# Insect communities and biotic interactions on fragmented calcareous grasslands—a mini review

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## Abstract

We evaluate existing evidence for alternative hypotheses on the effects of fragmentation with special emphasis on insects of calcareous grasslands. Species richness of butterflies in general and the proportion of monophagous species in particular increase with fragment size. Habitat fragmentation disrupts plant–pollinator and predator—prey interactions in some cases. No evidence for changes in the outcome of competitive interactions exists for insects. Habitat connectivity increases inter-patch movement and population density and decreases extinction risk. Habitat quality changes with succession and management. Depending on life-history traits, insect species may profit from early, mid or late successional stages of calcareous grasslands. We conclude from the few well-designed and replicated studies that there is a bias towards modelling approaches and small-scale fragmentation experiments, so more large-scale studies on a community level are needed to quantify the functional roles of insects and their dependence on fragmented calcareous grasslands in the landscape mosaic. © 2002 Elsevier Science Ltd. All rights reserved.

*Keywords:* Habitat fragmentation; Plant–pollinator interactions; Predator–prey interactions; Conservation; Landscape structure; Secondary succession

## 1. Introduction

Insects make up more than half of all living species, a further quarter are green plants, and only 4% of all described species are vertebrates (Strong et al., 1984). Insects impress not only by their immense species richness but also by their variety of life forms: the four largest insect orders, Coleoptera, Diptera, Lepidoptera and Hymenoptera, represent major functional groups such as herbivores, pollinators, parasitoids and predators (Strong et al., 1984; LaSalle and Gauld, 1993). The diversity of both species and life forms make insect communities an important part of terrestrial ecosystems. Herbivory, for example, may greatly influence the community structure of plants by changing competitive interactions and reproductive success of plant species (Ritchie and Olff, 1999). Plants profit from mutualistic interactions such as pollination and seed dispersal by insects (Burd, 1994). Plant–insect interactions become even more complex due to parasitoids and predators which attack herbivores and pollinators (Fig. 1). In addition, vertebrate top predators and megaherbivores may affect plant–invertebrate food webs (Tscharntke, 1997; Dicke and Vet, 1999).

The destruction and fragmentation of habitats has become one of the major threats to biodiversity (Saunders et al., 1991; Baur and Erhardt, 1995). Habitat fragmentation may change or disrupt mutualistic and antagonistic interactions such as pollination (Rathcke and Jules, 1993; Matthies et al., 1995; Kearns et al., 1998), parasitism or predation (Didham et al., 1996; Tscharntke and Kruess, 1999), and interspecific competition (Kareiva and Wennergren, 1995; Holt et al., 1995). A further effect of habitat destruction is the decreasing area of old, little disturbed, mid- and late-successional habitats, whereas the area of highly disturbed, early-successional habitats increases (Bazzaz, 1996).

Here, we focus on the effects of habitat fragmentation on the diversity and biotic interactions of insect communities with special emphasis on calcareous grasslands. Calcareous grasslands are one of the most species-rich habitats in central Europe harbouring many rare and specialised plant and insect species. Most European grasslands are man-made habitats, created in historical times (e.g. Baur and Erhardt, 1995; Balmer and Erhardt, 2000). These grasslands are often the only habitat remnants for a great number of invertebrates and plants, since other open habitats have been mostly destroyed. Nowadays, calcareous grasslands and their insect communities are endangered due to destruction, fragmentation and succession as a result of intensification or abandonment of agriculture, and due to the loss

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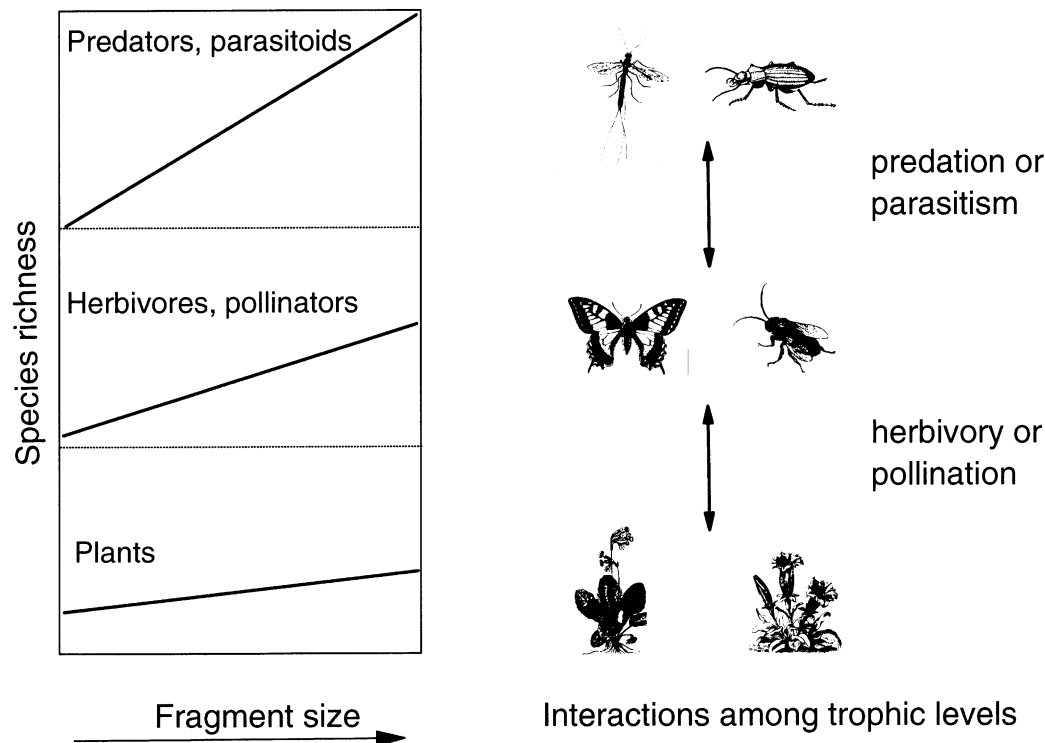
# Habitat fragmentation and community structure



Fig. 1. Expected effects of habitat fragmentation on species richness and community interactions on three trophic levels. The slope of the species area curves indicates how sensitive a species group is to habitat fragmentation. Higher sensitivity of herbivores, pollinators, parasitoids and predators to fragment size is only expected for specialized species.

of traditional extensive animal husbandry (e.g. Blackwood and Tubbs, 1970; Baur and Erhardt, 1995; Mortimer et al., 1998; Niemelä and Baur, 1998; Balmer and Erhardt, 2000; Pykälä, 2000). Many local case studies have been published with respect to the species composition of several insect groups and their possible dependence on different management regimes (e.g. Morris, 1967; Rushton et al., 1990; Dolek, 1994; Beinlich and Plachter, 1995; Baur et al., 1996; Wolf and Zimmermann, 1996; Kuhlmann, 1998). However, during our literature survey on insect communities of calcareous grasslands, we found only a few well-designed and replicated studies testing general ecological hypotheses. Similarly, a recent review of habitat fragmentation experiments indicated an emphasis on birds and small mammals (Debinski and Holt, 2000). In this review, we included also insect community studies on habitat types other than calcareous grasslands to substantiate the following hypotheses (Table 1).

## 1.1. Species–area and species–isolation relationships

In most landscapes, habitat fragmentation is characterised by decreasing size and increasing isolation of the remaining habitat fragments and a reduction of the total area. The relative importance of patch size and isolation is expected to differ at different degrees of habitat loss (Andren, 1994). Below a critical threshold of 20% of habitat in a landscape the isolation distances between habitat patches will increase exponentially (Andren, 1994, 1999). The effects of fragment size on species richness, i.e. species–area relationships, have been shown for many species groups and habitats, since MacArthur and Wilson (1967) established the theory of island biogeography. Possible reasons for the increase of species diversity with habitat area are (1) colonisation–extinction dynamics, (2) sampling effects, and (3) increased habitat diversity in large compared to small areas (Connor and McCoy, 1979; Rosenzweig, 1995). Depending on the geometry of the fragment, edge effects may further affect habitat quality, and thereby, species diversity and community structure (Didham et al., 1998). In real landscapes, habitat area and isolation are often closely correlated. Habitat isolation should affect survival of habitat specialists with limited dispersal capabilities more than that of vagile generalists which may perceive a fragmented landscape as sufficiently connected (Thomas, 2000).

Table 1
Hypotheses and empirical data on the effects of habitat fragmentation on plant and insect communities of calcareous grasslands

| Hypothesis | Species group and spatial scale | Supported by field data | Reference |
|---|---|---|---|
| (1) Species richness increases with habitat area and decreases with habitat isolation | Butterflies | Increased with fragment size | Zschokke et al. (2000) |
| | Ants, grasshoppers, gastropods (0.25–20.25 m$^2$) | No effects of fragment size | Zschokke et al. (2000) |
| | Butterflies (0.03–7.6 ha) | Increased with fragment size | Steffan-Dewenter and Tscharntke (2000a) |
| | Insects on *H. Chamecistus* (0.4–6500 m$^2$) | Increased with plant colony size | Davis and Jones (1986) |
| | Butterflies (up to 10 km isolation) | Colonisation probabilities decreased with habitat isolation | Thomas et al. (1992); Thomas and Harrison (1992) |
| | Butterflies (up to 5 km isolation) | No effects of habitat isolation | Steffan-Dewenter and Tscharntke (2000a) |
| | Insects on *Helianthemum chamecistus* (up to 6.5 km isolation) | No effects of habitat isolation | Davis and Jones (1986) |
| (2) Abundance increases with habitat area and decreases with habitat isolation | Butterflies (0.03–7.6 ha) | Monophagous increased with fragment size | Steffan-Dewenter and Tscharntke (2000a) |
| | | Oligophagous and polyphagous decreased with fragment size | Steffan-Dewenter and Tscharntke (2000a) |
| | Butterflies (0.25–20.25 m$^2$) | Less frequent in fragments than in control plots | Zschokke et al. (2000) |
| | Ants, grasshoppers, gastropods (0.25–20.25 m$^2$) | No effects of fragment size | Zschokke et al. (2000) |
| (3) Habitat fragmentation affects particularly species of higher trophic levels, food plant specialists and species with limited dispersal abilities. | Butterflies (0.3–7.6 ha) | Higher *z*-values for food plant specialists | Steffan-Dewenter and Tscharntke (2000a) |
| (4) Habitat fragmentation disrupts biotic interactions such as plant–pollinator or predator–prey interactions, and changes the outcome of competitive interactions | Primula veris (<200 plants), Gentiana lutea (<500 plants) | Reduced seed set in small populations | Kéry et al. (2000) |
| | *Gentianella germanica* | Inbreeding depression | Matthies et al. (1995) |
| | Several plant species | Increased extinction risk in small populations | Fischer and Matthies (1997); Bräuer et al. (1999) |
| | Bumble bees (0.25–20.25 m$^2$) | Changed pollinator behaviour | Goverde et al. (2002) |
| | Bees (0–1000 m) | Pollinator diversity and seed set decreased with isolation | Steffan-Dewenter and Tscharntke (1999) |
| | Trap-nesting bees (0–1000 m) | Natural enemies and percent parasitism decreased with isolation | Tscharntke et al. (1998) |

Table 1 (*continued*)

| Hypothesis | Species group and spatial scale | Supported by field data | Reference |
|---|---|---|---|
| (5) Landscape structure influences the habitat connectivity and the availability of resources outside calcareous grasslands | | No study exists for calcareous grasslands | |
| (6) Secondary succession changes habitat quality of calcareous grasslands | Butterflies | Species profit from different successional stages depending on life history traits | Balmer and Erhardt (2000) |
| | Phytophagous insects | | Morris (1967) |
| | Phytophagous insects | | Völkl et al. (1993) |
| | Grasshoppers, ground beetles, butterflies, snails | | Beinlich (1995) |
| | Bees | | Steffan-Dewenter and Tscharntke (2000b) |

## 1.2. Abundance–area relationships

The equilibrium theory of island biogeography presumes that the population density for individual species remains constant with increasing area (MacArthur and Wilson, 1967) or even increases due to resource concentration (Connor et al., 2000). Since species richness is a positive function of area, this implies that the density of the total insect community should also increase with area.

## 1.3. Biotic interactions

Not all species are equally affected by habitat fragmentation: species of higher trophic levels, rare species, species with specific habitat requirements, species with greatly fluctuating populations and species with poor dispersal abilities are expected to be more prone to extinction (Lawton, 1995). Life history traits such as oviposition preference may change as an evolutionary consequence of increased habitat fragmentation (Mopper and Strauss, 1998; Thomas et al., 1998; Kuussaari et al., 2000). As a result of changes in community structure, interspecific interactions such as plant–pollinator or predator–prey interactions may disrupt, and competitive interactions may be changed (Hanski, 1995; Harrison and Bruna, 1999). Less competitive but highly mobile species, which are typically early successional r-strategists, may profit from habitat fragmentation at the cost of competitively superior, but specialised and sedentary species (Tilman, 1994).

## 1.4. Landscape structure

In addition to the size and isolation of habitat patches, their spatial arrangement (Collinge and Forman, 1998) and the spatial and temporal heterogeneity of the surrounding landscape remains a little understood, but important determinant of fragmented communities (Kareiva and Wennergren, 1995; Gustafson, 1998). Landscape complexity determines the availability of physical corridors and the hostility of the environment, and thereby the structural connectivity of habitat fragments (With et al., 1997; Tischendorf and Fahrig, 2000). The species-specific response to landscape elements, the mortality risks and movement patterns are considered as functional connectivity (Tischendorf and Fahrig, 2000). Whether the landscape is perceived as connected depends on the scale at which the organisms interact with spatial patch structure (With et al., 1999). Furthermore, the surrounding landscape may provide additional food resources for insect species relying on a certain habitat type, e.g. calcareous grasslands, thereby enhancing population density and survival rates (e.g. Debinski and Holt, 2000; Norton et al., 2000).

## 1.5. Habitat quality and succession

Habitat quality of calcareous grasslands mainly depends on the opposing forces of succession and management (Morris, 2000). Speed of succession of calcareous grasslands may be related to fragment size because late-successional shrubs and trees invade from the edge. Secondary succession is characterized by changes in species richness and structure of vegetation, so the availability of nesting and mating sites and food plants for insects also changes (Brown and Southwood, 1987). Successional theory predicts that highest species richness peaks in mid-successional stages of "intermediate disturbance" (Connell, 1978; Brown and Southwood, 1987).

## 2. Results and discussion

Most of these hypotheses and expectations have been rarely tested, particularly on calcareous grasslands (Harrison and Bruna, 1999; Holt et al., 1999; Debinski and Holt, 2000). In the following we evaluate existing evidence for each hypothesis (Table 1).

### 2.1. Species diversity increases with habitat area and decreases with habitat isolation

Although species–area relationships are generally a well known and often described ecological pattern, only a few studies of insect communities on calcareous grasslands exist. Zschokke et al. (2000) analysed short-term (after 3 years) responses of plants, ants, butterflies, and grasshoppers to experimentally created small-scale fragmentation of calcareous grasslands in Switzerland. Species richness and composition of each group in fragments of 20.25, 2.25, and 0.25 m$^2$ were compared with neighbouring control plots (distance 10 m) of the same size within a large grassland area. Species richness of butterflies was lower in fragments than in control plots, whereas species richness of the other insect groups did not differ (Zschokke et al., 2000). In a study of butterfly communities on 33 calcareous grasslands in Germany, total species richness increased with fragment size but was not significantly affected by habitat isolation (Steffan-Dewenter and Tscharntke, 2000a). Positive species-area relationships were also found for insect communities on two characteristic plant species of calcareous grasslands, *Juniperus communis* and *Helianthemum chamaecistus* (Ward and Lakhani, 1977; Davis and Jones, 1986). Further studies focus on single insect species, but not on communities. Several rare UK butterflies are restricted to large and non-isolated limestone habitat patches, while habitat fragments isolated from source populations remain vacant (Thomas and Harrison, 1992; Hill et al., 1996). Isolation distances of 1000 m

or more reduced colonisation probability to zero for the lycaenid *Plebejus argus* (Thomas et al., 1992). Large and non-isolated grassland patches were more likely to be colonised, whereas local populations in small and isolated patches were more likely to go extinct (Table 1). For the butterflies *Plebejus argus* and *Hesperia comma,* morphological characters associated with flight ability were related to the level of habitat fragmentation. Relative allocation to the thorax increased with declining limestone habitat area (Thomas et al., 1998; Hill et al., 1999). This indicates that habitat fragmentation may have evolutionary consequences for the life history traits of insect communities. Further studies showed that emigration rates of *Aphantopus hyperantus* (Sutcliffe et al., 1997), *Melanargia galathea* and *Aporia crataegi* (Baguette et al., 2000) declined with increasing patch area, while the fraction of the resident populations increased.

### 2.2. Abundance increases with habitat area and decreases with habitat isolation

On calcareous grasslands, total densities of butterflies decreased with increasing fragment size, but did not depend on habitat isolation (Steffan-Dewenter and Tscharntke, 2000a). More detailed analyses showed an opposite trend for the four monophagous species (out of the 61 species), i.e. increasing densities with fragment size, whereas oligophagous and polyphagous decreased. In the small-scale fragmentation experiment by Zschokke et al. (2000), butterflies were less frequent in fragments compared to control plots, whereas ants, grasshoppers and snails showed no clear tendencies (Table 1). In a short-term microlandscape experiment, fragmented grassland plots maintained higher densities of insects than did control plots (Collinge and Forman, 1998). A meta-analyses of abundance–area relationships found an overall increase in densities of individual species but no increase of faunal densities in larger fragments. However, insect studies were rare, and only nine studies of individual species and two faunal studies could be included (Connor et al., 2000).

### 2.3. Habitat fragmentation affects particularly species of higher trophic levels, food plant specialists and species with limited dispersal abilities

A study of butterflies on calcareous grasslands showed that community structure changed with fragment size. The *z*-values, i.e. the slope of species–area relationships, increased with food plant specialisation, from 0.07 in polyphagous to 0.11 in oligophagous, 0.16 in strongly oligophagous and 0.22 in monophagous species. Most of the monophagous species were endangered habitat specialists, thereby underlining the great importance of large habitats for conservation

(Steffan-Dewenter and Tscharntke, 2000a). These results also indicated that the specialists of higher trophic levels (monophagous and strongly oligophagous butterflies) are more sensitive to fragmentation than are species of lower trophic levels (the plant community with $z = 0.14$). Different responses of trophic levels to habitat fragmentation were also found for herbivores and their parasitoids on red clover *Trifolium pratense* and bush vetch *Vicia sepium* (Kruess and Tscharntke, 1994, 2000). The ratio of parasitoids to herbivores and thus the potential for parasitism was lower in fragmented grassland plots compared to controls (Collinge and Forman, 1995).

### 2.4. Habitat fragmentation disrupts biotic interactions

#### 2.4.1. Plant–pollinator interactions

About 80% of the plant species in western Europe are insect pollinated. Therefore, pollinator limitation and reduced gene flow may play an important role for plant fitness (Kwak et al., 1998). In most cases, pollination systems are generalised, i.e. each plant is visited by more than one insect species and each insect species visits several plant species, but a critical level of pollinator species richness is necessary for successful pollination and maintenance of diverse plant communities (Neff and Simpson, 1993; Waser et al., 1996). Pollinator populations depend on sufficient nectar and pollen sources as well as suitable nesting sites. Both may be limiting in small fragments. As a result of decreased pollinator diversity or abundance in small fragments, plants may increasingly compete for pollinators (Levin and Anderson, 1970). Less attractive plant species, very small or less dense plant patches may receive fewer pollinator visits and a higher proportion of heterospecific pollen grains, thereby reducing pollination efficiency and gene flow by pollen dispersal (Sowig, 1989; Kunin, 1993; Kwak et al., 1998).

Plant ecologists have found clear evidence that small and isolated plant populations on calcareous grasslands have reduced seed set (e.g. Matthies et al., 1995; Kéry et al., 2000), suffer from genetic erosion (e.g. Oostermeijer et al., 1994; Fischer and Matthies, 1997) and have a higher extinction risk (e.g. Fischer and Stöcklin, 1997; Bräuer et al., 1999). A study of small-scale fragmentation showed lower visitation frequency of the most common pollinator, *Bombus veteranus*, and a change in foraging behaviour in fragments compared to control plots (Goverde et al., 2002). Increasing isolation of experimentally established small habitat islands from calcareous grasslands resulted in both decreasing numbers of flower-visiting bees and lower rates of seed set of two annual crucifers (Steffan-Dewenter and Tscharntke, 1999; Table 1). Lack (1982a, 1992b) studied the ecology of flowers on chalk grasslands and competition for pollinators. He found that early flowering plants were more specialised for pollinators and more divergent in flowering time than plant species flowering in late summer, which overlapped in flowering time and in their insect visitors. However, no study explicitly examined effects of fragmentation of calcareous grasslands on pollinator diversity and abundance. Literature data from other habitat types suggest changes in pollinator community composition, reductions in species richness and abundance of pollinators as well as reductions in seed set when habitat size decreases or habitat isolation increases. Aizen and Feinsinger (1994b) found that the frequency and species richness of native flower-visitors declined with decreasing forest-fragment size, whereas the frequency of exotic honey bees increased. Fragmentation-related declines in pollen tube numbers, fruit set and seed set occurred in 9 of 16, 5 of 15 and 3 of 14 species, respectively (Aizen and Feinsinger, 1994a). Jennersten (1988) showed that the perennial plant *Dianthus deltoides* received fewer flower visits in a fragmented grassland area than in a mainland area. As a result of pollen limitation, seed set was much lower in the fragmented area.

#### 2.4.2. Predator–prey interactions

Habitat fragmentation is expected to have differential effects on plants, herbivores and their natural enemies (Holt et al., 1999). Plant diversity is the basis for the diversity of herbivorous insects, because the resource heterogeneity determines the number of consumer species (Lawton, 1983; Siemann et al., 1998). High herbivore diversity maintains a high diversity of predators and parasitoids on the third trophic level. Top-down effects of predators and parasitoids may in turn maintain high herbivore diversity (Siemann et al., 1998). Holt et al. (1999) showed with a model for communities closed to immigration that species–area relationships should be stronger at higher trophic ranks. Therefore, habitat fragmentation should change trophic interactions between plants, herbivores and their natural enemies. Almost no empirical data to support this hypothesis exist for calcareous grasslands. In communities of trap-nesting solitary bees, the species number of natural enemies decreased more markedly with increasing isolation distance from the nearest calcareous grassland than the species richness of their hosts, and species richness of enemies and percent mortality (parasitism and predation) covaried (Tscharntke et al., 1998). Percent parasitism of herbivores on red clover and bush vetch patches increased with habitat area and decreased with isolation from old meadows (Kruess and Tscharntke, 1994, 2000). Since predators and parasitoids are more susceptible to fragmentation than their prey and hosts, herbivores may be released from their natural enemies and tend to outbreaks (Kareiva, 1987).

### 2.4.3. Competition

Nectar and pollen feeders are often assumed to be strongly affected by interspecific competition (e.g. Schaffer et al., 1983; Butz Huryn, 1997). Therefore, nature conservationists concerned about the general decline of wild bees have claimed the importance of competition by honeybees in Europe, especially in fragmented semi-natural habitats such as calcareous grasslands or heathlands (Evertz, 1995). A test of this expectation on 15 calcareous grasslands did not give evidence that the abundance or species richness of flower-visiting or trap-nesting wild bees declined with increasing densities of honey bee colonies (Steffan-Dewenter and Tscharntke, 2000b). In contrast to expectations, the number of flower-visiting bumble bees was even positively correlated with honeybee density, and also with the cover of flowering plants. This indicates similar resource use of honey bees and bumble bees but no competitive exclusion. The abundance of flower-visiting solitary, mainly ground-nesting bees, decreased with increasing cover of vegetation (presumably due to a reduction of suitable nesting sites) and increased with increasing cover of flowering plants. Thus, habitat structure but not competitive interactions appeared to determine bee communities on calcareous grasslands. However, no evidence for changes in the outcome of competitive interactions due to fragmentation exists for insects.

### 2.5. Landscape structure influences habitat connectivity and the availability of resources outside calcareous grasslands

We are not aware of any study testing this hypothesis on calcareous grasslands, but some other studies show substantial effects of increased connectivity, e.g. by corridors. In a landscape experiment, early successional patches were created within large areas of pine forest. Two butterfly species moved more frequently between patches connected by corridors than between unconnected patches (Haddad, 1999). Furthermore, three open-habitat specialists reached higher densities in patches connected by corridors than in isolated patches (Haddad and Baum, 1999). Gilbert et al. (1998) used moss patches as microecosystems to test the idea that corridors can reduce the rate of loss of species. Connected patches showed slower rates of extinctions and higher species richness than disconnected patches. As a consequence of reduced or eliminated migration between patches, the abundance of surviving animal species declined on isolated but not on connected habitat patches (Gonzales et al., 1998). Furthermore, the proportion of predator species declined significantly in disconnected compared to connected fragments in this study. In a further microcosm study, species persistence was higher in fragments connected by corridors than in either unconnected fragments or a single large fragment (Holyoak and Lawler, 1996).

### 2.6. Secondary succession changes habitat quality of calcareous grasslands

Long-term abandonment of calcareous grasslands results in succession to relatively species poor late-successional stages dominated by grasses like *Brachypodium pinnatum* and later by shrubs and trees (Erhardt, 1985; Bobbink and Willems, 1991). Therefore, regular grazing or mowing is necessary to stop succession and to maintain plant species richness (Morris, 2000). Species richness of plants was higher on annually grazed than on abandoned or extensively grazed calcareous grasslands (Steffan-Dewenter, 1998). In contrast, Balmer and Erhardt (2000) found higher diversity of diurnal butterflies on calcareous grasslands abandoned for 10 years than on extensively cultivated grasslands. They conclude that old fallow land has been underestimated in conservation efforts in central Europe. Similarly, Erhardt (1985) and Beinlich (1995) found that species richness and abundance of butterflies was higher on abandoned calcareous grasslands than on regularly mown or grazed grasslands, but greatly decreased on late-successional grasslands with shrubs or trees. One might expect that plants reach maximum species richness at higher grazing intensity than some insect groups which depend on flowers, food plants and a long-lasting larval development (Morris, 1967; Erhardt, 1985; Völkl et al., 1993), but species richness of grasshoppers, snails and ground beetles was highest on regularly mown or grazed calcareous grasslands (Beinlich, 1995). Belowground nesting solitary bees were more abundant on regularly mown or grazed calcareous grasslands with sparse vegetation and open soil, whereas the abundance of above-ground nesting bees increased with increasing cover of shrubs (Steffan-Dewenter and Tscharntke, 2000b). Similarly, butterfly species such as *Maculinea arion*, *Hesperia comma*, *Cupido minimus*, *Lysandra bellargus* and *L. coridon* mainly occur on regularly mown or grazed calcareous grasslands as they appear to rely on warm microclimates and host plants within sparse vegetation (Thomas, 1991; Settele et al., 1995). Depending on life history traits, species profit from early, mid or late successional stages and highest global species richness should be reached with a mosaic of different successional stages. Such a mosaic of different habitat structures may be in large habitat fragments or in a series of small patches.

## 3. Conclusions

Many local case studies give details of insects on calcareous grasslands, but astonishingly few large-scale

and well replicated studies on the effects of habitat fragmentation and secondary succession on insect communities are published. Furthermore, there is a bias towards modelling approaches or small-scale fragmentation experiments, whereas the field data necessary to assess the ecological responses of communities and to test these models are often lacking (Gustafson and Gardner, 1996). We obviously need concerted research efforts to quantify the functional role of insects in trophic interactions and its dependence on habitat fragmentation in real landscapes (Didham et al., 1996). Such an approach should consider the size and shape of habitats, the isolation distance to neighbouring fragments and the proportion of suitable habitats in a landscape, i.e. the meaning of the landscape structure (Kareiva and Wennergren, 1995). Calcareous grasslands are very suitable systems for fragmentation studies because they are (1) well-delimitated from other habitat types, (2) nowadays highly fragmented, (3) harbour species-rich plant and insect communities with a large variety of biotic interactions, and (4) thereby, have high conservation value. Besides the already discussed interaction types, many other biotic interactions may be susceptible to fragmentation-induced changes in the abundance and species richness of functional groups, such as seed-predation, seed dispersal, litter decomposition, pathogen–insect or vertebrate–invertebrate interactions. Successful nature conservation of calcareous grasslands will depend greatly on the understanding of these complex spatio-temporal and biotic interactions. We think that close collaboration of plant and insect ecologists as well as an Europe-wide, macroecological perspective would be a big step to reach this objective.

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## References

Aizen, M.A., Feinsinger, P., 1994a. Forest fragmentation, pollination, and plant reproduction in a chaco dry forest, Argentina. Ecology 75, 330–351.

Aizen, M.A., Feinsinger, P., 1994b. Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine "Chaco Serrano". Ecological Applications 4, 378–392.

Andren, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat. Oikos 71, 355–366.

Andren, H., 1999. Habitat fragmentation, the random sample hypothesis and critical thresholds. Oikos 84, 306–308.

Baguette, M., Petit, S., Quéva, F., 2000. Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. Journal of Applied Ecology 37, 100–108.

Balmer, O., Erhardt, A., 2000. Consequences of succession on extensively grazed grasslands for Central European butterfly communities: rethinking conservation practices. Conservation Biology 14, 746–757.

Baur, B., Erhardt, A., 1995. Habitat fragmentation and habitat alterations: principal threats to most animal and plant species. Gaia 4, 221–226.

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

Bazzaz, F.A., 1996. Plants in Changing Environments. Cambridge University Press, Cambridge.

Beinlich, B., 1995. Veränderungen der Wirbellosen-Zönosen auf Kalkmagerrasen im Verlauf der Sukzession. Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg 83, 283–310.

Beinlich, B., Plachter, H., 1995. Schutz und Entwicklung der Kalkmagerrasen der Schwäbischen Alb. Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg 83, 1–520.

Blackwood, J.W., Tubbs, C.R., 1970. A quantitative survey of chalk grassland in England. Biological Conservation 3, 1–5.

Bobbink, R., Willems, J.H., 1991. Impact of different cutting regimes on the performance of *Brachypodium pinnatum* in Dutch chalk grasslands. Biological Conservation 51, 1–21.

Bräuer, I., Maibom, W., Matthies, D., Tscharntke, T., 1999. Populationsgröße und Aussterberisiko gefährdeter Pflanzenarten in Niedersachsen. Verhandlungen der Gesellschaft für Ökologie 29, 505–510.

Brown, V.K., Southwood, T.R.E., 1987. Secondary succession: patterns and strategies. In: Gray, A.J., Crawley, M.J., Edwards, D.J. (Eds.), Colonization, Succession and Stability. Blackwell Scientific Publications, Oxford , pp. 315–337.

Burd, M., 1994. Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. Botanical Review 60, 83–139.

Butz Huryn, V.M., 1997. Ecological impacts of introduced honey bees. The Quarterly Review of Biology 72, 275–297.

Collinge, S.K., Forman, R.T.T., 1998. A conceptual model of land conversion processes: predictions and evidence from a microlandscape experiment with grassland insects. Oikos 82, 66–84.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.

Connor, E.F., McCoy, E.D., 1979. The statistics and biology of the species–area relationship. The American Naturalist 113, 791–833.

Connor, E.F., Courtney, A.C., Yoder, J.M., 2000. Individuals–area relationships: the relationship between animal population density and area. Ecology 81, 734–748.

Davis, B.N.K., Jones, P.E., 1986. Insects on isolated colonies of common rock-rose *Helianthemum chamaecistus*. Ecological Entomology 11, 267–281.

Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14, 342–355.

Dicke, M., Vet, L.E.M., 1999. Plant–carnivore interactions: evolutionary and ecological consequences for plant, herbivore and carnivore. In: Olff, H., Brown, V.K. (Eds.), Herbivores: Between Plants and Predators. Blackwell Science, Oxford , pp. 483–520.

Didham, R.K., Ghazoul, J., Stork, N.E., Davis, A.J., 1996. Insects in fragmented forests: a functional approach. Trends in Ecology and Evolution 11, 255–260.

Didham, R.K., Hammond, P.M., Lawton, J.H., Eggleton, P., Stork, N.E., 1998. Beetle species responses to tropical forest fragmentation. Ecological Monographs 668, 295–323.

Dolek, M., 1994. Der Einfluss der Schafbeweidung von Kalkmagerrasen in der Südlichen Frankenalb auf die Insektenfauna (Tagfalter, Heuschrecken). Paul Haupt, Bern.

Erhardt, A., 1985. Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grasslands. Journal of Applied Ecology 22, 849–861.

Evertz, S., 1995. Interspezifische Konkurenz zwischen Honigbienen (*Apis mellifera*) und solitären Wildbienen (Hymenoptera Apoidea). Natur und Landschaft 70, 165–172.

Fischer, M., Matthies, D., 1997. Mating structure and inbreeding and outbreeding depression in the rare plant *Gentianella germanica* (Gentianaceae). American Journal of Botany 84, 1685–1692.

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

Gilbert, F., Gonzales, A., Evans-Freke, I., 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. Proceedings of the Royal Society of London B 265, 577–582.

Gonzales, A., Lawton, J.H., Gilbert, F.S., Blackburn, T.M., Evans-Freke, I., 1998. Metapopulation dynamics, abundance and distribution in a microecosystem. Science 281, 2045–2047.

Goverde, M., Baur, B., Erhardt, A. 2002. Small-scale habitat fragmentation effects on pollinator behavior: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grassland. Biological Conservation 104, 293–299.

Gustafson, E.J., 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems 1, 143–156.

Gustafson, E.J., Gardner, R.H., 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77, 95–107.

Haddad, N.M., 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. Ecological Applications 9, 612–622.

Haddad, N.M., Baum, K.A., 1999. An experimental test of corridor effects on butterfly densities. Ecological Applications 9, 623–633.

Hanski, I., 1995. Effects of landscape pattern on competitive interactions. In: Hansson, L., Fahrig, L., Merriam, G. (Eds.), Mosaic Landscapes and Ecological Processes. Chapman & Hall, London, pp. 203–224.

Harrison, S., Bruna, E., 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22, 225–232.

Hill, J.K., Thomas, C.D., Lewis, O.T., 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia* comma butterflies: implications for metapopulation structure. Journal of Animal Ecology 65, 725–735.

Hill, J.K., Thomas, C.D., Lewis, O.T., 1999. Flight morphology in fragmented populations of a rare British butterfly, *Hesperia comma*. Biological Conservation 87, 277–283.

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

Holt, R.D., Debinski, D.M., Diffendorfer, J.E., Gaines, M.S., Martinko, E.A., Robinson, G.R., Ward, G.C., 1995. Perspectives from an experimental study of habitat fragmentation in an agroecosystem. In: Glen, D.M., Greaves, M.P., Anderson, H.M. (Eds.), Ecology and Integrated Farming Systems. John Wiley, Bristol, pp. 147–175.

Holyoak, M., Lawler, S.P., 1996. The role of dispersal in predator–prey metapopulation dynamics. Journal of Animal Ecology 65, 640–652.

Jennersten, O., 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. Conservation Biology 2, 359–366.

Kareiva, P., 1987. Habitat fragmentation and the stability of predator–prey interactions. Nature 326, 388–390.

Kareiva, P., Wennergren, U., 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373, 299–302.

Kearns, C.A., Inouye, D.W., Waser, N.M., 1998. Endangered mutualisms: the conservation of plant–pollinator interactions. Annual Review of Ecology and Systematics 29, 83–112.

Kéry, M., Matthies, D., Spillmann, H.-H., 2000. Reduced fecundity and offspring performance in small populations of the declining grassland plants *Primula veris* and *Gentiana lutea*. Journal of Ecology 88, 17–30.

Kruess, A., Tscharntke, T., 1994. Habitat fragmentation, species loss, and biological control. Science 264, 1581–1584.

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

Kuhlmann, M., 1998. Die Struktur von Stechimmenzönosen (Hymenoptera Aculeata) ausgewählter Kalkmagerrasen des Diemeltales unter besonderer Berücksichtigung der Nutzungsgeschichte und des Requisitenangebots. Dissertation. Universität Münster.

Kunin, W.E., 1993. Sex and the single mustard: population density and pollinator behavior effects on seed-set. Ecology 74, 2145–2160.

Kuussaari, M., Singer, M., Hanski, I., 2000. Local specialization and landscape-level influence on host use in an herbivorous insect. Ecology 81, 2177–2187.

Kwak, M.M., Velterop, O., van Andel, J., 1998. Pollen and gene flow in fragmented habitats. Applied Vegetation Science 1, 37–54.

Lack, A.J., 1982a. Competition for pollinators in the ecology of *Centaurea scabiosa* L. and *Centaurea nigra* L. I. Variation in flowering time. New Phytologist 91, 297–308.

Lack, A.J., 1982b. The ecology of flowers of chalk grassland and their insect pollinators. Journal of Ecology 70, 773–790.

LaSalle, J., Gauld, I.D., 1993. Hymenoptera: their diversity, and their impact on the diversity of other organisms. In: LaSalle, J., Gauld, I.D. (Eds.), Hymenoptera and Biodiversity. CAB International, Wallingford, UK, pp. 1–26.

Lawton, J.H., 1983. Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology 28, 22–39.

Lawton, J.H., 1995. Population dynamic principles. In: Lawton, J.H., May, R.M. (Eds.), Extincton Rates. University Press, Oxford, pp. 147–163.

Levin, D.A., Anderson, W.W., 1970. Competition for pollinators between simultaneously flowering species. American Naturalist 104, 455–467.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. University Press, Princeton.

Matthies, D., Schmid, B., Schmid-Hempel, P., 1995. The importance of population processes for the maintenance of biological diversity. Gaia 4, 199–209.

Mopper, S., Strauss, S.Y., 1998. Genetic Structure and Local Adaptation in Natural Insect Populations: Effects of Ecology, Life History, and Behaviour. Chapman and Hall, New York, USA.

Morris, M.G., 1967. Differences between the invertebrate faunas of grazed and ungrazed chalk grassland I. Responses of some phytophagous insects to cessation of grazing. Journal of Applied Ecology 4, 459–474.

Morris, M.G., 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. Biological Conservation 95, 129–142.

Mortimer, S.R., Hollier, J.A., Brown, V.K., 1998. Interactions between plant and insect diversity in the restoration of lowland calcareous grasslands in southern Britain. Applied Vegetation Science 1, 101–114.

Neff, J.L., Simpson, B.B., 1993. Bees, pollination systems and plant diversity. In: LaSalle, J., Gauld, I.D. (Eds.), Hymenoptera and Biodiversity. CAB International, Wallingford, UK, pp. 143–168.

Niemelä, J., Baur, B., 1998. Threatened species in a vanishing habitat: plants and invertebrates in calcareous grasslands in the Swiss Jura mountains. Biodiversity and Conservation 7, 1407–1416.

Norton, M.R., Hannon, S.J., Schmiegelow, F.K.A., 2000. Fragments are not islands: patch vs landscape perspectives on songbird presence and abundance in a harvested boreal forest. Ecography 23, 209–223.

Oostermeijer, J.G.B., van Eijck, M.W., den Nijs, J.C.M., 1994. Offspring fitness in relation to population size and genetic variation in the rare perennial plant species *Gentiana pneumonanthe* (Gentianaceae). Oecologia 97, 289–296.

Pykälä, J., 2000. Mitigating human effects on European biodiversity through traditional animal husbandry. Conservation Biology 14, 705–712.

Rathcke, B.J., Jules, E.S., 1993. Habitat fragmentation and plant–pollinator interactions. Current Science 65, 273–277.

Ritchie, M.E., Olff, H., 1999. Herbivore diversity and plant dynamics: compensatory and additive effects. In: Olff, H., Brown, V.K., Drent, R.H. (Eds.), Herbivores: Between Plants and Predators. Blackwell Science Ltd, Oxford , pp. 175–204.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time. University Press, Cambridge.

Rushton, S.P., Eyre, M.D., Luff, M.L., 1990. The effects of scrub management on the ground beetles of oolitic limestone grasslands at Castor Hanglands National nature reserve, Cambridgeshire, UK. Biological Conservation 51, 97–111.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5, 18–32.

Schaffer, W.M., Zeh, D.W., Buchmann, S.L., Kleinhans, S., Schaffer, M.V., Antrim, J., 1983. Competition for nectar between introduced honey bees and native North American bees and ants. Ecology 64, 564–577.

Settele, J., Pauler, R., Kockele, K., 1995. Magerrasennutzung und Anpassungen bei Tagfaltern: Populationsökologische Forschung als Basis für Schutzmaßnahmen am Beispiel von *Glaucospyche ( Maculina) arion* (Thymian-Ameisenbläuling) und *Glaucospyche ( Maculina) rebeli* (Kreuzenzian-Ameisenbläuling). Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege 83, 129–158.

Siemann, E., Tilman, D., Haarstad, J., Ritchie, M., 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. American Naturalist 152, 738–750.

Sowig, P., 1989. Effects of flowering plant's size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera: Apidae). Oecologia 78, 550–558.

Steffan-Dewenter, I., 1998. Wildbienen in der Agrarlandschaft: Habitatwahl, Sukzession, Bestäubungsleistung und Konkurrenz durch Honigbienen. Verlag Agrarökologie, Bern..

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

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

Steffan-Dewenter, I., Tscharntke, T., 2000b. Resource overlap and possible competition between honey bees and wild bees in central Europe. Oecologia 122, 288–296.

Strong, D.R., Lawton, J.H., Southwood, R., 1984. Insects on Plants. Blackwell Scientific Publications, Oxford.

Sutcliffe, O., Thomas, C.D., Peggie, D., 1997. Area-dependent migration by ringlet butterflies generates a mixture of patchy population and metapopulation attributes. Oecologia 109, 229–234.

Thomas, C.D., 2000. Dispersal and extinction in fragmented landscapes. Proceedings of the Royal Society of London Series B 267, 139–145.

Thomas, C.D., Harrison, S., 1992. Spatial dynamics of a patchily distributed butterfly species. Journal of Animal Ecology 61, 437–446.

Thomas, C.D., Thomas, J.A., Warren, M.S., 1992. Distribution of occupied and vacant butterfly habitats in fragmented landscapes. Oecologia 92, 563–567.

Thomas, C.D., Hill, J.K., Lewis, O.T., 1998. Evolutionary consequences of habitat fragmentation in a localized butterfly. Journal of Animal Ecology 67, 485–497.

Thomas, J.A., 1991. Rare species conservation: case studies of European butterflies. In: Spellerberg, I.F., Goldsmith, F.B., Morris, M.G. (Eds.), The Scientific Management of Temperate Communities for Conservation. Blackwell Scientific Publications, Oxford, UK, pp. 149–198.

Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2–16.

Tischendorf, L., Fahrig, L., 2000. On the usage and measurement of landscape connectivity. Oikos 90, 7–19.

Tscharntke, T., 1997. Vertebrate effects on plant–invertebrate food webs. In: Gange, A.C., Brown, V.K. (Eds.), Multitrophic Interactions in Terrestrial Systems. Blackwell Science, Oxford, pp. 277–297.

Tscharntke, T., Kruess, A., 1999. Habitat fragmentation and biological control. In: Hawkins, B.A., Cornell, H.V. (Eds.), Theoretical Approaches to Biological Control. Cambridge University Press, Cambridge, pp. 190–205.

Tscharntke, T., Gathmann, A., Steffan-Dewenter, I., 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. Journal of Applied Ecology 35, 708–719.

Völkl, W., Zwölfer, H., Romstöck-Völkl, M., Schmelzer, C., 1993. Habitat management in calcareous grasslands: effects on the insect community developing in flower heads of Cynarea. Journal of Applied Ecology 30, 307–315.

Ward, L.K., Lakhani, K.H., 1977. The conservation of juniper: the fauna of foodplant island sites in Southern England. Journal of Applied Ecology 14, 121–135.

Waser, N.M., Chittka, L., Price, M.V., Williams, N.M., Ollerton, J., 1996. Generalization in pollination systems and why it matters. Ecology 77, 1043–1060.

With, K.A., Gardner, R.H., Turner, M.G., 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos 78, 151–169.

With, K.A., Cadaret, S.J., Davis, C., 1999. Movement responses to patch structure in experimental fractal landscapes. Ecology 80, 1340–1353.

Wolf, R., Zimmermann, P., 1996. Wacholderheiden am Ostrand des Schwarzwaldes (Landkreis Calw). Verbreitung, Flora, Fauna, Gefährdung, Schutz und zukünftige Entwicklung. Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg 88, 1–616.

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