Biodiversity and Conservation **13:** 1427–1439, 2004.

Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands

JOCHEN KRAUSS*, ALEXANDRA-MARIA KLEIN,
INGOLF STEFFAN-DEWENTER and TEJA TSCHARNTKE
Department of Agroecology, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany;
**Author for correspondence (e-mail: j.krauss@uaoe.gwdg.de; fax: +49-551-398806)*

Received 18 November 2002; accepted in revised form 15 May 2003

Key words: Conservation, Generalists, Habitat fragmentation, Specialists, Species density, Species–area relationships

Abstract. Calcareous grasslands harbour a high biodiversity, but are highly fragmented and endangered in central Europe. We tested the relative importance of habitat area, habitat isolation, and landscape diversity for species richness of vascular plants. Plants were recorded on 31 calcareous grasslands in the vicinity of the city of Göttingen (Germany) and were divided into habitat specialist and generalist species. We expected that habitat specialists were more affected by area and isolation, and habitat generalists more by landscape diversity. In multiple regression analysis, the species richness of habitat specialists ($n = 66$ species) and habitat generalists ($n = 242$) increased with habitat area, while habitat isolation or landscape diversity did not have significant effects. Contrary to predictions, habitat specialists were not more affected by reduced habitat area than generalists. This may have been caused by delayed extinction of long-living plant specialists in small grasslands. Additionally, non-specialists may profit more from high habitat heterogeneity in large grasslands compared to habitat specialists. Although habitat isolation and landscape diversity revealed no significant effect on local plant diversity, only an average of 54% of habitat specialists of the total species pool were found within one study site. In conclusion, habitat area was important for plant species conservation, but regional variation between habitats contributed also an important 46% of total species richness.

Introduction

Habitat loss and habitat fragmentation of natural and semi-natural habitats are considered as major threats to biodiversity. Semi-natural calcareous grasslands belong to the most species-rich plant and insect habitats in central Europe (Van Swaay 2002; WallisDeVries et al. 2002). Habitat loss of calcareous grasslands in Germany reached locally up to 60% in the last 100 years. Thereby, 1% of the plant species restricted to this habitat type became extinct and 42% are threatened in Germany (WallisDeVries et al. 2002). Calcareous grasslands are highly fragmented, endangered, and nowadays protected by law in Germany (Riecken et al. 1994). Interest in conservation is high (Beinlich and Plachter 1995; WallisDeVries et al. 2002), leading to several studies on plant and insect community structure and extinction risks (e.g. Fischer and Stöcklin 1997; Bruun 2000; Zschokke et al. 2000; Krauss et al. 2003). However, a recent review emphasises the lack of well-replicated community level studies on calcareous grasslands (Steffan-Dewenter and Tscharntke 2002).

Habitat fragmentation is a major threat for plant species richness (e.g. Ouborg 1993; Grashof-Bokdam 1997; Honnay et al. 1999; Bruun 2000). The influence of landscape context in habitat fragmentation studies is often ignored (Wiens 1997; Hanski 1999), although it is essential to understand plant community dynamics (De Blois et al. 2002). Habitat isolation might be seen as a simple measure of landscape context, as it describes the distance to neighbouring habitats or the proportion of the habitats of a certain type within a landscape (see Moilanen and Nieminen 2002). But landscape context includes more factors that may affect local communities, as there is the proportion of other habitat types or the diversity of habitats in the landscape matrix (Steffan-Dewenter et al. 2002). Similar habitats and high habitat diversity in the surroundings might enhance species richness of a local site. Landscape context might affect gene flow via pollen and seed dispersal, the pressure of herbivory, and the functional connectivity between habitat patches (Ricketts 2001). Recently published studies started to focus on the complex effects of landscape context on local plant species richness (Kollman and Schneider 1999; Metzger 2000; Söderström et al. 2001).

Not all species depend on habitat area, isolation and landscape context equally (Tscharntke et al. 2002). (1) Habitat specialists are more affected by habitat loss than generalists, (Warren et al. 2001). (2) The surrounding landscape is inhabitable for habitat specialists, but at least partly habitable for generalists, supporting the prediction that habitat isolation affects habitat specialists more than generalists (see Jonsen and Fahrig 1997). (3) High landscape diversity in the surrounding matrix provides more different habitat types for generalists or species with other habitat preferences, supporting the prediction that landscape diversity enhances the number of generalists, especially at edges, but hardly specialists (see Jonsen and Fahrig 1997). These predictions have rarely been tested for plant communities in the context of spatial dynamics. True forest species showed a stronger response to habitat area than other species, but no response to habitat isolation (Honnay et al. 1999), and shade tolerant species were more sensitive to habitat fragmentation than shade intolerant species (Metzger 2000). Numerous functional groups, including specialist grassland species, were positively related to habitat area and inconsistently to isolation (Bruun 2000).

Species–area relationships can be explained by two ecological hypotheses. (1) The habitat heterogeneity hypothesis predicts higher species numbers because of higher habitat heterogeneity. (2) The area per se or equilibrium hypothesis considers colonisation–extinction dynamics to cause increasing species numbers with increasing habitat area independent of habitat heterogeneity (Rosenzweig 1995). Habitat area and habitat heterogeneity are often closely correlated (Kohn and Walsh 1994; Rosenzweig 1995; Köchy and Rydin 1997). Equal sample sizes should reduce the habitat heterogeneity effect, making it possible to test separately for area per se effects (Kelly et al. 1989; Köchy and Rydin 1997).

In this study we tested the impact of the three parameters habitat area, habitat isolation, and landscape diversity on the species richness of habitat specialist and generalist vascular plants on calcareous grasslands.

We tested the following predictions:

(1) Plant species richness increases with increasing habitat area, decreasing habitat isolation and increasing landscape diversity.
(2) Species richness of habitat specialists is more sensitive to habitat area and isolation, whereas species richness of generalists is more sensitive to landscape diversity.
(3) Species density, that is, plant species richness per area in samples of equal size on all study sites, is related to habitat area, isolation and landscape diversity.

Materials and methods

Study region and study sites

Altogether 31 calcareous grasslands in the vicinity of the city of Göttingen in Lower Saxony (Germany) were studied. The grasslands were located in the Leine-Weser Mountain lands (Gauss-Krüger: $R = 5695$, $H = 3550/R = 5724$, $H = 3579$) and belong to the plant association *Gentiano-Koelerietum*. Low impact management to stop succession and to remove woody bushes was carried out on the study sites mainly from late summer to winter. The average rainfall in the area around Göttingen is 635 mm per annum, with an average temperature of 6.8 °C (Deutscher Wetterdienst 2001). The landscape is structurally rich with a mosaic of diverse habitat types. Calcareous grasslands can be sharply delimited from the surrounding landscape with little or no ambiguity and cover 0.26% of the study region.

Habitat area, isolation, landscape diversity

The area of the 31 calcareous grasslands was measured with a differential GPS GEOmeter 12L (GEOsat GmbH 1998) and ranged from 314 to 51395 m^2. Area covered with shrubs was excluded from the measurement.

Habitat isolation was measured as an index (I) of each study site (i) from edge to edge on the basis of all known calcareous grasslands in a radius of 8 km around our study sites using the following formula:

$$I = \Sigma e^{-dij} A_j$$

where A_j is the size (in m^2) of neighbouring calcareous grasslands and dij the distance (in km) from the neighbouring grassland j to the study site i. The formula is based on Hanski et al. (1994). Larger values of I indicate lower isolation than smaller values. Additionally, habitat isolation was measured as distance from edge to edge to the nearest calcareous grassland (55–1894 m). This isolation distance and the isolation index were always $\log_{10}$ transformed. Both were correlated ($r = -0.445$, $n = 31$, $P = 0.012$) and showed similar, always non-significant results. Therefore we show only the results from the isolation index.

Landscape diversity was analysed using modified digital thematic maps (ATKIS®-DLM 25/1 Landesvermessung and Geobasisinformationen Niedersachsen 1991–1996, and ATKIS®-DLM 25/2 Hessisches Landesvermessungsamt 1996). Eleven land-use types were defined, including arable land (42.15% of the study region), forest (36.80%), grassland (12.14%), built-up area (6.24%), other habitats (1.48%), garden land (0.31%), hedgerow (0.30%), calcareous grassland (0.26%), orchard meadow (0.20%), plantation (0.06%), and fen (0.05%). We used the Shannon–Wiener index to calculate landscape diversity for each of the 31 grassland fragments using a nested set of 12 circles with a radius ranging from 0.25 to 3.00 km in 0.25 km steps:

$$Hs = -\Sigma p_i * \ln p_i$$

where p_i is the proportion of each of the 11 different land-use types (Krebs 1989).

Further we pooled the plant species-rich habitat types, grassland, garden land, hedgerow, calcareous grassland, orchard meadow, and fen around the study sites. We related the different plant species richness data with the proportion of this pooled habitat type data set. We never found any positively significant relation between both, and the pooled habitat types were highly correlated with landscape diversity (250 m scale: $r = 0.685$, $P < 0.0001$). Therefore we only show results from landscape diversity.

Due to some missing ATKIS data we could test the landscape data for a radius of 0.25 and 0.50 km for all 31 study sites, while 0.75–2.00 km scales were tested for only 30, 2.25 km for 29, and 2.50–3.00 km for 28 sites. For each landscape analysis, the habitat area of the central study site was excluded.

Plants

The complete survey of vascular plants (Spermatophyta plus *Equisetum arvense* L.) for all of the 31 calcareous grasslands was compiled from four independent data sets from 1996, 2000 and 2001 to achieve a total list of plant species per study site. In 1996 and 2000 the vegetation was mapped in May/June and again in August in randomised plots of 25 m^2 according to Braun-Blanquet. These plots were the same for both records in 1996, while they changed in 2000. In 1996 one plot was mapped for small ($>1500\,m^2$), two plots for medium ($1500–5000\,m^2$), three plots for medium to large ($5000–1\,0000\,m^2$) and four plots for large grasslands ($>10\,000\,m^2$) (see Steffan-Dewenter and Tscharntke 2000). In 2000 one plot was mapped on small grasslands ($<1500\,m^2$), two plots on medium grasslands ($1500–10000\,m^2$), and three plots on large grasslands ($>10000\,m^2$). To complete these two Braun-Blanquet surveys, in 2000 between April and August we mapped five times the plant species in flower of each grassland on randomised transects. Each transect covered from 11.4% (largest habitat) to 100.0% (small habitats) of the total habitat area (average: 62.7 ± 0.4%). In a fourth survey in May 2001, again plants were mapped on the 31 grasslands to complete the species list.

We used the total number of species per grassland for statistical analyses. To compare equal sample sizes (species density) we also tested all correlations using only one 25 m^2 plot (mapped in spring and summer) of the 2000 data set.

All vascular plant species recorded as species restricted to oligotrophic grasslands in Von Drachenfels (1994) were defined as habitat specialists ($n = 66$) for calcareous grasslands (see Appendix 1). These species mainly occur on calcareous grasslands in the study region, but might inhabit other habitat types in other regions of Germany and Europe. All other species with no habitat preferences or preferences for other habitats were defined as generalist plants (242 species). Species identification and nomenclature follow Bässler et al. (1999).

Statistical analyses

The statistical analyses of the data were performed using the software 'Statgraphics Plus for Windows 3.0' (Statgraphics 1995). All data were tested on whether they satisfy the assumption of normality. We calculated simple and multiple regressions, Pearson correlations, and comparisons of regression lines (Sokal and Rohlf 1995). We chose backward selections for stepwise multiple regressions. The independent variables habitat area and isolation were always $\log_{10}$ transformed. Species numbers in regressions were also $\log_{10}$ transformed to calculate scale-independent slopes (z-values) for comparison with other studies. Arithmetic means ± one standard error are given in the text.

Results

Habitat area (0.03 – 5.14 ha, average: 0.90 ± 0.23 ha) was not correlated with habitat isolation (index: 2051 – 85 978, average: 23 019 ± 3368) ($r = -0.013$, $P = 0.944$). Also landscape diversity (at a 250 m scale; Shannon–Wiener: 0.09–1.56, average: 1.09 ± 0.05) was not correlated with habitat isolation ($r = -0.015$, $P = 0.936$), but with habitat area ($r = 0.375$, $P = 0.038$).

Altogether 308 plant species were identified on all 31 calcareous grasslands with pooled data. This was an average of 89.0 ± 3.7 species per habitat with a minimum of 56 species and a maximum of 138 species. In Braun-Blanquet plots we found 192 species in 1996 and 234 species in 2000, resulting in a total of 278 species. Additional recordings due to the transect walks in 2000 and the survey in 2001 resulted in a total of 308 species. Nine of 66 (13.6%) specialist species (see Appendix 1) and seven out of 242 (2.9%) habitat generalist species (*Achillea millefolium* L., *Campanula rotundifolia* L., *Daucus carota* L., *Leontodon hispidus* L., *Lotus corniculatus* L., *Plantago lanceolata* L., and *Plantago media* L.) were found on each of the 31 calcareous grasslands. A minimum of 33% and a maximum of 67% of habitat specialists of the 66 specialists were found within one study site. On average, per study site 54% of all specialist species was found, emphasising that 46% of total species richness was due to between-habitat variation (see Veech et al. (2002) for calculations of β-diversity).

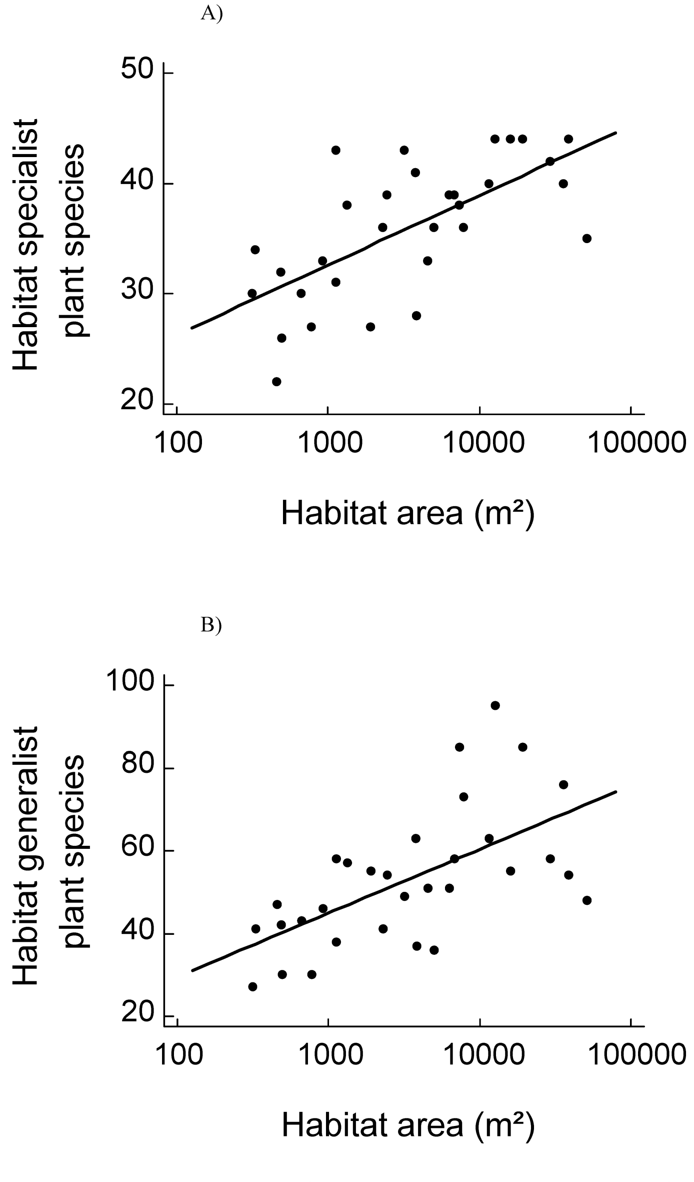

Figure 1. Relationship between the number of plant species and grassland area ($n = 31$ fragments). (A) Specialist plant species (66 species): $y = 13.64 + 6.32 \log_{10} x$. (B) Generalist plant species (242 species): $y = -1.40 + 15.44 \log_{10} x$. For statistics see Table 1. Comparison of regression lines: slopes: $F = 5.34$, $P = 0.024$.

Species richness increased with increasing habitat area for both habitat specialist and generalist species, leading to an increase of all species (Figure 1, Table 1). The *z*-value (slope of log–log regressions) for specialists (*z*-value: 0.08) was lower than

Table 1. Simple regressions for the habitat specialists among the plant species (66 species), generalist species (242 species) and all plant species (308 species). Relations between species numbers and species density with the three independent factors habitat area, habitat isolation, and landscape diversity ($n = 31$). Habitat area and habitat isolation are $\log_{10}$ transformed.

	Habitat area			Habitat isolation			Landscape diversity (radius: 250 m)		
	F	*r*	*P*	*F*	*r*	*P*	*F*	*r*	*P*
Total species numbers									
Habitat specialists	23.49	0.669	<0.0001	0.39	−0.116	0.536	3.81	0.341	0.061
Habitat generalists	17.18	0.610	0.0003	0.95	−0.178	0.337	0.16	0.074	0.692
All plants	24.67	0.678	<0.0001	1.04	0.186	0.316	0.76	0.160	0.390
Species density									
Habitat specialists	0.09	0.054	0.773	0.39	−0.116	0.535	0.00	−0.008	0.965
Habitat generalists	0.02	0.028	0.879	0.00	0.012	0.950	0.00	0.004	0.981
All plants	0.06	0.046	0.807	0.11	0.061	0.744	0.00	−0.000	0.999

for generalists (z-value: 0.13), but did not differ significantly (comparison of regression lines $F = 2.16$, $P = 0.148$). The slope for not log-transformed species numbers was even significantly steeper for generalists (Figure 1). For all plant species the z-value was 0.11. Habitat isolation showed no significant effect on species richness in simple regressions, while landscape diversity at the smallest scale of 250 m was positively related to specialist species with marginal significance (Table 1). We analysed the effects of landscape diversity at 12 nested spatial scales. Correlations were highest at the smallest spatial scale of 250 m for specialist, generalist and all plants (results for other spatial scales are not shown).

In multiple regressions with habitat area, isolation and landscape diversity (250 m), habitat area was the only significant factor explaining 44.8% of variation for specialists, 37.2% for generalists and 46.0% for all plant species.

Considering only equal sample size with one plot per grassland, we found altogether 199 plant species. This was an average of 46.5 ± 1.4 species per habitat with a minimum of 30 species and a maximum of 63 species. Neither in simple (Table 1) nor in multiple regressions we found evidence for an impact of habitat area, isolation, and landscape diversity on plant species density for specialists, generalists or all plants on the studied 31 calcareous grasslands.

Discussion

Landscape diversity is known to increase generalist insect species numbers (Jonsen and Fahrig 1997; Krauss et al. 2003), but did not affect the number of generalist plants in our study. Increasing landscape diversity even tended to increase specialist plant species numbers, but due to correlation with habitat area this effect was eliminated in multiple regressions. We also could not detect an effect of landscape on total plant species richness. This might be explained by the relatively complex landscapes that surrounded our calcareous grasslands. In multiple tests for different landscape parameters and numerous functional groups, inconsistent results of correlations of plant species richness with landscape diversity were reported (Kollman and Schneider 1999; Metzger 2000). To reduce multiple testing and intercorrelations of landscape factors, Steffan-Dewenter et al. (2002) suggest focusing on landscape diversity and proportion of habitats in the surrounding matrix. Söderström et al. (2001) found lower plant species numbers on semi-natural pastures with increasing proportion of arable fields in the surrounding landscape, but landscape diversity was not studied. In general, landscape studies on plant species composition are still rare, but essential to fully understand community dynamics (De Blois et al. 2002).

Species numbers increased significantly with increasing habitat area for both habitat specialist and habitat generalist plant species. Our results confirm the general validity of species–area relationships, as shown before for plant communities (e.g. Ouborg 1993; Grashof-Bokdam 1997; Honnay et al. 1999; Bruun 2000). Our high sampling effort appeared to guarantee almost complete recordings. In addition, our numbers of plant species on 27 of the grasslands were very similar to a complete survey made between 1980 and 1986 (Eggers 1986, unpublished data; B. Preuschoff, personal communication). We did not measure habitat heterogeneity, but species density, that is, species numbers measured with equal sample sizes on all grasslands, was not affected by habitat area in our study, giving indirect evidence for the habitat heterogeneity hypothesis as an explanation for species–area relations (Kelly et al. 1989; Holt et al. 1999). Habitat heterogeneity is assumed to be the main predictor for plant species richness (Köchy and Rydin 1997), as neither Köchy and Rydin (1997) nor Lawesson et al. (1998) found positive species–area relations for area-corrected sample sizes.

Surprisingly, habitat specialists were not more affected by habitat area than generalists. This is in contrast to previous findings for specialist and generalist plant species, where the z-value was higher for true forest plant species ($z = 0.45$) than for species of edges and clearings ($z = 0.39$) and for woody species and lianas ($z = 0.17$) in Belgium forests (Honnay et al. 1999). Also habitat specialist butterflies on the same calcareous grasslands were significantly more affected by habitat loss than generalists (Krauss et al. 2003). Large areas with high habitat heterogeneity can be expected to offer a diverse mosaic of microhabitat types for species that are non-specialists. This may explain the steeper species–area relationships for generalists in our study. Habitat specialists are expected to have higher extinction rates than generalists, as shown for plants and butterflies (Fischer and Stöcklin 1997; J. Krauss, unpublished data). However, when these specialists are perennial plants, they may persist for several years in small populations, thereby delaying their extinction (Oostermeijer et al. 1994). An extinction debt for these species in small habitats keeps the z-value lower than in equilibrium situations (Tilman et al. 1994; Gonzales 2000). Hypotheses developed for mobile birds and butterflies with short life cycles might be not applicable to sessile plants with long life cycles (Eriksson 1996).

Contrary to our predictions, we could not find effects of habitat isolation, neither for specialist nor for generalist plant species. Isolation effects on plant species are mainly found for plant species with low dispersal abilities (Van Ruremonde and Kalkhoven 1991; Grashof-Bokdam 1997), while other species groups generally show no or weak isolation effects (Ouborg 1993; Köchy and Rydin 1997; Honnay et al. 1999; Bruun 2000). Also for the more mobile butterfly species no isolation effects could be reported on the same calcareous grasslands (Steffan-Dewenter and Tscharntke 2000; Krauss et al. 2003). As calcareous grasslands were better connected decades ago (WallisDeVries et al. 2002), we might have found patterns that show previous situations because of extinction debt of plants, and therefore no isolation effect.

In conclusion, habitat area was the only predictor explaining vascular plant community structure for habitat specialists, generalists, and all plant species. Per study site an average of 54% of all specialist species was found, indicating that 46% of total species richness was due to between study site variation. Nevertheless, habitat isolation and landscape diversity had no effect in our study region. These results stress the point that habitat area and increasing habitat heterogeneity are the most important basis of plant diversity. Several populations of specialist plant species on small habitat fragments may be prone to extinction in the near future, showing the so-called extinction debt. Sheep flock migration might contribute to a better dispersal of seeds (Poschlod and WallisDeVries 2002), to reduce potentially increasing specialist extinction in small and isolated habitats. For conservation we suggest to protect (a) the largest grasslands with low extinction risk of habitat specialists, and (b) a series of habitat fragments covering a sufficient range of geographical area to maximise regional diversity.

Acknowledgements

We thank David Kleijn, Olivier Honnay, Sabine Güsewell and one anonymous referee for helpful comments on the manuscript and Bertram Preuschoff (Untere Naturschutzbehörde des Landkreis Göttingen) for his expert advice. This work was financially supported by the German Science Foundation (Deutsche Forschungsgemeinschaft).

Appendix 1

Habitat specialist plants on 31 calcareous grasslands in Southern Lower Saxony.

Taxon	Number of occupied habitats	Taxon	Number of occupied habitats
Agrimonia eupatoria L.	30	*Koelaeria pyramidata* (Lamk.) P.B.	29
Anemone sylvestris L.	3	*Medicago falcata* L.	7
Anthyllis vulneraria L.	20	*M. lupulina* L.	30
Astragalus glycyphyllos L.	10	*Melampyrum arvense* L.	3
Avenula pratensis (L.) Dum.	16	*M. nemorosum* L.	2
A. pubescens (HUDS.) Dum.	11	*Onobrychis viciifolia* Scop.	7
Brachypodium pinnatum (L.) P.B.	31	*Ononis spinosa* L.	24
Briza media L.	30	*Ophris apifera* Huds.	1
Bromus erectus Huds.	19	*Ophrys insectifera* L. em L.	16
Campanula rapunculoides L.	24	*Orchis mascula* (L.) L.	13
Carex caryophyllea Latourr.	15	*O. militaris* L.	3
C. flacca Schreber	30	*O. purpurea* Huds.	5
C. ornithopoda Willd.	3	*Orchis tridentata* Scop.	3
Carlina vulgaris L.	25	*Origanum vulgare* L.	3
Centaurea scabiosa L.	28	*Pimpinella saxifraga* L.	31
Cerastium arvense L.	11	*Platanthera bifolia* (L.) L.C. Richard	2
Cirsium acaule SCOP.	31	*Polygala comosa* Schkuhr	27
Clinopodium vulgare L.	15	*Potentilla neumanniana* Rchb.	31
Euphorbia cyparissias L.	14	*Primula veris* L.	30
Euphrasia stricta Wolff ex Lehm	2	*Prunella grandiflora* (L.) Scholler	11
Festuca ovina L.	31	*Ranunculus bulbosus* L.	31
Filipendula vulgaris Moench	1	*Salvia pratensis* L.	4
Fragaria viridis (Duchesne) Weston	18	*Sanguisorba minor* Scop.	31
Galium pumilum Murray	22	*Scabiosa columbaria* L.	31

Appendix 1. (continued)

Taxon	Number of occupied habitats	Taxon	Number of occupied habitats
G. verum L.	25	*Sedum sexangulare* L.	6
Gentianella ciliata (L.) Borkh.	10	*Silene nutans* L.	3
G. germanica (Willd.) Börner	9	*Thymus pulegioides* L.	31
Gymnadenia conopsea (L.) R.Br.	26	*Trifolium campestre* Schreber	7
Helianthemum nummularium (L)	20	*T. medium* L.	18
Hieracium pilosella L.	29	*T. montanum* L.	2
Hippocrepis comosa L.	25	*Veronica teucrium* L.	17
Hypericum perforatum L.	30	*Vincetoxicum hirundinaria* Med.	3
Inula conyzae (Griesselich) Meikle	12	*Viola hirta* L.	26

References

Bässler M., Jäger E.J. and Werner K. 1999. Rothmaler, Exkursionsflora von Deutschland, Bd. 2, Gefässpflanzen: Grundband. Spektrum Akademischer Verlag, Heidelberg, Berlin, Germany.

Beinlich B. and Plachter H. 1995. Ein Naturschutzkonzept für Kalkmagerrasen der Mittleren Schwäbischen Alb (Baden-Württemberg): Schutz, Nutzung und Entwicklung. Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden–Württemberg 83: 1–520.

Bruun H.H. 2000. Patterns of species richness in dry grassland patches in an agricultural landscape. Ecography 23: 641–650.

De Blois S., Domon G. and Bouchard A. 2002. Landscape issues in plant ecology. Ecography 25: 244–256.

Deutscher Wetterdienst 2001. Klimadaten der Wetterstation Göttingen. In: Stadt Göttingen, Amt für Statistik und Stadtforschung (eds), Statistikjournal 1/2001.

Eriksson O. 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. Oikos 77: 248–258.

Fischer M. and Stöcklin J. 1997. Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. Conservation Biology 11: 727–737.

GEOsat GmbH 1998. GEOlink Version 1. 46. Wuppertal, Germany.

Gonzales A. 2000. Community relaxation in fragmented landscapes: the relation between species richness, area and age. Ecology Letters 3: 441–448.

Grashof-Bokdam C. 1997. Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. Journal of Vegetation Science 8: 21–28.

Hanski I. 1999. Metapopulation Ecology. Oxford University Press, Oxford, UK.

Hanski I., Kuussaari M. and Nieminen M. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia*. Ecology 75: 747–762.

Holt R.D., Lawton J.H., Polis G.A. and Martinez N.D. 1999. Trophic rank and species–area relationship. Ecology 80: 1495–1504.

Honnay O., Endels P., Vereecken H. and Hermy M. 1999. The role of patch area and habitat diversity in explaining native plant species richness in disturbed suburban forest patches in northern Belgium. Diversity and Distribution 5: 129–141.

Jonsen I.D. and Fahrig L. 1997. Response of generalist and specialist insect herbivores to landscape spatial structure. Landscape Ecology 12: 185–197.

Kelly B.J., Bastow W.J. and Mark A.F. 1989. Causes of the species–area relation: a study of islands in lake Manapouri, New Zealand. Journal of Ecology 77: 1021–1028.

Köchy M. and Rydin H. 1997. Biogeography of vascular plants on habitat islands, peninsulas and mainlands in an east-central Swedish agricultural landscape. Nordic Journal of Botany 17: 215–223.

Kohn D.D. and Walsh D.W. 1994. Plant species richness – the effect of island size and habitat diversity. Journal of Ecology 82: 367–377.

Kollmann J. and Schneider B. 1999. Landscape structure and diversity of fleshy-fruited species at forest edges. Plant Ecology 144: 37–48.

Krauss J., Steffan-Dewenter I. and Tscharntke T. 2003. How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? Journal of Biogeography 30: 889–900.

Krebs C.J. 1989. Ecological Methodology. Harper Collins Publishers, New York.

Lawesson J.E., de Blust G., Grashof C., Firbank L., Honnay O., Hermy M., Hobitz P. and Jensen L.M. 1998. Species diversity and area-relationships in Danish beech forests. Forest Ecology and Management 106: 235–245.

Metzger J.P. 2000. Tree functional group richness and landscape structure in a Brazilian tropical fragmented landscape. Ecological Applications 10: 1147–1161.

Moilanen A. and Nieminen M. 2002. Simple connectivity measures in spatial ecology. Ecology 83: 1131–1145.

Oostermeijer J.G.B., Vant 't Veer R. and Den Nijs J.C.M. 1994. Population structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands. Journal of Applied Ecology 31: 428–438.

Ouborg N.J. 1993. Isolation, population size and extinction: the classical and metapopulation approaches applied to vascular plants along the Dutch Rhine-system. Oikos 66: 298–308.

Poschlod P. and WallisDeVries M.F. 2002. The historical and socioeconomic perspective of calcareous grasslands – lessons from the distant and recent past. Biology Conservation 104: 361–376.

Ricketts T.H. 2001. The matrix matters: effective isolation in fragmented landscapes. The American Nationalist 158: 87–99.

Riecken U., Ries U. and Ssymank A. 1994. Rote Liste der gefährdeten Biotoptypen der Bundesrepublik Deutschland. Kilda-Verlag, Greven, Germany.

Rosenzweig M.L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.

Söderström B., Svensson B., Vessby K. and Glimskär A. 2001. Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. Biodiversity and Conservation 10: 1839–1863.

Sokal R.R. and Rohlf F. 1995. Biometry. Freeman, New York.

Statgraphics 1995. Statgraphics plus for Windows, Version 3.0. Manugistics, Inc, Rockville, Mary land.

Steffan-Dewenter I. and Tscharntke T. 2000. Butterfly community structure in fragmented habitats. Ecology Letters 3: 449–456.

Steffan-Dewenter I. and Tscharntke T. 2002. Insect communities and biotic interactions on fragmented calcareous grasslands – a mini review. Biological Conservation 104: 275–284.

Steffan-Dewenter I., Münzenberg U., Bürger C., Thies C. and Tscharntke T. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83: 1421–1432.

Tilman D., May R.M., Lehman C.L. and Nowak M.A. 1994. Habitat destruction and the extinction debt. Nature 371: 65–66.

Tscharntke T., Steffan-Dewenter I., Kruess A. and Thies C. 2002. Characteristics of insect populations on habitat fragments: a mini review. Ecological Research 17: 229–239.

Van Ruremonde R.H.A.C. and Kalkhoven J.T.R. 1991. Effects of woodlot isolation on the dispersion of plants with fleshy fruits. Journal of Vegetation Science 2: 377–384.

Van Swaay C.A.M. 2002. The importance of calcareous grasslands for butterflies in Europe. Biological Conservation 104: 315–318.

Veech J.A., Summerville K.S., Crist T.O. and Gering J.C. 2002. The additive partitioning of species diversity: recent revival of an old idea. Oikos 99: 3–9.

Von Drachenfels O. 1994. Kartierschlüssel für Biotoptypen in Niedersachsen. Naturschutz und Landschaftspflege Niedersachsen 4: 1–192.

WallisDeVries M.F., Poschlod P. and Willems J.H. 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. Biological Conservation 104: 265–273.

Warren M.S., Hill J.K., Thomas J.A., Asher J., Fox R., Huntley B. et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414: 65–69.

Wiens J.A. 1997. Metapopulation dynamics and landscape ecology. In: Hanski I. andGilpin M.E. (eds) Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, London, pp. 43–62.

Zschokke S., Dolt C., Rusterholz H.-P., Oggier P., Braschler B., Thommen G.H. et al. 2000. Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation. Oecologia 125: 559–572.