diversity and finally composition, whereas for carabid beetles and hover flies composition was more important than diversity.

Analyses of the habitat-specific subsets at the local scale confirmed the dominance of local habitat composition over local habitat diversity ($P < 0.001$, ANOVA; Fig. 3d). Their relative effect seemed not to differ between the five arthropod taxa.

Ecological groups

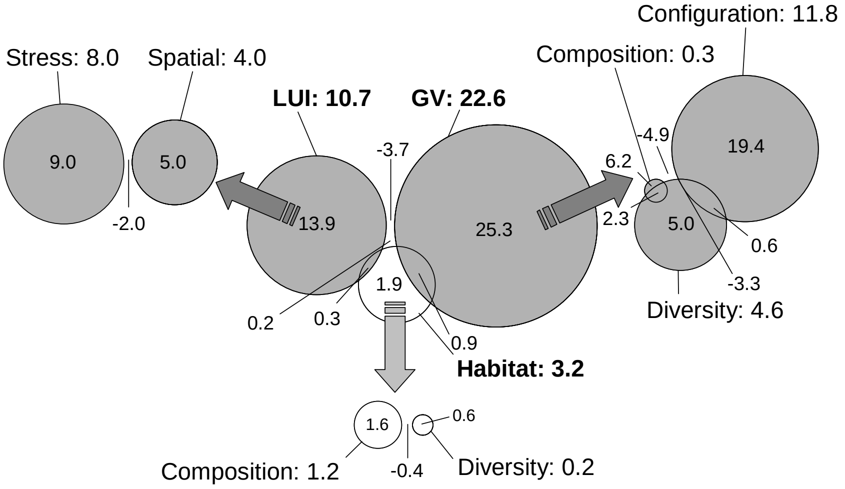
The analysis of ecological groups pooled for all arthropods revealed that the total variability explained by the independent variables (country and environment) was smaller for size classes (26%) than for trophic guilds (46%). However, after removing the confounding effect of country, the proportion of total variability explained by environmental variables was 39% for size classes and only 18% for trophic guilds. Hierarchical variability decomposition revealed pronounced differences in the dependence of size classes and trophic guilds on particular sets of environmental variables (Fig. 4).

Size classes. The distribution of size classes was most affected by GV at the landscape scale (Fig. 4a). Within GV, landscape configuration was most important determining the local size structure of the arthropod communities. Compared to the dominating impact of GV, LUI was less important. Within LUI, stress factors dominated. The explained variability by local habitat features was not significant (Monte Carlo permutation test).

The biplot including all conditional environmental variables (country as covariable) revealed a strong dependency of the size classes on a landscape configuration gradient (Fig. 5). This gradient along the first principal axis explained 63% of the variation. It ranged from high to low connectivity (i.e. proximity index; correlation coefficient: -0.29) and correlated with arthropod size classes in such a way that the size of the arthropods increased with decreasing connectivity. The second principal axis explained 30% and reflected a pure LUI gradient (e.g. correlation coefficient of pesticides: -0.18), where medium sized arthropods were associated with low levels of LUI and small and large arthropods with high levels of LUI. Large arthropods were particularly associated with frequent pesticide applications.

Trophic guilds. The distribution of trophic guilds was more evenly affected by the main sets of environmental variables compared to the analysis of the size classes (Fig. 4b). GV accounted for the largest part of the proportion of variability explained but was not as dominant as in the analysis of the size classes. Within GV, landscape configuration was most important, but was confounded to a great extent by compositional aspects. The influence of diversity at the landscape scale was not significant (Monte Carlo permutation test). Within LUI, spatial factors dominated over stress factors. Moreover, after removing the confounding effect of spatial factors from stress factors, their conditional effect was no longer significant pointing to the increased importance of spatial factors of LUI on trophic

a) Size classes



b) Trophic groups

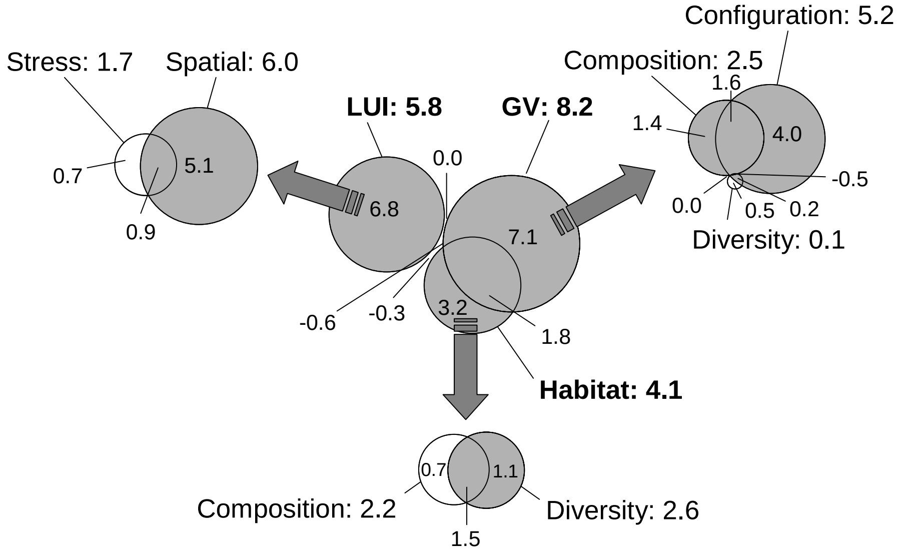


Fig. 4 Hierarchical variability partitioning (%) of the influence of land-use intensity (LUI), green veining (GV) and local habitat factors (Habitat) on size classes (a) and trophic guilds (b). The area of the circles is proportional to the fraction of total variability explained. Values outside the circles, marginal effects; values inside the circles, conditional effects (see text). White areas indicate non-significant effects.

guilds. The influence of local habitat features on trophic guilds was relatively high compared to analyses of size classes and arthropod species. However, the local habitat variables were not entirely independent from GV variables at the landscape scale, as the amount of confounding was high (43%). Within the local habitat subset, diversity dominated. But composition and diversity were highly confounded (68% of variability explained by composition). This resulted in a non significant conditional effect of local habitat composition.

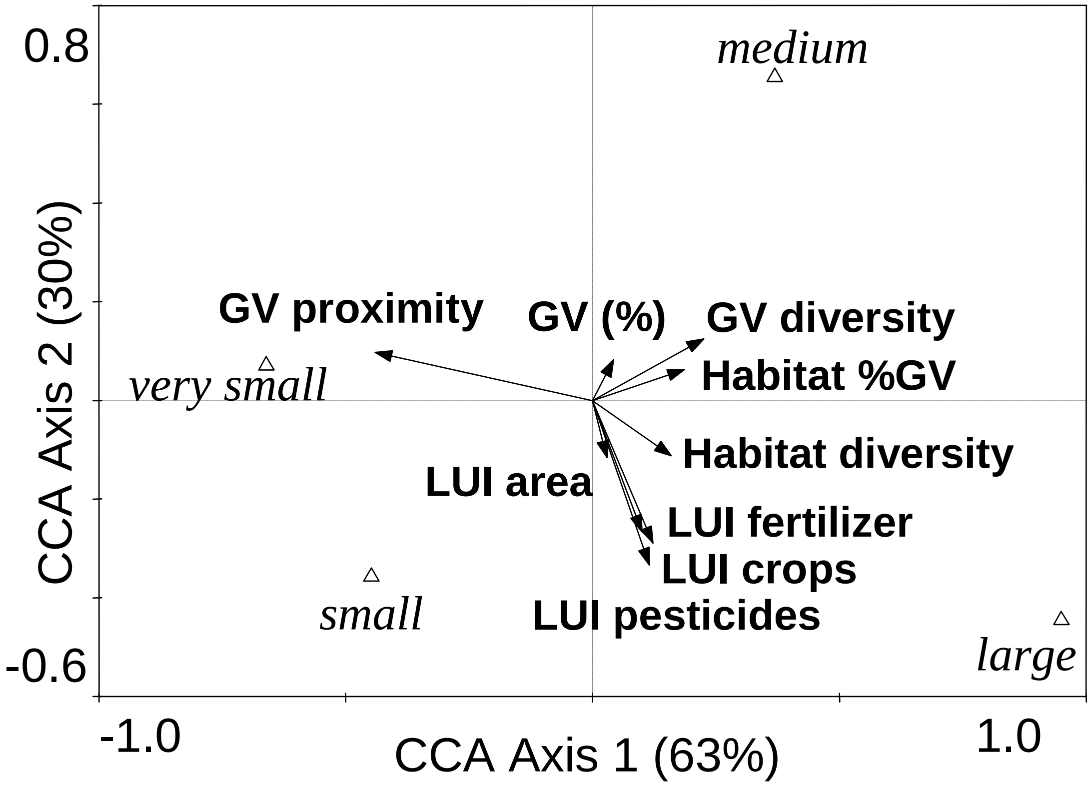


Fig. 5 Ordination diagram (biplot) from canonical correspondence analysis of size classes (triangles) constrained by conditional environmental factors (arrows; country as covariable).

The biplot including all conditional environmental variables (country as covariable) revealed two major gradients (Fig. 6). The first principal axis explained 58% of the variation in the trophic guilds and represented mainly a landscape configuration gradient from high to low connectivity (i.e. proximity index; correlation coefficient: -0.25). The second principal axis explained 38% and reflected predominantly a LUI gradient which was dominated by crop diversity (correlation coefficient of crop diversity: -0.23). Saprophagous arthropods were associated with a high level of connectivity, whereas omnivorous arthropods were associated with a high level of LUI. Predators and phytophages reacted similarly and were associated with high landscape diversity.

6.5. Discussion

Scale

The present study revealed an increasing importance of scale from local level to landscape and finally to region. This might reflect general patterns in assembling local arthropod communities. We demonstrated that local community composition and the distribution of body size classes and trophic guilds were most affected by regional processes, which highly confounded landscape and local factors. Thus, regional factors and consequently

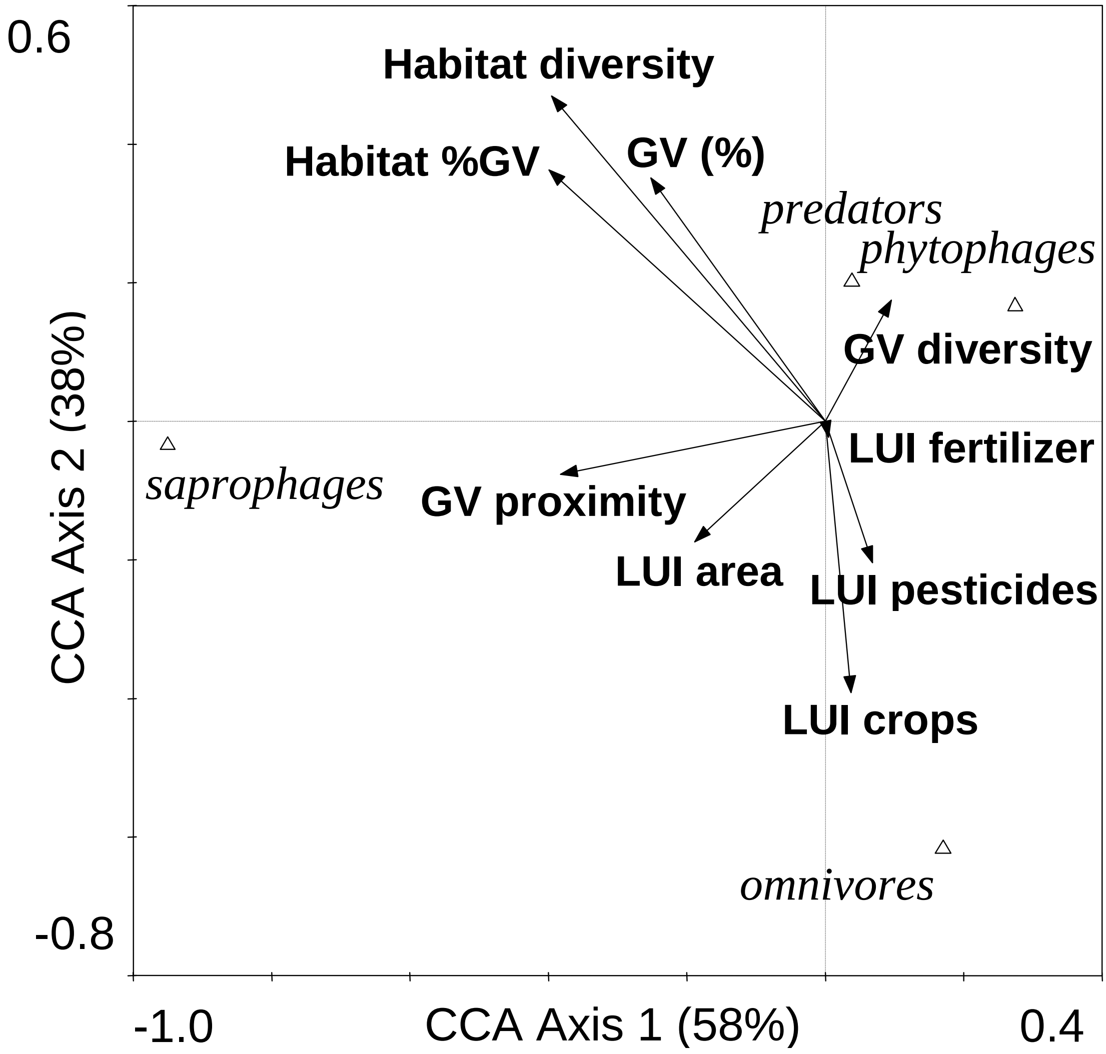


Fig. 6 Ordination diagram (biplot) from canonical correspondence analysis of trophic guilds (triangles) constrained by conditional environmental factors (arrows; country as covariable).

regional species pool effects are crucial for local community composition and must not be ignored (Rickfels 1987).

After removing the regional effects (and therewith the regional species pool), variables describing land-use intensity and the structure of green veining were more important at the landscape scale than variables describing green veining at the local scale (Fig. 2). Landscape properties will affect local recruitment of species from the regional pool as well as their persistence or local extinction (references in Lawton 1999), whereas local habitat properties might support local persistence just as long as landscape features allow for viable spatial population dynamics.

These results suggest a positive relation between scale and the impact of environmental factors on local community composition and structure emphasizing the importance of multi-scale analyses.

Effect of land-use intensity, landscape structure and habitat properties on local arthropod communities

Notwithstanding the large geographical range and the associated large regional effect we found substantial effects of environmental variables at landscape and local scale, being apparently applicable to the agricultural landscape across this large range. The total variability in community data explained by environmental factors (arthropod taxa: 22% - 31%, size classes: 26%, trophic guilds: 46%) was within the usual range one can achieve with a CCA (Okland & Eilertsen 1994; Githaiga-Mwicigi, Fairbanks & Midgley 2002). However, the unexplained variation is not only a consequence of unmeasured environmental variables or stochasticity but also due to a varying lack-of-fit of data (Okland 1999). In consequence, we were not able to speculate about the unexplained and the complement total variability explained, but relied on the unbiased relative amount of variation explained by the different sets of variables.

The low level of confounding between land-use intensity, green veining and local habitat properties indicated their relative independence in affecting local community composition (Fig. 2). Therefore, changes in each of these three environmental sets may induce specific changes in local arthropod communities. The arthropod communities studied reacted predominantly to an intensification gradient from landscapes with a high proportion and connectivity of green veining elements to landscapes with high levels of land-use intensity. The influence of agrarian land use was slightly larger than that of green veining (Fig. 2) and indicated the particular importance of agrarian management practices on local arthropod community composition. The impact of spatial aspects of agricultural land use was larger than that of stress factors, but their independence indicated separate effects on local communities. Besides agrarian land use, the high effect of green veining pointed to the additional importance of the landscape structure. Landscape composition (i.e. amount of habitat), diversity and configuration (i.e. connectivity) were previously shown to be key factors in determining local communities (Miller, Brooks & Croonquist 1997). However, our study revealed differences in the relative impact of these factors and indicated a dominant effect of connectivity (Fig. 2). Connectivity affects dispersal and therefore spatial population dynamics (Hanski & Gilpin 1997). Hence, the high impact of connectivity on local communities indicated that dispersal driven population dynamics might be more important in local community structuring than effects of landscape composition and landscape diversity at the landscape as well as the local scale.

The replications over the single arthropod taxa confirmed these findings. A surprising similarity in the reactions of all taxa was observed despite their obvious ecological differences (Fig. 3). The similarity in the response of the different arthropod taxa to land-use intensity, green veining and local habitat factors might indicate some underlying general processes. Nevertheless, some differences were found between/among the five taxonomic groups. The strength of the response to land-use intensity factors was higher in bee, bug and spider communities, as compared to carabid beetle and hover fly communities (Fig. 3b). Wild bees, true bugs and spiders have a relatively thin cuticula compared to the majority of carabid beetles, which might result in an increased vulnerability to pesticide exposure. They also have in most cases a smaller home range than the highly mobile hover flies, which might make them more sensitive to spatial aspects of agrarian practices.

The ecological differences between the arthropod taxa were also reflected in the somewhat heterogeneous response to landscape configuration, diversity and composition (Fig. 3c). Configuration was proven to be the most important factor for four arthropod taxa, but the effect on hover flies was low. This might be a consequence of the high mobility of this taxon compared to the others. Highly vagile species without significant dispersal limitation are affected by habitat loss only and not by connectivity per se (Tscharntke & Brandl 2004). Our results indicated that the effect of dispersal limitation is low for hover flies and might explain the relatively high impact of landscape composition. Consequently, the high effect of connectivity on the other arthropod groups indicated increasing dispersal limitation from true bugs to wild bees and carabid beetles and finally to spiders.

Effects on local ecological groups

The environmental factors differed in their effects on size classes and trophic guilds (Fig. 4). Green veining affected the composition of size classes most, with a dominating effect of landscape configuration (i.e. connectivity; Fig. 4a). The observed ordination of size classes along a connectivity gradient showed that the size of arthropods increased with decreasing connectivity. This indicated that small species better cope with connected than isolated habitats and large species better cope with isolation than small species (Fig. 5). Connectivity affects dispersal and therefore the local recruitment of species from the regional pool. Assuming that dispersal ability is positively correlated with body size (Peters 1986; Sutherland et al. 2000; Gathmann & Tscharntke 2002), the dominating effect of connectivity on local pattern of size distribution indicated that arthropod communities within agricultural landscapes are predominantly affected by dispersal limitation.

The local distribution of size classes was also affected by land-use intensity with stress factors dominating (Fig. 4a). The ordination along an intensity gradient showed that small and large arthropods were associated with high levels of land-use intensity, whereas medium sized arthropods reacted most sensitive (Fig. 5). The size class of large arthropods was highly dominated by carabid beetles. Some of them seem to be comparatively tolerant to pesticide application (Walters et al. 1998; Holland, Winder & Perry 2000) and might therefore be associated with high levels of land-use intensity. Body size is not only related to dispersal but also to reproduction. Population production is highest in very small species and declines with increasing size (Peters 1986). Consequently, frequent population decreases due to agricultural perturbations might be compensated more easily by the high population production of small and very small arthropods, but not sufficiently by medium sized and large species. Additionally, the class of medium sized arthropods was not dominated by carabid beetles, but by species with a thinner cuticula. These might react more sensitively to agricultural perturbations because of both a limited ability of compensation by reproduction and reduced pesticide tolerance.

Like in size classes, the variability of the trophic guilds was best explained by green veining with a dominating role of landscape configuration (i.e. connectivity; Fig. 4b). The ordination separated the four guilds and reflected different levels of resource-dependence and spatio-temporal resource variation. Saprophages were associated with landscapes with high connectivity of green veining elements. These landscapes were characterised by larger, less fragmented woodlands. Within such woodlands, a more continuous supply of dead wood is likely to be present, the particular resource of most of the trapped saprophages, providing proper conditions for saprophagous species. The association of omnivorous species with high levels of LUI was most likely due to their larger trophic niche breadth. In consequence of their generalistic feeding habits, they are assumed to overcome problems of frequent reduction in food supply due to agricultural management. Predators and phytophages reacted similarly in their association with low connectivity, high landscape diversity and low levels of land-use intensity, probably indicating trophic links. Spatio-temporal changes in resource supply often require high vagility of resource dependent species (Tscharntke & Brandl 2004). Most of the trapped phytophages forage to a different extent in arable fields which are characterised by high spatio-temporal dynamics. To cope with these dynamics, high vagility may be an advantage especially in landscapes of low connectivity.

Conclusions

Hierarchical variability partitioning by means of partial CCA demonstrated high analytical power in decomposing the relative effects of nested sets of environmental variables across several spatial scales. The high variability in explanation power at different scales calls for a further focus on multi-scale research. Our results indicated relatively independent effects of agricultural management and landscape structure on the composition, structure and functioning of local arthropod communities. This provides great scope for application by conservation management. Changes in each of these factors might result in specific effects on local community composition and structure. Land-use intensity of agricultural fields explained most of the variability in species data. High intensity favoured large, small and omnivorous species while low intensity favoured medium sized species and predators as well as phytophages. Landscape characteristics of semi-natural elements explained most of the variability in size and trophic groups with connectivity as the dominating factor. According to dispersal ability and resource use, high connectivity favoured very small, small and saprophagous species, whereas low connectivity favoured large arthropods and predators as well as phytophages.

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Appendix A Species and individual numbers within size classes of the five arthropod taxa. Body size was obtained from the literature (carabid beetles: Freude, Harde & Lohse 1976; Lindroth 1985; Lindroth 1986; Wachmann, Platen & Barndt 1995; Turin 2000; spiders: Nentwig et al. 2003; bees: Amiet 1996; Scheuchl 1996; Müller, Krebs & Amiet 1997; Schmid-Egger & Scheuchl 1997; Amiet, Neumeyer & Müller 1999; Scheuchl 2000; Amiet et al. 2001; hover flies: Verlinden 1991; Speight 2003; bugs: Southwood & Leston 1959; Wagner 1961, 1966; Wagner & Weber, 1964; Péricart 1972, 1983, 1984, 1987, 1990, 1999; Moulet 1995; Wachmann et al. 2004).

Taxon	Size class	Size (mm)	Species	Individuals
Apidae	Very small	< 8.5	39	3,546
	Small	8.5 - 12.5	44	7,789
	Medium	12.5 - 15.5	23	8,820
	Large	> 15.5	9	2,163
Apidae Total			120	22,318
Araneae	Very small	< 3.0	88	33,264
	Small	3.0 - 5.0	35	9,103
	Medium	5.0 - 8.0	31	6,616
	Large	> 8.0	8	3,261
Araneae Total			175	52,244
Carabidae	Very small	< 5.5	40	10,359
	Small	5.5 - 9.0	62	19,073
	Medium	9.0 - 14.0	32	24,312
	Large	> 14.0	19	12,946
Carabidae Total			154	66,690
Heteroptera	Very small	< 4.0	38	6,166
	Small	4.0 - 6.0	32	4,892
	Medium	6.0 - 9.0	42	6,823
	Large	> 9.0	16	443
Heteroptera Total			128	18,324
Syrphidae	Very small	< 8.0	9	1,505
	Small	8.0 - 10.0	25	4,928
	Medium	10.0 - 13.0	10	1,745
	Large	> 13.0	7	1,203
Syrphidae Total			51	9,381
Grand Total			628	170,105

Appendix B Species and individual numbers within trophic guilds. Feeding habits were obtained from the literature (references in Appendix A).

Trophic position	Taxon	Species	Individuals
Omnivorous	Carabidae	4	7,731
	Heteroptera	30	5,083
	Syrphidae	2	351
Omnivorous total		36	13,165
Phytophagous	Apidae	120	22,797
	Carabidae	42	7,449
	Heteroptera	68	8,487
	Syrphidae	2	40
Phytophagous Total		232	38,773
Predacious	Araneae	175	52,748
	Carabidae	99	51,390
	Heteroptera	29	4,694
	Syrphidae	24	3,905
Predacious Total		327	112,737
Saprophagous	Syrphidae	24	5,145
Grand Total		628	170,105

7. Synthesis

7.1. Which factors determine biodiversity in agricultural landscapes?

Our studies emphasise that environmental change will affect biodiversity significantly at all major organisational levels. Population genetics, population structure, species richness (Billeter et al. 2005), community similarity, community composition and ecological community characteristics, all responded to environmental factors but in a specific way.

In order to address the fundamental question of which factors determine certain biodiversity levels, we disentangled the relative effects of single environmental factors that act on different spatial scales.

Scale of environmental factors

All three analysed levels of biodiversity (genetics, populations, communities) revealed a clear trend of increasing importance of scale from the local level to the landscape and finally to the region. The genetic diversity of the land snail *Cepaea nemoralis* was not affected by local features such as patch size or habitat diversity, whereas the observed metapopulation structure indicated a pronounced effect of landscape features (Chapter 3). The population response of the butterfly *Pararge aegeria* was a bit more complex. Under beneficial environmental conditions (high abundance scenario) the impact of local and landscape-scale factors was similar but low. However, adverse conditions (low abundance scenario) revealed an increasing effect of scale from local factors (suitable habitat) to landscape features (number of woody patches) and finally to regional factors (climate; Chapter 4). Likewise, the analysis of community turnover, species composition and ecological groups supported these findings and were remarkably similar even between arthropod groups that differ markedly in their ecology (Chapters 5 and 6).

These consistent results across major levels of biodiversity indicate general processes of community assembly supporting a top-down hierarchical theory of biodiversity (Whittaker, Willis, & Field 2001; Noda 2004). Two largely independent disciplines in ecology have addressed the relationship between the environment and biodiversity. Small scale community ecology considers species properties and focuses on interactions among species, and between species and their environment (e.g. competition, predation, parasitism, niche differentiation) while typically ignoring processes at larger scales. However, small scale community ecology failed in generating general rules of community assembly because of too much contingency and idiosyncrasy of specific systems (Lawton 1999; Blackburn & Gaston 2002). Macroecology, on the other hand, focuses on processes occurring at larger scales, while typically ignoring species specifics. Nevertheless, macroecology succeeded in deducing general rules such as species-area relationships, body size-range size-abundance relationships or energy input-species richness relationships (references in Lawton 1999). However, the majority of macroecological studies define ‘large scale’ by both a large extent and a low resolution (large grain; Blackburn & Gaston 2002) which circumvents predictions for local species assembly. This gap between community ecology and macroecology calls for a unification of theories that includes biological interactions as well as spatial patterns across a broad range of scales with a high resolution (Rahbek & Graves 2000; McGill & Collins 2003; Brose et al. 2004). A promising approach might consider the species pool concept where local biodiversity is determined by the regional species pool through a series of environmental filters (Zobel 1997; Hillebrand & Blenckner 2002; Butaye et al. 2002).

Our results support this concept and confirm the top-down hierarchical structure of these filters. Local diversity seems to be determined mostly by factors operating at regional scales such as climate or evolutionary and biogeographical history (Chapter 4). These large-scale factors modulate the regional species pool. In a next step, the species from the regional pool have to pass environmental filters that act at the landscape scale to colonise a particular local patch and to persist within the landscape (Chapters 3, 4, 5 and 6). In agricultural areas, our results indicate that agrarian land-use intensity and landscape structure represent most prominent filters. They affect populations and communities independently with more or less the same pressure (Chapter 6). When a species successfully passed through these filters, factors at the local scale such as habitat quality, resource supply or species interactions might affect population establishment and local persistence. However, it was shown that the effects of local habitat properties are less important compared to regional and landscape factors (Chapters 3, 4, 5 and 6).

Agrarian land-use intensity

As expected, the effects of agrarian land-use management on local community composition and species turnover were strong. Our results suggest that land-use intensification affects wild species according to niche breadth and dispersal ability as well. The increasing community similarity on intense agricultural landscapes is interpreted as increasing dominance of generalist species (Chapter 5) which is supported by the association between high intensity levels and omnivorous species (Chapter 6). On the other hand, the interaction of pesticide application and habitat fragmentation on community similarity (Chapter 5) as well as the independent effect of spatial components of land-use practices on community composition (Chapter 6) indicate effects operating over dispersal.

An ongoing discussion debates whether it is ‘niche assembly’ or ‘dispersal assembly’ that drives local community composition (Williams, Jones, & Hartley 2001; Brandle & Brandl 2001; Hubbell 2001; Brandle, Ohlschlager, & Brandl 2002; Whitfield 2002; Yu et al. 2004; Potts et al. 2004). Niche-assembly theories posit that environmental heterogeneity and biological interactions are responsible for species coexistence and community structure (Weiher & Keddy 1999; Klausmeier 2001; Williams, Jones, & Hartley 2001). In contrast, neutral dispersal-assembly theories hypothesise that chance, history and dispersal explain species coexistence and community structure (Bell 2001; Hubbell 2001).

However, including species identities or their ecological characteristics into the analysis, our results did not support a dichotomy between these two theories. Moreover, the interaction between pesticides and fragmentation and the independent, similarly strong effects of stress and spatial land-use factors suggests interdependency between niche- and dispersal-assembly.

Landscape structure

In agricultural areas, the filter effect of landscape structure seems to be similarly strong as that of land-use intensity. The observed genetic patterns in the land snail *Cepaea nemoralis* were a consequence of a metapopulation structure because of dispersal limitation in a fragmented landscape (Chapter 3). In this case, no resource limitation (according to niche-assembly theory) was evident as neither patch size nor other patch characteristics affected genetic diversity. In contrast, population analysis of the butterfly *Pararge aegeria* supported interdependency of niche- and dispersal- assembly as local habitat quality interacted with landscape features (at least under adverse conditions; Chapter 4). Both community similarity and composition indicated niche- as well as dispersal-assembly (Chapters 5 and 6). However, the effect of dispersal seems to dominate in structuring local communities. This was indicated by the observed strong effect of fragmentation on species turnover and community composition (i.e. for size classes).

In a review of studies on the effects of fragmentation on biodiversity, Fahrig (2003) concluded that habitat loss, rather than fragmentation *per se*, negatively affects biodiversity. She reported that fragmentation had as many positive as negative effects. In our studies of community composition, we followed her suggestions to investigate habitat loss and fragmentation independently. In contrast to Fahrig´s conclusion, it was shown that fragmentation *per se* was the dominant landscape factor for most of the investigated species groups in the European agricultural landscape (Chapter 6). Thus, habitat fragmentation *per se* and therewith dispersal is most likely one of the main drivers of biodiversity that operates at the landscape scale.

Conclusion

The analysis of biodiversity in agricultural landscapes across organisational levels and spatial scales supported a top-down hierarchical theory of biodiversity. It predicts that local communities are assembled from a regional species pool, which is modulated by large-scale factors such as climate or evolutionary and biogeographical history, through a series of hierarchical filters at the landscape scale and, to a lower extent, at the local scale according to both dispersal- and niche-assembly processes. Dispersal is suggested to be one of the main drivers of biodiversity at the landscape scale. Consequently, land-use change that affects the connectivity of habitats will significantly affect biodiversity by diminishing or even disrupting genetic, population and community processes.

However, real species are not entirely neutral as the effects of niche-assembly related processes showed. This calls for a further unification of biodiversity theories that should consider species identities and their ecological role as well as their dispersal ability and spatial patterns across a variety of spatial and temporal scales if one wants to understand the multifaceted manifestations of live.

7.2. References

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8. Summary – Zusammenfassung

Biodiversität ist eine der fundamentalen Erscheinungsformen des Lebens. Dessen ungeachtet unterliegt die Vielfalt des Lebens einer zunehmenden weltweiten Bedrohung durch menschliche Aktivitäten. Unter der Vielzahl von Ursachen liegt die Intensivierung der Landnutzung an vorderster Stelle. In Europa ist Landwirtschaft die dominierende Landnutzungsform mit erheblichen Auswirkungen auf die Biodiversität. Dünger und Pestizide auf den Agrarflächen beeinflussen die Biodiversität ebenso wie der Anteil und die räumliche Anordnung von natürlichen und naturnahen Habitaten. Die meisten Untersuchungen zur Beziehung zwischen Landnutzung und Biodiversität konzentrierten sich bisher auf Artenzahlen. Die Vielfalt des Lebens äußert sich jedoch nicht nur in Artenzahlen pro Fläche, sondern besteht aus einer Vielzahl an Komponenten. Biodiversität manifestiert sich auf der Ebene von Genen, Individuen, Populationen, Lebensgemeinschaften und Ökosystemen und auf unterschiedlichen räumlichen Skalen.

Ziel dieser Dissertation ist, die Auswirkungen von unterschiedlichen Landnutzungsformen auf drei wichtige organisatorische Ebenen der Biodiversität über mehrere Skalenbereiche hinweg zu untersuchen: Gene, Populationen und Lebensgemeinschaften. Dazu wurden vier Detailstudien im Rahmen des EU-Projekts ‚GREENVEINS – Vulnerability of Biodiversity in the Agroecosystem as influenced by Green Veining and Land-use Intensity' in 25 Agrarlandschaften in sieben Europäischen Ländern vorgenommen, die unabhängige Gradienten der Landschaftsstruktur und der agrarischen Nutzungsintensität bildeten.

Der erste Teil der Dissertation beschäftigt sich mit der räumlichen genetischen Struktur der Landschnecke *Cepaea nemoralis* (L.) in einer fragmentierten Agrarlandschaft. Wir untersuchten genetische und morphologische Merkmale auf lokaler Skala entlang eines Transekts von 500 m und auf Landschaftsskala in einer Untersuchungsfläche von 4 x 4 km. Analysen von Mikrosatelliten Loci sowie von morphologischen Merkmalen ergaben eine räumliche Strukturierung auf beiden Skalen und erbrachten Hinweise auf eine Metapopulationsstruktur. Eine Beziehung zwischen genetischer und morphologischer Diversität deutete auf *bottleneck effects* aufgrund von Wiederbesiedelungsereignissen durch eine geringe Zahl von Migranten. Unsere Studie legt nahe, dass die Metapopulationsstruktur sowohl von der Landschaftsstruktur als auch von der Form der Dispersalfunktion abhängt. Die räumliche Autokorrelation sowohl der genetischen als auch der morphologischen Merkmale reichte lokal bis 80 m und auf Landschaftsebene bis 800 m und deutete auf eine leptokurtische Art des Dispersal. Die Metapopulationsstruktur von *C. nemoralis* in einer fragmentierten Agrarlandschaft äußert sich demnach in einem Netz von lokalen Populationen die einer Dynamik von lokalem Aussterben und Wiederbesiedelung unterliegen. Entsprechend der Landschaftsstruktur und der Dispersalfähigkeit ergibt sich die räumliche genetische Struktur, wobei mit zunehmender Distanz die genetische Drift den homogenisierenden Einfluss des Genflusses überwiegt.

Der zweite Teil der Dissertation untersucht das lokale Vorkommen von Populationen des Schmetterlings *Pararge aegeria*, der aufgrund der engen Bindung an natürliche und naturnahe Habitate als Modellorganismus ausgewählt wurde. Die räumliche Verteilung des Schmetterlings wurde in 23 Agrarlandschaften erfasst. Umweltvariablen wurden auf lokaler Skala (Radius von 250 m) und Landschaftsskala (5 x 5 km) aufgenommen. Wir erstellten logistische Regressionsmodelle für zwei Umweltszenarien. Das ‚High Abundance Scenario' war durch günstige Umweltbedingungen und entsprechend hohe lokale Abundanzen charakterisiert, wohingegen das ‚Low Abundance Scenario' durch ungünstige Umweltbedingungen (vor allem während der Larvalentwicklung) und entsprechend niedrige Abundanzen gekennzeichnet war. Unter dem ‚High Abundance Scenario' war der Einfluss von lokalen und regionalen Umweltvariablen gleichermaßen gering und das Modell sagte eine generell hohe Antreffwahrscheinlichkeit für *P. aegeria* nahezu unabhängig von lokalen oder regionalen Umweltfaktoren voraus. Völlig andere Verhältnisse zeigten sich unter dem ‚Low Abundance Scenario'. Hier konnten wir starke Effekte von lokalen und regionalen Faktoren beobachten, wobei klimatische Einflüsse dominierten. Das Modell sagte eine Begrenzung sowohl auf *patches* als auch auf Landschaften mit hoher Qualität voraus. Die ausgeprägten Unterschiede in beiden Umweltszenarien deuten darauf hin, dass sich die Ansprüche von *P. aegeria* an einzelne Umweltfaktoren wie der Landschaftsstruktur entsprechend allgemeiner Umweltbedingungen stark ändern können. So kann z.B. ein Fragmentierungsgrad, der unter günstigen klimatischen Bedingungen keinen Einfluss auf die Populationsstruktur hat, unter ungünstigen klimatischen Bedingungen zum limitierenden Faktor werden.

Der dritte Teil der Dissertation untersucht die Ähnlichkeit von lokalen Lebensgemeinschaften in Abhängigkeit von unterschiedlichen Landnutzungsformen, wobei nicht nur die Artenzahl sondern auch deren Identität und Abundanz berücksichtigt werden. Wir untersuchten die Ähnlichkeiten in Lebensgemeinschaften von Pflanzen, Vögeln (Aves), Bienen (Apidae), Wanzen (Heteroptera), Laufkäfern (Carabidae), Schwebfliegen (Syrphidae), und Spinnen (Araneae) in 25 Agrarlandschaften. Nach einer Korrektur auf Habitattypen und lokale Artenzahlen zeigte sich, dass Habitatfragmentierung die Ähnlichkeit zwischen lokalen Lebensgemeinschaften von Pflanzen und Wanzen und somit den Austausch von Arten negativ beeinflusst. Bei Bienen und Spinnen zeigte sich der negative Einfluss von Habitatfragmentierung nur bei geringem Pestizideinsatz. Die hochmobilen Vögel und Schwebfliegen aber auch die Laufkäfer reagierten nicht auf Fragmentierung. Die Reaktionen der Einzelnen Gruppen auf Intensivierung der Landwirtschaft (Pestizide) waren unterschiedlich, wobei Interaktionen mit Habitatfragmentierung (Bienen, Wanzen, Spinnen) gegenläufige Mechanismen anzeigten. In intensiv genutzten Landschaften führt Fragmentierung zu einem verringerten Austausch zwischen den lokalen Lebensgemeinschaften und somit zu einer geringen Ähnlichkeit. Gleichzeitig bedingt aber ein hoher Pestizideinsatz und ein geringer Anteil an naturnahen Habitaten eine Erhöhung der Ähnlichkeit, die wahrscheinlich auf eine Dominanz von Generalisten zurückzuführen ist. Die relative Empfindlichkeit einzelner Organismengruppen gegenüber beiden Prozessen bestimmt die jeweilige Reaktion der Ähnlichkeit der Lebensgemeinschaften auf eine Intensivierung der Landnutzung.

Der vierte Teil der Dissertation untersucht die relative Bedeutung einzelner Landnutzungsfaktoren über drei verschiedene Skalen auf die organismische und ökologische Zusammensetzung von lokalen Lebensgemeinschaften. Wir untersuchten Bienen (Apidae), Wanzen (Heteroptera), Laufkäfer (Carabidae), Schwebfliegen (Syrphidae), und Spinnen (Araneae) in 24 Agrarlandschaften. Die Beziehungen zwischen den Lebensgemeinschaften und den Umweltvariablen wurden mittels hierarchischer

Varianzpartitionierung mit einer Reihe partieller canonischer Correspondenzanalysen (CCA) untersucht, wobei 16 Umweltvariablen zu acht Untergruppen und diese wiederum zu vier Hauptgruppen (Land, Landnutzungsintensität, Landschaftsstruktur, lokale Habitateigenschaften) zusammengefasst wurden. Die vier Hauptgruppen deckten drei Skalenbereiche ab (Region, Landschaft, Lokal). Die Untersuchungen zeigten eine Zunehmende Bedeutung der Umweltvariablen mit der Skala, auf der sie erfasst wurden. Nachdem für regionale Effekte (und somit auf den Artenpool) korrigiert wurde, dominierten Landschaftsfaktoren über lokale Faktoren. Agrarische Landnutzung erklärte den größten Teil der Variabilität in der Artenzusammensetzung, während Landschaftsfaktoren (vor allem Konnektivität) den größten Teil der Variabilität in der Körpergröße und trophischen Position erklärten. Unsere Ergebnisse weisen auf eine Unabhängigkeit der Effekte von agrarischer Landnutzung und der Landschaftsstruktur für alle untersuchten Arthropodengruppen hin, sodass Änderungen einzelner Faktoren spezifische Änderungen in der Struktur der Lebensgemeinschaften entsprechend der Dispersalfähigkeit und Ressourcennutzung einzelner Arten bedingen.

Die vier Detailstudien haben gezeigt, dass Änderungen in der Landnutzung die Biodiversität auf allen organisatorischen Ebenen beeinflussen. Um die zentrale Frage zu beleuchten, welche Faktoren die jeweilige Biodiversitätskomponente maßgeblich beeinflussen, versuchten wir die einzelnen Umweltfaktoren und deren Skalen zu entwirren.

Alle drei untersuchten organisatorischen Ebenen zeigten, dass der Einfluss eines Umweltfaktors auf lokale Lebensgemeinschaften mit der Skala steigt, auf der er wirkt. Die Ergebnisse unterstützen eine Theorie der Biodiversität, die eine hierarchische *top-down* Kontrolle annimmt und somit zu einem Brückenschlag zwischen den Sichtweisen von Makroökologen und *Community*-Ökologen führen könnte. Einen viel versprechenden Ansatz könnte das Artenpool-Konzept darstellen, das besagt, dass lokale Diversität durch eine Serie von hierarchisch wirkenden Filtern determiniert wird, die entweder makroökologisch oder *community*-ökologisch wirken. Unsere Ergebnisse zeigen, dass die Diversität hauptsächlich durch Faktoren bestimmt wird, die auf regionaler Skala wirken wie Klima oder die biogeografische Geschichte. Diese Faktoren bestimmen den regionalen Artenpool, aus dem sich die lokalen Lebensgemeinschaften rekrutieren, wobei sie eine weitere Reihe an Umweltfiltern passieren müssen. In Agrarlandschaften stellen agrarische Landnutzung und die Landschaftsstruktur wichtige Filter auf der Landschaftsebene dar. Hat eine Art diese Filter passiert, kommen Faktoren der lokalen Skala wie Habitatqualität oder biologische Interaktionen zum tragen, wobei die lokale Habitatqualität allerdings von geringerer Bedeutung zu sein scheint als Faktoren der Landschaftsskala.

Die Effekte von agrarischer Landnutzung und Landschaftsstruktur auf lokale Lebensgemeinschaften waren voneinander unabhängig und annähernd gleich groß. Die Analyse der Einzelfaktoren und den Reaktionen aller Biodiversitätskomponenten deutete darauf hin, dass sowohl Ressourcenlimitierung als auch Dispersallimitierung die Zusammensetzung lokaler Lebensgemeinschaften determinieren. Unsere Ergebnisse legen allerdings nahe, dass Dispersallimitierung in Agrarlandschaften einen größeren Einfluss hat als Ressourcenlimitierung, was Dispersal und somit Habitatfragmentierung zu einer der wichtigsten Einflussgrößen auf alle Organisationsebenen der Biodiversität macht.

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Halle, 2005 Oliver Schweiger

10. Appendix

10.1. Declaration of self-contained work

Herewith I affirm that I composed the Dissertation

Hierarchical top-down control of biodiversity in agricultural landscapes across organisational levels and spatial scales

single handed without utilising illegitimate resources. I used no other than the cited references and facilities. This work has not been previously handed in to another university and was not subject to miscellaneous examinations.

Oliver Schweiger Halle, 07.01.2005

10.2. Curriculum vitae

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Personal information

Date of birth	21.11.1969
City, Country	Salzburg, Austria
Languages	German / English
Current position	PhD student

Education

1988-99	Studies of zoology and ecology at the University of Salzburg, Austria
1991	Ecoterrestrial field course at the research station in Gastein, Austria
1997	Research stay at the National Park Bayerischer Wald, Germany
1999	Diploma thesis in animal ecology, graduated with honours at the Department of Zoology, University of Salzburg, Austria
2001-05	PhD student at the Department of Animal Ecology, University of Marburg, Germany

Research experience and interests

- **Animal ecologist with a focus on insects**
- Diploma thesis: “Ground beetle communities (Carabidae, Col.) within the scope of natural succession on windfall areas in the National Park Bayerischer Wald”
- PhD thesis: “Hierarchical top-down control of biodiversity in agricultural landscapes across organisational levels and spatial scales”
- Since 2001 working at the UFZ – Centre for Environmental Research Leipzig-Halle
- Since 2001 involved in the EU research project ‘Greenveins’, species coordinator
- Terrestrial biodiversity research across organisational levels and spatial scales:
  - Population genetics and dynamics (fragmentation – dispersal)
  - Community ecology (disentangling scale and environmental factors)
  - Ecosystem functioning (function – reliability)
  - Macroecology (general rules)

Skills

Genetic laboratory	Microsatellite analysis; ABI 310 genetic analyser
Genetic data analysis	GENOTYPER; GENEPOP; ARLQUIN; MSA; STRUCTURE, SPAGEDI
Landscape data analysis (GIS)	ARCVIEW; FRAGSTATS
Ecological data analysis	Univariate and multivariate analysis; spatial statistics; variability partitioning; habitat modelling
Statistical software	R; SPSS; STATISTICA; CANOCO; SIGMAPLOT
Research co-ordination	Species co-ordinator within the EU research project GREENVEINS

Publications

Refereed journals:

Schweiger O, Frenzel M, Durka W (2004) Spatial genetic structure in a metapopulation of the land snail *Cepaea nemoralis* (Gastropoda: Helicidae). *Molecular Ecology*, **13**: 3645-3655.

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Frenzel M, Schweiger O (2004) Diversity patterns of bird communities in agricultural landscapes. *Verhandlungen der Gesellschaft für Ökologie* **33**: 188.

Posters:

Schweiger O, Frenzel M (2002) Effects of land use intensity and “green veining” on arthropod communities. *Verhandlungen der Gesellschaft für Ökologie* **32**: 62.

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Schweiger O (2002) Carabid beetle communities in natural successions on windfall areas. *Zoology* **105** Supplement V (DZG 95.1): 73.