

Characteristics of insect populations on habitat fragments: A mini review

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Modern human-dominated landscapes are typically characterized by intensive land-use and high levels of habitat destruction, often resulting in sharply contrasted habitat mosaics. Fragmentation of remaining habitat is a major threat to biodiversity. In the present paper, we focus on the different features of habitat fragmentation. First we discuss the importance of pure habitat loss, fragment size, fragment isolation and quality, edge effects, and the importance of landscape structure. Second, we characterize life-history features of fragmentation-sensitive species, showing that rare, specialized, little dispersing species are most affected, as well as species characterized by high population variability and a high trophic position, while the effect of body size is unclear. Third, we discuss the conservation value of habitat fragments. The question arises how to relate studies on population survival to those of community structure and studies on biodiversity to those on ecological functions. Despite the general superiority of large to small reserves, only small or medium-sized reserves are available in many human-dominated landscapes. A great number of small habitats covering a wide range of geographic area should maximize beta diversity and spreading of risk and may be very important for the regional conservation of biodiversity, in contrast to the prevailing arguments in favor of large habitats. Finally, landscape context influences community structure of fragments, and communities are composed of species that experience the landscape on a broad range of spatial scales. Spatial arrangement of habitat fragments in a landscape appears to be important only in simple, not complex landscapes.

Key words: conservation; landscape structure; reserve design; scale dependence; trophic interactions.

INTRODUCTION

Modern human-dominated landscapes are typically characterized by intensive land-use and high levels of habitat destruction. In Germany, agricultural land-use affects more than half of the area resulting in sharply contrasted habitat mosaics. In these agricultural landscapes, fragmentation of remaining habitats is a major threat to biodiversity and an important issue in landscape management (see, for example, Wilcove *et al.* 1986; Baur & Erhardt 1995; Matthies *et al.* 1995; Tscharntke *et al.* 2002). Several characteristics of habitat frag-

ments such as size, isolation, proportion of edges, and habitat quality, as well as characteristics of the surrounding landscape are known to influence abundance of populations and diversity of communities, but the relative importance of each characteristic is mostly unknown. Further, some species are systematically disadvantaged on small or isolated habitats, so both community structure and interactions of species with their biotic or abiotic environment may change (Pimm 1991; Lawton 1995). Loss of favorable interactions may handicap, while the disruption of antagonistic interactions may favor local target populations. For example, an increase in biotic interactions may increase both pollination and seed predation of plants (Steffan-Dewenter *et al.* 2001). The disruption of interactions may also lead to additional, so-called secondary extinctions (Wilcove *et al.* 1986).

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In the following, we give a short overview of the main characteristics of habitat fragmentation and discuss the features of fragmentation-sensitive species. This will end in a discussion of open questions concerning the conservation and management of fragmented landscapes; for example, the conservation value of small habitat fragments and the role of landscape context for fragmented communities.

Which features of habitat fragmentation matter?

Pure habitat loss

Habitat connectivity or size of habitat fragments may be of minor importance when species are highly vagile (Andr n 1994; S derstr m & P rt 2000). For example, population density of the black woodpecker (*Dryocopus martius*) did not differ between a forest landscape (80% forest) and a forest-farmland landscape (26% forest) (Tjernberg *et al.* 1993). Woodpeckers, like many other birds, can pool the resources from different habitat fragments by enlarging their home range (see Redpath 1995). In such cases with an obvious lack of dispersal limitation, habitat fragmentation can be described as a pure quantitative effect of habitat loss and thus differs fundamentally from the qualitative effects of fragmentation discussed below (see Fahrig 1997). However, there are often critical thresholds, viz. transition ranges across which small changes in overall habitat area or spatial pattern produce abrupt shifts in ecological responses (With & Crist 1995).

Fragment size

The area-*per se* hypothesis claims that large islands have high immigration and low extinction rates (MacArthur & Wilson 1967). Despite this equilibrium theory of island biogeography, many islands and habitat fragments are non-equilibrium systems. Random extinction events are less probable on large islands supporting large populations (Shaffer 1981). A true area effect will arise when the habitat forms a distinctive and homogeneous habitat, whereas in large habitats area *per se* and habitat heterogeneity are difficult to separate (Whittaker 1998). In any case, area or fragment

size has turned out to be a simple parameter of high predictive value for species richness.

Fragment isolation

Large distances of habitat islands to the nearest species pool reduce colonization rates (MacArthur & Wilson 1967; Thomas *et al.* 1992), assuming that other possible effects such as area, type of adjacent vegetation and regional features of the source communities are equal (see Ricketts 2001). In real landscapes, habitat area and isolation are often closely correlated. Experimental designs may reflect both aspects simultaneously in that a reduction in area parallels an increase in isolation (Golden & Crist 1999), but area and isolation can be also separated (as independent predictor variables) with a corresponding selection of field sites (e.g. Zabel & Tschardt 1998; Steffan-Dewenter & Tschardt 2000) or experimentally (e.g. Steffan-Dewenter & Tschardt 1999; Kruess & Tschardt 2000a). When remaining habitats cover less than 20% of the landscape, distance between patches of original habitat exponentially increases (Andr n 1994; see Fahrig 1997 for a 20% rule). Close to this critical threshold, an extra loss of habitat will suddenly disrupt landscape connectivity. Landscape connectivity does not need to imply structural connectivity (by corridors, Rosenberg *et al.* 1997; Collinge 2000), but functional connectivity (by dispersal), which is species and landscape specific (see With *et al.* 1999; Tischendorf & Fahrig 2000). The degree of isolation or hostility of the environment, respectively, is often difficult to assess due to limited information on the organisms' dispersal or gap-crossing ability.

Edge effects

Edges are the places where two habitat types come together, and the transition zones are called ecotones. Edges first caught the attention of wildlife managers because of the enhanced numbers of game species, and over the years the edge effect meant a general increase in wildlife species richness and abundance (Hunter 1990). In contrast to these positive effects, many species avoid edges, and small habitats have been devalued for conservation because of their high proportion of edges. Life is different at fragment edges due to changes

in microclimate (temperature, humidity, wind velocity etc.) or due to invasions by, for example, aerial plankton (seed rain, tiny arthropods) or immigrants. In addition, impact of pesticides (insecticides, herbicides) that are applied in crop fields affects edges of natural habitats. Relative importance of edge size and, consequently, importance of such disturbances, depends on the geometrical form of the habitat (see Laurance & Yensen 1991). Strip margins along arable fields are completely determined by edge effects, whereas in circular habitats, proportion of edges is at a minimum (Diamond & May 1981; Denys & Tschardtke 2002). These different conditions near habitat edges often reduce the survival of species typical for the original habitat, while opportunistic species from the outside may successfully invade, causing either the interruption or enhancement of biotic interactions such as predation and parasitism rates. The interruption may be expected from specialized host–parasitoid interactions and the possible control of herbivorous insects (Thies & Tschardtke 1999; Kruess & Tschardtke 2000a), whereas bird-nesting success near forest edges is often reduced due to increased mortality by hawks and brood parasites (Paton 1992).

Fragment quality and productivity

The habitat-heterogeneity hypothesis claims that large areas are more likely to include different habitat types than small areas, and different habitats support different communities in most cases. Area and heterogeneity often correlate so closely that either variable is equally useful in predicting species richness (Rosenzweig 1995). Strong habitat-heterogeneity effects should be more likely than pure area effects when taxa show: (i) high degrees of habitat specialization; and (ii) require only a small area due to high population densities (see Ricklefs & Lovette 1999). In many cases, reductions in the size of habitats are correlated with changes in soil conditions (e.g. with increasing fertility and decreasing humidity which may result from anthropogenic fertilization and drainage in the adjacent area), translating to plant growth changes. Even in plant monocultures, which usually look very much alike at first glance, resource quality of the arthropod community may change with stand size. Small stands of bracken

(*Pteridium aquilinum*) or common reed (*Phragmites australis*) have significantly smaller fronds or shoots, respectively, than large stands (Rigby & Lawton 1981; Tschardtke 1992). In contrast, small marine islands often have much higher productivity per unit area than large islands which may lead to higher population densities and lower extinction rates (Andersen & Wait 2001). Effects of fragment size may be clouded by such changes in food quantity and complexity, as resource biomass is often more important than resource heterogeneity in determining insect diversity (see Waide *et al.* 1999; Koricheva *et al.* 2000). In such cases, an experimental approach with standardized, potted plants that are exposed to monitor insect colonization may give more reliable results (Kruess & Tschardtke 1994; Steffan-Dewenter & Tschardtke 1999).

Landscape mosaic

Ecological processes of a given ecosystem are, in part, a function of the landscape structure (see below). In terrestrial habitat fragments, distance to the nearest habitat is only one parameter of the landscape matrix, and the focal species may use both the habitat and parts of the surrounding shifting mosaic of habitats giving rise to even inverse relations between population density and fragment area (see Debinsky & Holt 2000; Norton *et al.* 2000; Ricketts 2001). On a geographic scale, characteristics of both the habitat fragments and the surrounding landscape may change, with differential contributions to population survival and species richness. Spatial variation in heritable traits of plant and insect populations may further shape regionally specific plant-insect assemblages (Mopper & Strauss 1998; Kuussaari *et al.* 2000; Thomas *et al.* 2001).

Which species are disadvantaged by habitat fragmentation?

Rarity

Rarity is a well-known precursor of extinction (Gaston 1994). Red-Data books mostly rely on information on the abundance of species as an estimate of their status. Local abundance and regional distribution are significantly correlated, so rare

species suffer from a double jeopardy (Cornell & Lawton 1992; Lawton 1995; Hanski & Gyllenberg 1997). The plausible hypothesis that species whose rarity is caused by anthropogenic reasons are more disadvantaged than species whose rarity is a pristine or long-term characteristic of the species, needs to be tested. Population density may remain constant across island size as predicted by the traditional equilibrium theory, but may also be smaller or larger than expected from habitat area alone (Connor *et al.* 2000). In a study on butterflies of grassland habitats, specialists had reduced densities on small fragments, while generalists increased densities due to the contribution of the surrounding landscape matrix (Steffan-Dewenter & Tscharntke 2000).

Population variability

Species with fluctuating populations should be more prone to local extinctions than species with stabilized populations. The more variable the population size, the higher the susceptibility to environmental stochasticity and the more likely it is for population size to become zero within a period of time (Schoener & Spiller 1992; Fagan *et al.* 2001). Fluctuations of local carabid subpopulations are significantly larger than the overall fluctuations, due to metapopulation dynamics of interconnected local populations (den Boer 1990). Greatly fluctuating populations of noctuid moths and aphids show regionally concurrent fluctuations (Hanski & Woiwood 1993; see Lawton 1995). Such concurrent fluctuations may relativize the idea of compensatory immigrations within metapopulations (Tscharntke 1992). Rarity and population variability may be closely correlated, as has been shown for clover and nettle insects (Kruess & Tscharntke 1994; Zabel & Tscharntke 1998).

Trophic position

Populations at the top of food chains are more likely to become extinct than those of lower trophic levels (Pimm 1991; Lawton 1995; Holt *et al.* 1999). Parasitoids are mostly host specific (in comparison to most predators, which are relatively little specialized) and have been found to be more

affected by area loss or increased isolation than their hosts. This is shown by Schoener *et al.* (1995) with their study on parasitoid fraction on the Bahamian islands, Golden and Crist (1999) with insect samples from experimentally fragmented fallows, Kruess and Tscharntke (1994, 2000a,b) with field studies and experiments using clover and vetch insects, Tscharntke *et al.* (1998) with the natural enemies of trap-nesting bees and wasps, van Nouhuys and Hanski (1999) in a butterfly parasitoid metapopulation, and Scherer and Tscharntke (1995) in ant lion populations parasitized by a chalcid wasp.

Body size

The size of organisms is the most apparent aspect of their life history. Large species reproduce more slowly, need more energy and resources, and have larger home ranges than small ones. This is why they are often greatly affected by disturbances such as habitat fragmentation. In addition, size is negatively correlated with abundance and many large species have a high trophic position (e.g. raptors or carnivorous mammals). Accordingly, body size is related to other features of endangered species. In contrast, large species tend to have better dispersal abilities to bridge hostile areas within their home ranges (shown by many birds, see above). Accordingly, the relation of body size to the species' susceptibility to habitat fragmentation is ambiguous (see Whittaker 1998; Davies *et al.* 2000).

Specialization

In general, habitat specialists are more susceptible to extinctions than generalists (With & Crist 1995; Zabel & Tscharntke 1998; Steffan-Dewenter & Tscharntke 2000). For monophagous or otherwise specialized herbivores the landscape produces a certain pattern of isolated habitat islands, whereas for polyphagous species, these islands may be connected by further usable habitat patches, thereby producing a habitat continuum. With respect to the natural enemies of pest insects, the mostly specialized, monophagous parasitoids should be more affected than the mostly less specialized, polyphagous predators. Species with a

fine-grained habitat use depend on different habitat parts and a blend of resources that are less likely to occur on small patches and, thereby, contrast with species exhibiting a coarse-grained habitat use. For example, bees need both suitable nesting sites and pollen plants (Gathmann *et al.* 1994; Tscharrntke *et al.* 1998), parasitoids depend on a spatially and temporally co-occurrence of hosts and nectar (Russell 1989), and birds may use a number of different habitat patches within their home range (Redpath 1995). In contrast to such fine-grained patch use, several monophagous insect herbivores (e.g. on thistles or common reed) may spend their whole life (feeding, copulating, ovipositing) on the one host plant only (Zwölfer & Harris 1971; Tscharrntke 1999).

Dependence on mutualists

Plants, animals, and micro-organisms are mostly considered to be separate entities, thereby largely ignoring the fact that most organisms do not live on their own, but depend on more or less intimate interactions with other species (see Redfearn & Pimm 1987). Availability of mutualists may be reduced in small and isolated habitats, so species depending on pollinators, fungi, or seed dispersers should be more affected than non-dependent species. Isolated patches of flowering plants receive fewer visits by pollinating insects, leading to reduced seed set (Jennersten 1988; Steffan-Dewenter & Tscharrntke 1999). Plant-fungal symbiosis may be disrupted, and the absence of mycorrhiza or of grass endophytes may dramatically decrease plant survival (Sanders *et al.* 1995; see Brown & Gange 2002). Like extinction of mutualists, extinction of keystone species may cause the extinction of cascades of dependent species. In the common reed *Phragmites australis*, many insect species depend on shoots damaged by a stem-boring moth, although this abundant noctuid moth is characterized by flush-crash cycles and local extinctions (Tscharrntke 1992, 1999).

Dispersal ability

Communities of small islands are characterized by high turnover rates. Bad dispersers are less common in a fragmented landscape, and isolated

patches are dominated by species with high dispersal abilities (Bunce & Howard 1990; den Boer 1990; de Vries *et al.* 1996; Thomas 2000). Many species have to travel between patches, as critical resources are found in patches of different types, called landscape complementation (Dunning *et al.* 1992). Simulation models by Fahrig (2001) showed that information on movement rates of organisms in fragmented landscapes are critical for predicting extinction thresholds, but little is known of the dispersal ability of most groups. These simulations also predict that the higher the emigration rate, the more habitat is required for regional population survival. This result may be counter-intuitive, as dispersal is generally viewed to be positive. However, the probability of successful colonization does not only depend on the species' traits, but also on the landscape matrix, and survival rates of dispersers depend on matrix quality (Fahrig 2001). Small populations may be 'rescued' by conspecific immigrants from nearby source populations (Brown & Kodric-Brown 1977). As good dispersers tend to be bad competitors, patterns of coexistence should change in habitat fragments (Kareiva & Wennergren 1995). Successful colonizers have usually one of two possible strategies (Corbet 1995; Tscharrntke & Greiler 1995). First, many are small-bodied members of the aerial plankton, such as small-seeded plants, aphids and thrips, and therefore widely dispersed. Second, in species that are too large to be transported as aerial plankton, body size and foraging range are positively correlated, exemplified by carabid beetles (den Boer 1990), wild bees (Gathmann *et al.* 1994; Steffan-Dewenter & Tscharrntke 1999), and butterflies (Hodgson 1993; Steffan-Dewenter & Tscharrntke 1997). In four insect species that have increased the variety of colonized habitat types in Great Britain, the increase in habitat breadth and dispersal tendencies led to enhanced expansion rates (Thomas *et al.* 2001). Insects differ from vertebrates as they have smaller home ranges and fewer dispersal capabilities (as far as they are not part of the aerial plankton). Accordingly, they are more affected by isolation barriers, but can cope better with small habitat fragments. As the public is more concerned with vertebrates than with invertebrates, area effects appear to be more popular than isolation effects.

The conservation value of habitat islands: Conclusion and outlook

Evaluations of the conservation value of habitat islands consider the above-mentioned abiotic and biotic features, but are often difficult, because there is little scientific basis to prioritize arguments.

Populations or communities?

What is the significance of fine-filter conservation with a focus on populations of umbrella, flagship and indicator species (Simberloff 1998)? Coarse-filter conservation with a focus on communities or landscapes often appears to be more appropriate (Schwartz 1999). Measures of success in species conservation are clear in that the persistence of populations is success, while extinction is failure. In contrast, measures of success in community conservation is often unclear, because relative importance of community features is controversial. Species are known to greatly differ in their response to landscape structure and there is no common threshold value for the amount of habitat across species (Fahrig 2001). Further, interacting species experience the world at different spatial scales (Holt 1996), and ecological traits may vary among regions (Thomas *et al.* 2001).

Communities or interactions, species richness or ecological functions?

Species are differentially affected by characteristics of habitat fragmentation such as isolation, area and habitat quality. Are the resulting changes in community structure, interspecific interactions and ecological functions more or less significant than estimates of biological diversity? Fragmentation is usually considered in the context of conservation, but is also related to the efficiency of biological control in the agricultural landscape (Kareiva 1987, 1990; Thies & Tschardtke 1999; Tschardtke & Kruess 1999). Schoener *et al.* (2001) found that a major hurricane in the Bahamas led to the extinction of lizard populations only on those islands where a predator had been introduced. What is the relative importance of biodiversity and ecological functions in landscape planning? These are still

two separate issues. Species richness and the strength of interactions often covary (Didham *et al.* 1996; Tschardtke & Kruess 1999; but see Denys & Tschardtke 2002). However, it is still controversial as to which mechanisms create a positive relationship between biodiversity and ecological functions (Naeem 2000; Wardle *et al.* 2000). Is it the importance of a complementary action exerted by many species or a sample effect in that many species increase the probability to have the right or most efficient species included?

What about the conservation value of small habitats?

In Germany in 1993, about 5000 reserves protect about 2% of the country. These are complemented by at least 40 000 very small reserves ('natural monuments', estimation for only former western Germany) with an area of only hundreds to maximally thousands of square meters (and rarely up to 2–5 ha, Jedicke 1994). This reality of a mosaic of small-scale reserves is in contrast to the recent emphasis on large-scale conservation (see Schwartz 1999).

Boecklen (1986) found in an analyses of a large USA bird census data set that habitat heterogeneity is a significant predictor of species richness even after area has been factored out. In most cases, several small reserves incorporate a wider array of habitat types and thus support more species than the single large option. Several small fragments of calcareous grasslands supported more butterfly species, even when only endangered species were considered, than the same area composed of only one or two fragments. Further, analyses of insects on legumes showed trophic-level differences in the response to 'single large or several small' fragments (SLOSS, see Quinn & Harrison 1988), as species numbers of parasitoids, but not of herbivores, benefited from habitat subdivision in landscapes (Kruess & Tschardtke 2000b; Tschardtke *et al.* 2002). There is no debate on the general superiority of large to small reserves, but in many human-dominated landscapes, only small or medium-sized reserves are still available. The argument of Soulé and Simberloff (1986) that 'nature reserves should be as large as possible, and there should be many of them' is irrefutable, but in the agriculturally dominated landscapes of Central Europe, where

only a small fraction of the area is reserved for conservation, maximum species richness will not be achieved by focusing strictly on large reserves. In human-dominated landscapes, an intermediate-fragmentation strategy of habitat conservation considers that small habitat fragments cover such a wide range of geographic area that beta diversity and spreading of risk are maximized, and that large habitat fragments are close enough to enable dispersal among fragments, to reduce extinction probability of area-sensitive species, and to stabilize predator–prey interactions (Tscharntke *et al.* 2002).

Overriding effects of the landscape context?

The area around habitat fragments may offer only suboptimal resources, but may still function as a foraging area and, thereby, permanently enhance the fragments' populations (Zschokke *et al.* 2000; Fahrig 2001). In a Swedish study on the role of local and regional effects for butterfly communities, landscape structure was more important for butterfly diversity than the local farming system (Weibull *et al.* 2000).

Landscape ecology analyzes ecological processes in relation to a range of local and regional spatial scales. Communities are composed of species that experience the landscape on a broad range of spatial scales (Holt 1996; Debinsky & Holt 2000). Which landscape scale is appropriate for conservation management when the survival of some species is determined by small landscape sectors, whereas others are affected by much larger sectors? For example, forest fragmentation affects parasitoid survival and tent caterpillar outbreaks (Roland & Taylor 1995, 1997). The spatial scale at which forest structure had its greatest effect differed among parasitoid species depending on the parasitoids' body size. Similarly, local abundance of flower-visiting honey-bees was best explained by a much larger landscape sector than the abundance of solitary bees, which are known to have a smaller home range (Steffan-Dewenter *et al.* 2002). In general, the abundance and distribution of species with large home ranges or high trophic levels should depend on larger spatial scales than species with little home ranges or low trophic levels (Holt 1996), and such differences may affect community structure and interactions.

What is the relative importance of area loss and spatial arrangement of habitat?

Is the loss of area of overriding importance or does the pattern of fragmentation contribute to the conservation of species and interactions? Fahrig (1997) and Harrison and Bruna (1999) argue that only habitat loss is of major importance, whereas Kareiva and Wennergren (1995) argue that the spatial arrangement of habitat fragments may compensate for overall habitat loss and mitigate extinction risks. The relative importance of local habitat quality for the strength of biotic interactions may decrease with increasing complexity of the surrounding landscape (Thies & Tscharntke 1999; Östman *et al.* 2001). Edge effects in the parasitism of rape pollen beetles, due to old field margins adjacent to crop fields, could only be shown in simple, but not complex, landscapes with a threshold of 20% non-crop area (Tscharntke *et al.* 2002). These findings support mathematical models that predict increasing effects of fragment area and isolation with decreasing proportions of suitable habitat in a landscape (Andrén 1996).

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