PLANT-INSECT INTERACTIONS IN FRAGMENTED LANDSCAPES

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Key Words metapopulation, trophic interactions, biodiversity, dispersal ability, spatial ecology

Abstract Population and community ecology need a large-scale perspective because local patterns (of biodiversity) and processes (trophic interactions) are influenced by the regional setting. The ratio of the foraging range and/or dispersal ability to the distance between landscape elements influences local population dynamics. The spatial scale experienced by a species may be linked to its trophic level and also to traits such as body size, resource specialization, rarity, and population size variability. Hence, communities are assemblages of species with different spatial strategies. Effects of habitat loss and habitat fragmentation on plant-herbivore, herbivore-enemy, as well as plant-pollinator interactions are contingent on species and landscape. Metapopulation theory provides a unifying frame to approach plant-insect systems across fragmented landscape, although the landscape context is often ignored. In some cases theory is far ahead of empirical research. We call for more population data on large spatial and temporal scales to better understand plant-insect populations across fragmented landscapes.

INTRODUCTION

During the past decade, the issue of space has become an important topic in ecology (105, 125). It became increasingly clear that the occurrence of species and their population densities, as well as population dynamics, trophic interactions, and community structure within a habitat, may depend on processes at larger spatial scales (48, 82, 125). Hence, one has to consider size, spatial arrangement, connectivity, quality of habitats, and the landscape context (sometimes called landscape matrix) in which the habitats are embedded to understand local patterns and processes. Multihabitat use, i.e., foraging among different habitat types, as well as landscape context substantially determine or even dominate local patterns and processes (141, 147). This calls for a large-scale perspective in population and community ecology (30, 77, 118, 156). Agricultural intensification has led to
considerable losses in habitat diversity at multiple spatial and temporal scales (8). Habitat destruction and the fragmentation of remaining habitat is a major issue in the management of landscapes, because habitat fragmentation has great effects on the occurrence of species and thus biodiversity (6, 132, 155, 159, 174).

Communities, however, are made up of species with different spatial strategies (36, 81, 141). The spatial scale of population processes is contingent on the species’ trophic level (74, 96, 117). Hence, decreasing size and connectivity of habitats as well as changes of the landscape type between habitats may not only decrease population densities and species richness, but also disrupt plant-herbivore, herbivore-enemy, and plant-pollinator interactions (26, 103, 144, 158). Our review on plant-insect interactions explores four topics.

- Effects of the landscape context on populations and communities of herbivorous insects. We review empirical evidence for the relative importance of local and regional processes for community structure and include a discussion of “functional” spatial scales, the size and spatial configuration of habitats, as well as the landscape type between habitats.
- The effect of landscape context on trophic interactions. We expand on the above note that the response of a species to habitat fragmentation depends on its trophic position.
- The theory of population dynamics and trophic interactions under a landscape perspective. We provide a short guide through the theory and patterns predicted from the available theory.
- The spatial structure of insect populations on a landscape scale. In particular, we approach the question whether herbivorous insects are organized as metapopulations and to what extent metapopulation models allow predictions for population dynamics in real landscapes.

POpulations and communities in fragmented landscapes

In human-dominated landscapes, agricultural land use often produces landscapes with a mosaic of sharply contrasted habitat types (159). In Table 1, we list five characteristics of habitat fragments that affect occurrence and population density of species and, consequently, biodiversity.

Characteristics of habitat fragments

Habitat isolation depends on both the hostility of the environment and the organism’s gap-crossing ability (123, 135, 154, 178). Thus to understand isolation, one must consider the distance to all potential source populations, the size of these populations (106), and the landscape between habitat fragments (patches; Figure 1). In real landscapes, total habitat area and isolation are often closely correlated. This
TABLE 1  Characteristics of habitat fragments (patches) in relation to possible processes and patterns of insect communities

<table>
<thead>
<tr>
<th>Characteristics of habitat fragments</th>
<th>Possible processes and patterns</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fragment area</td>
<td>Large fragments have high immigration and low extinction rates.</td>
<td>(132, 138, 170)</td>
</tr>
<tr>
<td>Fragment isolation</td>
<td>Colonization rates decrease with distance to the nearest conspecific population; immigration by nearby populations may “rescue” fragmented populations.</td>
<td>(12, 123, 152)</td>
</tr>
<tr>
<td>Fragment geometry</td>
<td>Edge effects may increase biodiversity due to the transition zone between habitat types but negatively affect survival of species typical for the original habitat. Percentage of edges changes with habitat geometry.</td>
<td>(23, 24, 76, 95)</td>
</tr>
<tr>
<td>Fragment quality</td>
<td>Large patches provide usually higher heterogeneity, and thereby, support different communities. Small patches are particularly affected by the surrounding landscape, changing nutrient availability, ground water level, and plant growth.</td>
<td>(124, 126, 132, 150, 155)</td>
</tr>
<tr>
<td>Landscape around fragments</td>
<td>Highly vagile species without significant dispersal limitation are affected by habitat loss only, and not by fragmentation per se. Hostility of the fragment’s environment depends on the organisms’ often unknown dispersal or gap-crossing abilities and the contribution of nonhabitat use. Interacting communities are made up of species with different spatial strategies. Several small patches often enclose more species than single large habitats.</td>
<td>(2, 19, 29, 38, 77, 93, 121, 123, 139, 144, 148, 156, 159, 169, 170, 177)</td>
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may be simulated in experimental designs (49) or analyzed as independent factors (91, 145, 152, 179). Landscape connectivity does not need to imply structural connectivity [by dispersal along corridors; (15, 53, 131)], but rather functional connectivity [by dispersal independent of corridors; (154, 176)]. Overall, contingent on the species, the landscape context may facilitate (Figure 1d) or impede (Figure 1e) movements of insects among habitat patches.

In addition to habitat area and isolation or connectivity, characteristics of habitat fragments such as habitat quality influence population survival and biodiversity within habitats (27, 153, 155). Fragment area–sensitive changes in habitat quality and productivity may cloud species-area relationships because resource availability may be more important than habitat area in determining insect diversity (88, 165,
Patch models:

(a) Patchy population  (b) Multihabitat population  (c) Classic metapopulation

Landscape models:

(d) Facilitation  (e) Inhibition  (f) Neutral
Importance of habitat heterogeneity compared to pure habitat area for biodiversity should be strong when the focal insect groups show (a) high degrees of habitat specialization and (b) high densities, thereby requiring only a small area for persistence (124).

Importance of edge effects is related to habitat geometry and the landscape context (matrix). Depending on the adjacent habitat type, the transition zone between the fragment and its neighboring habitat may exhibit increased or decreased species richness compared to the original habitat (76). Life is different in edges because of microclimate, invasion of aerial plankton, human-caused agrochemicals, and changed strength of trophic interactions (95, 181). For example, mortality of *Vicia* pod–inhabiting seed beetles due to parasitoids is lower near grassland edges than in the center (92), whereas birds nesting near forest edges usually suffer from enhanced predation and brood parasites (116).

### The Landscape Context

The surrounding landscape determines how area and geometry of habitat fragments affect local community structure. Hence, local factors (such as local management practices) and regional factors (such as distance to high-diversity habitats) determine local biodiversity (75, 79, 84, 85, 123, 139, 141). Spillover effects from adjacent natural or managed habitats may greatly change insect diversity and food web interactions (10, 23, 68, 122). There is empirical evidence that effects of habitat arrangement on biological control is of considerable importance in simple but not in complex landscapes (89, 114, 159). For example, old fallow strips adjacent to annual crop fields of oilseed rape provide overwintering sites for the parasitoids of the rape pollen beetle, a major oilseed rape pest. Such old fallow strips increase parasitism rates by a factor of three in the center of the field (148). However, this edge effect holds only for simple landscapes, characterized by high percentages of annual crop fields. In complex landscapes, characterized by low percentages of annual crop fields and a diversity

![Figure 1](https://example.com/figure1.png)

**Figure 1** Scenarios of possible interactions between species and landscape. Each quadrat is a landscape with at least one type of habitat (black circles, gray quadrat). Scenario (a) applies to species with a large foraging range. Individuals may forage across a large fraction of patches on a daily basis. These species form a patchy population. Scenario (b) is a variant of (a), where a species use two different habitats (e.g., one habitat for breeding and one for foraging). Scenario (c) presents the classic metapopulation. Species form local populations within habitats, and populations in habitats interact via dispersing individuals. Note that the landscape between habitats is an anonymous matrix. Scenarios (d) through (f) illustrate metapopulations within a landscape context. Elements of the matrix influence the interaction of local populations, e.g., by (d) facilitation, (e) inhibition, or (f) no influence on dispersal. We have not shown scenarios where foraging is influenced by the landscape context, that is, mixing scenarios (a) and (b) with the scenarios (d) through (f).
of (perennial) habitat types, parasitism rates are generally high and do not differ between edge and center (148, 159). In simple landscapes (with high habitat loss and habitat fragmentation), more habitat is required for population persistence (40), but there seems to be no empirical evidence for insects [for birds, see (164)].

A spatially explicit approach is necessary not only in aboveground but also in belowground population ecology (36) and in the interplay of below- and aboveground communities (21, 100, 133, 161). Soil organisms are usually not randomly distributed, but they exhibit spatially predictable, aggregated patterns across scales ranging from square millimeters to hectares (36).

Biodiversity in fragmented landscapes consists of two components: local richness of the habitat (alpha diversity) and dissimilarity (beta diversity) between local habitats. Both alpha and beta diversity determine overall species richness (gamma diversity) across the landscape (47, 48). As measures of spatial dissimilarity (or spatial turnover) have been employed in a variety of ways, interpretation of the relative importance of local diversity is difficult (47, 86). Although the relationship between alpha and beta diversity components is fundamental to understanding patterns of spatial diversity, convincing analyses are rare. In latitudinal biodiversity gradients, tropical richness has been often related to high spatial turnover (43). In such a broad geographical view, overall biodiversity is mainly due to beta diversity and even the most diverse sites contribute only a small fraction to gamma biodiversity, as proportion of species shared between habitats is often low. Across landscapes, a scale much smaller than the scale of biomes, most studies have focused on the maintenance of local biodiversity. The importance of small-scale spatial turnover for regional biodiversity appears to have been underestimated in the past (48, 159). In studies of the so-called local-regional richness relationships, richness on the scale of the landscape is usually higher than richness within habitats, and richness within habitats (local richness) is correlative with the species richness of the landscape (regional richness). This relationship often explains more than two thirds of the variance in regression models (42, 86).

**LANDSCAPE EFFECTS ON TROPHIC INTERACTIONS**

**Dispersal and Body Size**

Communities are composed of species that experience the landscape on a broad range of spatial scales (19, 71, 141). Foraging range and dispersal ability determine which landscape elements contribute to population dynamics and trophic interactions (22, 31, 39), but these characteristics tend to be related to body size and trophic position (Table 2). Wings obviously promote dispersal. Wing polymorphism is common in many insect taxa (180). Changes in spatial arrangement of habitats may induce investment in dispersal-related traits, including larger butterfly thorax mass among sites with a high degree of habitat fragmentation (69, 113, 150).
Size of organisms is key to many life history traits such as reproduction and resource use and is positively related to home range (as long as they are not part of the aerial plankton). This was shown for carabid beetles, dung beetles, butterflies, and solitary bees (4, 16, 22, 45, 46, 70, 143, 144). Large species need large areas but are often able to bridge hostile landscape features within their foraging range (18, 170).

Roland & Taylor (130) showed that forest fragmentation affects survival of four tachinid flies and thus parasitism of forest tent caterpillars (*Malacosoma disstria*). Outbreaks of this forest pest lasted longer in fragmented forests than in continuous forests (128, 129). The larger the body size of the tachinid parasitoid species, the larger the spatial scale at which forest structure had its greatest effect. Forest stands could be colonized when isolation distance was 125–400 m, and dispersal distance was positively correlative with the tachinids’ body size. These dispersal distances match the findings from studies in agricultural landscapes, where parasitoid richness and parasitism also sharply decreased within a few hundred meters (90–92).

Frequency of flower visitation by solitary bees is determined by a 500-m diameter around the blooming patch, but honey bee visitation frequency extends to a 6000-m diameter area, so potential competition between these pollinator guilds is driven by different spatial scales (46, 141, 142). Furthermore, foraging distances

### TABLE 2

<table>
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<tr>
<th>Traits of species</th>
<th>Correlation to landscape</th>
<th>References</th>
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</thead>
<tbody>
<tr>
<td>Dispersal ability and foraging range</td>
<td>Large foraging ranges and high dispersal rates allow colonization of isolated patches; Multiple-resource (multihabitat) use requires dispersal, as critical resources are often only found in different habitat types; High emigration rates should be only positive in landscapes with a high proportion of habitat.</td>
<td>(22, 30, 39, 46, 149)</td>
</tr>
<tr>
<td>Body size</td>
<td>Small-bodied species are widely dispersed (e.g. aerial plankton); In larger species, foraging range and body size are positively correlated; Large species should better cope with isolated than small habitat islands.</td>
<td>(4, 16, 22, 46, 70, 143, 144)</td>
</tr>
<tr>
<td>Trophic position</td>
<td>The higher the trophic level the larger the spatial domain in e.g., plant-insect-bird chains; But interaction with body size and resource specialization (e.g., small, specialized parasitoids vs. large, unspecialized predators); Temporal changes in densities of resource populations often require high vagility of resource-dependent species.</td>
<td>(71, 127, 147, 158)</td>
</tr>
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</table>
are larger in simple rather than complex landscapes (140). Similarly, social bees pollinating coffee in tropical agroforestry systems profit from adjacent natural forests offering a wealth of nesting sites. This is in contrast to solitary bees, which are mostly ground-nesting, benefit from reduced shade and dry soils, and are not affected by the surrounding landscape (84, 85).

Trophic-Level Position and the Spatial Scale Experienced

The spatial scale experienced by an organism is also linked to its trophic level (71) (Table 2). According to this idea, the abundance of a plant species is determined mainly by microhabitat, whereas herbivore populations are wider ranging but confined within the local community. Predator populations usually encompass several prey populations and must be mobile to switch between patches colonized by the prey. This is why Holt (71) expects that high-trophic-level populations are determined by larger spatial-scale processes. This idea was tested with a food chain, comprising oilseed rape, rape pollen beetle, and its parasitoids, in a gradient from simple to complex human-dominated landscapes (147). Local rates of both herbivory and parasitism were best correlated with landscape structures within a 1500-m diameter around this plant-insect system, so their functional spatial scales were similar (147). The similar body size of the beetles and parasitoids involved as well as the highly specialized host-parasitoid dynamics may be responsible for this pattern. Body size often increases with trophic interactions, particularly when vertebrate predators are involved. Because body size is usually related to foraging range, the trophic-level–spatial-scale idea should better fit vertebrate-invertebrate types of food chains. Although most theoretical and empirical studies found that phytophagous hosts are better dispersers than their specific parasitoids (66, 74, 90–92, 158), dispersal of the Glanville fritillary butterfly, Melitaea cinxia, is intermediate between that of its two primary parasitoids (162, 163). Mobile parasitoids may even block the spatial spread of hosts (10, 101, 129). In addition, plant populations are also affected by landscape structure and may disperse widely, but dispersal limitation (seed rain filling seed banks) in a landscape context is rarely assessed in plants (20).

Trophic-level position influences susceptibility of populations to disturbance (96, 117), and the trophic-level hypothesis of island biogeography claims that populations of higher trophic levels are more likely to become extinct (87, 90, 158). The surrounding landscape is often more important for generalists than for specialists, because generalists do not depend on only one well-defined habitat type. They consequently may need to bridge only relatively short distances (see also Tables 1 and 3). Hence, habitat fragmentation and disturbance is expected to mostly affect specialized organisms (74). This has been shown for butterflies in relation to plants, as the diversity of only the specialized butterflies decreased more than plant diversity on fragmented calcareous grasslands (145). This is why parasitoids should be generally more affected by loss of habitat area than predators should, as they tend to show greater host specificity.
TABLE 3 Summary of patterns predicted from metapopulation models

<table>
<thead>
<tr>
<th>Model variant</th>
<th>Predictions</th>
<th>References</th>
</tr>
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<tbody>
<tr>
<td>Levins model</td>
<td>Thresholds for the regional existence</td>
<td>(98, 99)</td>
</tr>
<tr>
<td>Structured models</td>
<td>Multiple equilibria</td>
<td>(52)</td>
</tr>
<tr>
<td></td>
<td>Core-satellite species</td>
<td>(57)</td>
</tr>
<tr>
<td></td>
<td>Correlation occupancy-abundance</td>
<td>(42, 43)</td>
</tr>
<tr>
<td>Noninteractive communities</td>
<td>Species richness increases with patch area</td>
<td>(58, 102)</td>
</tr>
<tr>
<td>Interactive communities</td>
<td>Competitive coexistence</td>
<td>(110)</td>
</tr>
<tr>
<td></td>
<td>Space enables coexistence of prey and predators</td>
<td>(66, 72)</td>
</tr>
<tr>
<td></td>
<td>Habitat fragmentation leads to shorter chains in food webs</td>
<td>(72, 73)</td>
</tr>
<tr>
<td></td>
<td>Apparent competition</td>
<td>(72)</td>
</tr>
<tr>
<td></td>
<td>Habitat fragmentation increases ratio of habitat generalists to specialists</td>
<td>(72, 79)</td>
</tr>
<tr>
<td></td>
<td>Complex spatial density patterns</td>
<td>(66)</td>
</tr>
</tbody>
</table>

In addition to resource specificity, density and population size of high-trophic-level populations are often lower and more variable (136, 163). Both rarity and population size variability are well-known predictors of local extinction (37, 41, 96, 136). Trophic position and rarity and population size variability may be closely correlated (90, 91, 129). When phytophagous insects are released from biological control in small or isolated habitat fragments and dramatically increase population densities (80, 81, 129), competitive ability of the damaged host plants as well as the outcome of interactions to competing herbivores may change patterns of coexistence and food web interactions.

**Is Ecological Change Best Indicated by Changes in Biodiversity or Trophic Interactions?**

Local plant-insect communities vary much more in biodiversity than in food chain length (73, 117, 132). The small number of trophic levels has been explained only by two factors: the diminution of energy along food chains and the dynamical instability of long food chains, called the productivity and the dynamical constraints hypothesis. The number of trophic levels is related to spatial attributes of ecosystems in that habitat fragments are characterized by shortened food chains, particularly for small sets of interacting and specialized species (73) (Table 2).

Biodiversity and trophic interactions often covary in fragmented landscapes, but a general cause-effect relationship has not yet been shown (108, 167). Although biodiversity is a major conservation issue, trophic interactions are rarely incorporated in evaluations for conservation schemes or in the bioindication of ecological change (157); however, strength of interactions (e.g., percent parasitism
or percent fruit set) may be unambiguously determined, whereas diversity estimates often suffer from their dependence on sampling effort (13). One contributing factor to this omission may be that the disruption of trophic interactions can be either favorable or detrimental to the target populations of conservation efforts. Increases in a plant’s biotic interactions may involve not only enhanced flower visitation and pollination but also seed predation or fungal infections, thereby counterbalancing the overall outcome (14, 83, 142). Loss of mutualistic interactions may include reduced seed dispersal or slower decomposition of dung and litter, whereas loss of antagonistic interactions favors the target populations with reduced predation or infection rates (26, 103, 157, 158). Disruption of biotic interactions may lead to additional, so-called secondary extinctions (174). Predation may enhance extinction risk owing to environmental disturbances or catastrophes, as shown with lizards affected by Bahamas hurricanes (137). The conflicting nature of increased trophic interactions is particularly intriguing in the case of introduced species. In classical biological control, introductions of effective phytophagous and entomophagous insects are welcome, but side effects of infection of native plants and the invasion of native parasitoid complexes are feared (67, 100).

Local Versus Regional Determinants of Trophic Interactions

Large habitats are characterized by more high-trophic-level species, such as parasitoids, and higher parasitism rates (Table 1). However, on a landscape scale, many small and spatially separated habitat fragments may provide more parasitoid species per phytophagous host species and thereby a greater potential of biological control agents (159). This pattern, established with *Trifolium* and *Vicia* herbivore-parasitoid assemblages, can be attributed to the fact that a habitat fragmentation in a landscape generates a larger heterogeneity of (a) the local habitat and (b) the immigration from an adjacent area. This may result in local parasitoid complexes made up of different species. In these *Trifolium* and *Vicia* plant-insect systems, the herbivore, not the parasitoid communities, showed a high regional similarity (i.e., the communities of the third trophic level showed a much higher regional dissimilarity) (92, 159). So both strategies, which increase local fragment area and the number of geographically distant habitat fragments, have merit because both density (due to large areas) and species richness (due to many fragments) are important in conservation biological control. These findings support recent analyses of arboreal beetle diversity at four sampling levels (trees, forest stands, sites, and ecoregions) (48). Rare species (<0.05% of total abundance) accounted for 45% of the 583 beetle species and were strongly influenced by broad spatial scales (i.e., ecoregions) (48). Accordingly, in food chains made up of high-trophic-level specialists with their typically low density compared to that of their host or prey, regional diversity of parasitoids should be generally more determined by beta diversity (dissimilarity between habitats) and that of herbivores more by alpha diversity (the local habitat attributes).
Host plant characteristics vary geographically, with associated changes for herbivores and carnivores (incorporating worldwide approximately 310,000 plant species, 360,000 phytophagous insect species, and 400,000 carnivorous insect species) (120). It is becoming increasingly apparent that explanations of diversity patterns vary with scale. The best predictor variables on a local spatial scale (or recent timescale) may be different from those on larger (regional, continental, or global) scales (175). Trophic interactions will also dramatically change over the geographic range of a species for a wealth of reasons, including genetic changes in plant and insect traits, in insect responses to plant resources, and in complex interactions between plant resistance and insect virulence (9, 25, 93). Inbreeding depression has well-known negative consequences for the survival of small populations (57, 97, 111, 115). However, inbreeding in fragmented plant patches does not necessarily result in increased susceptibility, as resistance depends on the specific genotype and greatly varies among populations and lines (115).

THEORY OF PLANT-ANIMAL INTERACTIONS WITH A LANDSCAPE PERSPECTIVE

The empirical evidence reviewed above suggests that the occurrence of species across a fragmented landscape depends on the size and connectivity of habitats, the landscape context in which the habitats are embedded, and the traits of the species. The enormous differences between landscapes and between species generate a bewildering array of empirical patterns. Does theory help to synthesize these patterns?

From the theoretical point of view the relationship between species and fragmented landscapes depends on the scale of individual movements and the distance between habitat fragments (Figure 1). Mobile species move freely between fragments. For these species the fragmented landscape influences foraging decisions on a daily basis (12) (Figure 1a). Some species may even use two or more different habitats, e.g., one for nesting and another for foraging (Figure 1b). Species with a limited foraging range, however, remain within one habitat through their life. In only rare circumstances may an individual disperse from one habitat fragment to another (Figure 1c–f). Thus dispersal influences dynamics of populations within habitat fragments. One has to distinguish the dynamics of the local populations within one habitat from the regional dynamics, that is, the dynamics of the sum of all local populations.

Two theoretical approaches have been used to predict the influence of size and arrangement of habitat fragments across a landscape on local and regional population dynamics: metapopulation theory (Figure 1c) and landscape ecology (Figure 1d–f). Classic metapopulation theory (98, 99) is concerned about the occurrence of individual species across an ensemble of habitat fragments. In metapopulation theory, habitat fragments suitable for the occurrence and reproduction of a species are often called patches (for a useful list of metapopulation terminology
Thus, the landscape has only two elements: suitable habitats and nonsuitable habitats. The term matrix is sometimes used to refer to all the nonsuitable habitats between the patches. The matrix is assumed to have no influence on the processes between patches (e.g., by influencing dispersal) and processes within patches (e.g., via edge effects). In contrast, landscape ecology considers the details of the landscape context and the impact of the matrix on processes between and within patches (172) (Figure 1d–f). Irrespective of details of the different approaches, metapopulation and landscape ecology study local population dynamics from the perspective of the landscape. Hence, the two approaches evaluate the impact of habitat destruction and fragmentation on the occurrence as well as dynamics of local populations from a theoretical point of view.

Metapopulation Models

Classic metapopulation theory (98, 99) is not concerned about the details of local population dynamics but provides models of the relative occurrence of a species within habitats (patches) across a landscape. The relative occurrence, or occupancy (percentage of patches occupied by a species), is expressed as a balance between extinctions of local populations (local extinctions) and colonizations of patches not yet occupied by a local population (54, 55). Therefore, one has to predict the relative number of empty patches that will be colonized and the relative number of occupied patches that will go extinct. This assumes that local population dynamics is much faster than metapopulation dynamics (28). Metapopulation models are formally identical to the so-called susceptible-infected-susceptible models of epidemiology (1).

Metapopulation models differ in how they consider space. Implicit models [such as the classic Levins model (98, 99)] assume that all patches are equally connected to other patches. Hence, implicit models are not able to mimic metapopulations with a clumped distribution of habitats, and one has to move from spatially implicit to spatially explicit models. Spatial explicit metapopulation models introduce details about size and location of patches. For example Hanski’s (54–56) incidence function model considers extinctions of local populations as function of patch area and colonization as a function of patch location. Spatial implicit and spatial explicit metapopulation models make useful predictions about the occurrence of a single species across a fragmented landscape (Table 3) and the impact of habitat loss and habitat fragmentation on the occurrence of single species:

- Species exist in a dynamic equilibrium. That is, no single patch is sufficient for the existence of a species in a landscape.
- If all local populations of a metapopulation have a probability to go extinct, there is a threshold for the existence of a species in a landscape. This threshold depends on the characteristics of the species (e.g., dispersal) and the landscape (area and isolation of patches). In the Levins model (all patches of equal size) this equilibrium is given by $P = 1 - e/m$, whereby $e$
measures the extinction rate of local populations and \( m \) measures the colonization rate of an empty patch. The parameter \( m \) incorporates the landscape as well as traits of the species and will increase with decreasing fragmentation and with increasing dispersal capacity of the species. Parameter \( e \) summarizes the size of individual patches and also all the traits of a species that influence its susceptibility to extinction. A species will exist in a landscape only if \( e > m \). Hence, a species may occur in one landscape but not in another. Assume that we remove some habitat from the landscape by removing some patches. This will decrease \( m \) and will lead to a decrease in the relative number of patches occupied. At the extreme, the metapopulation may go extinct. On the other hand, habitat reduction may affect all patches (reduction of size of individual patches). This will increase \( e \) and decrease \( m \). Again, this leads to a decrease in the relative number of patches. Despite its simplicity, the classic metapopulation model helps to understand the effects of habitat destruction and fragmentation from a theoretical point of view.

- One may modify the Levins model to include habitat destruction (94, 104, 110). This leads to what Hanski et al. (60) called the Levins rule: “A sufficient condition for metapopulation survival is that the remaining number of habitat patches following a reduction in patch number exceeds the number of empty but suitable patches prior to patch destruction.” This is an appealing result, as the Levins rule suggests that one can predict the minimum of habitat necessary for the survival of the metapopulation from the number of empty patches within a landscape. Simple snapshot data would suffice to make this prediction. But note that this rule of thumb should not be used for management decisions (55). Most importantly, the rule assumes that the metapopulation is in equilibrium, an assumption that may not hold in recently fragmented landscapes.

- The classic metapopulation model assumes an infinite number of patches, but in real landscapes the number of patches is limited. This may lead to considerable stochastic variation in the number of occupied patches. Metapopulation models that include stochasticity provide an estimate of the minimum viable metapopulation size that is the minimum number of interacting patches needed to guarantee the existence of a metapopulation (112).

- Simple metapopulation models predict one equilibrium, which is a mean percentage of patches occupied by a local population. Structured metapopulation models (52), which take into account certain details of the local population dynamics, however, suggest the existence of multiple stable equilibria. One equilibrium may be extinction. This is due to a rescue-effect (11), which generates a positive feedback between the global size of the metapopulation and the local population size. Such metapopulations may go abruptly extinct even without habitat destruction. Once extinct, it may be difficult to re-establish the metapopulation.
Structured models (52) predict a correlation between mean abundance and relative occurrence. The correlation between abundance and regional distribution should depend on dispersal and the intrinsic rate of increase. Thus, species that have a large local population but restricted distribution are predicted to have a high local growth rate in relation to dispersal. The opposite is predicted for species with a wide regional distribution and a low abundance.

As already noted, all spatially implicit models ignore details of the arrangement of patches. Thus, the predictions from spatially implicit models are of heuristic value only and increase our basic understanding of populations living in fragmented landscapes. But for management decisions we need more realistic models that allow for specific prediction about the importance of habitat destruction and fragmentation. Spatially realistic metapopulation models make such specific predictions. These models use only few parameters and some plausible assumptions. Further parameters can be estimated from snapshot data across a landscape (171). Subsequently, one may use the parameters to iterate the model using different scenarios of changed landscapes. Although such models do not make general predictions, these models are of considerable importance to investigate the influence of patch destruction and fragmentation for individual species. There are two facets that should be noted. First, spatially explicit models may incorporate complex details of landscape connectivity. Thus, these models are a step toward incorporating the matrix. Second, spatially explicit models suggest that metapopulations track with some delay the changing mosaic of patches within a landscape. Thus, the metapopulation equilibrium in the present landscape may be extinction, but species are still around simply because the metapopulation has not reached the equilibrium. Hence, predictions from models that assume equilibrium may be misleading.

If one wants to understand plant-insect interactions in a fragmented landscape, models of single populations are not sufficient. Insects interact with host plants as well as predators and parasitoids. Metapopulation theory is also able to make predictions about such interactions as well as patterns of communities (e.g., species richness, length of the food chain) (Table 3) living within a patch. From extensions of classic metapopulation models to competition and predation, the following major conclusions arise.

Two competitors not able to coexist in a single patch may coexist across an ensemble of patches (109, 110) if the inferior competitor is superior in dispersal (trade-off between competitive ability and dispersal). Hence, habitat destruction and fragmentation primarily affect the superior competitor, and fragmented landscapes may favor high-dispersal species at the cost of less mobile but more competitive species.

Predators and prey may also coexist across an ensemble of patches (109). Habitat destruction and fragmentation primarily influences the predator.
Extensions of such models to more trophic levels (72) suggest that the constraints for the existence of a species across a landscape increase with trophic level. Thus fragmentation may cut chain length of food webs.

Models of mutualism are notoriously unstable. However, simple metapopulation models of mutualism show nontrivial equilibria. Some equilibria may be unstable (109).

The above comments and Table 3 suggest that metapopulation theory may provide a framework to interpret a broad array of patterns on the occurrence of species across fragmented landscapes. But many of the predicted patterns in the occurrence of species across a landscape have alternative explanations. For example, at least nine different processes may explain the correlation between mean local abundance and occurrence across a landscape (44). Nevertheless, metapopulation theory forced ecologists to approach populations from a landscape perspective, and the predictions allow straightforward tests and even experimental approaches (50, 168).

Are Herbivorous Insects Organized as Metapopulations?

Murphy et al. (107) listed the following attributes of a species that make it a prime candidate for metapopulation dynamics: small body size, high rate of population increase, short generation time, and high habitat specificity. This list fits perfectly with the attributes of phytophagous insects and suggests that many insect populations may function as a metapopulation within a landscape, especially as the hosts are distributed as patches across the landscape. But what is the evidence?

To demonstrate convincingly that a plant-insect system functions as a metapopulation, one has to work through four steps (54): (a) Hosts are distributed as discrete patches, (b) populations within patches have a substantial risk of extinction, (c) empty patches are available for colonization, and (d) local populations do not fluctuate synchronously.

Many herbivorous insects are rather specialized. Thus, the habitats of phytophagous insects may be defined by the occurrence and distribution of the host plant. The distribution of host plants may be either diffuse or discrete across the landscape. A discrete distribution may be due to the specialized ecological requirements of the host plant or because the host plant itself grows in discrete patches [e.g., clonal plants (32)]. Furthermore, individual insects have to experience a host patch as an isolated habitat; that is, during the daily foraging the insect moves within the patch and there are only rare dispersal events to other patches. Otherwise one would have a single population with habitat heterogeneity (patchy population) (64). To date, there are only few field studies that analyzed in detail the behavior of the insect in relation to the distribution of the host plant. The best data are available for butterflies (151). Butterfly species are rather sedentary with rare but nevertheless important long-range dispersal events (59).

The next requirement for metapopulation dynamics is that local populations may go extinct. The demonstration of frequent extinctions calls for long-term
studies and again only few examples are available, including Hanski’s well-investigated butterfly species *Melitaea cinxia* (55), the specialized gall-forming fly *Urophora cardui* feeding on *Cirsium arvense* (32, 33), or the moth *Thyria jacobaea* on *Senecio jacobaea* (160). Hanski’s studies [reviewed in (55)] show that even the largest population has a chance to become extinct. Classic metapopulation theory assumes that local extinctions are due to local stochastic events. However, this is not always true. Habitats may change [e.g., by succession (34)], and thus observed extinctions are deterministic. Hence, habitats in which a local population disappears are not available for colonization. Thus more advanced models have to include the dynamics of the habitat (35).

This leads to the third step: Empty habitat patches should be available for colonization. This is not easy to prove and few studies have approached this issue. Introducing *U. cardui* has shown that empty patches are available for colonization (134).

The final step to prove that a system may function as a metapopulation is to show that dynamics of local populations are not correlated. Some studies, however, showed that the dynamics of plant-insect systems within two patches are correlated (62, 119, 112, 160), whereas others argue that there is sufficient asynchrony (54). Nevertheless, local variation seems to be embedded within broad-scale synchrony, which is presumably generated by climate (55, 146). Spatial synchrony inflates estimates of metapopulation survival.

Overall it seems that there are not many plant-insect systems for which convincing evidence is available that the system functions as a classic metapopulation. Classic metapopulation theory assumes that all patches are equal. The habitat size of *M. cinxia* shows a log-normal distribution (55), and the distribution of the size of *C. arvense* stands is skewed with few large and many small stands (34). Metapopulations can be placed along a continuum from one large population seeding the surrounding smaller populations (mainland-island) to all populations being of equal importance (classic metapopulation). Hence, the same system may function in one landscape as a mainland-island system and in another as a classic metapopulation. The details of a metapopulation depend on the idiosyncrasies of the landscape. Examples are the *Senecio-Thyria* system (65, 160) and the butterfly *Plebejus argus* (51, 150, 151).

### From Metapopulations to Landscapes

Populations and communities within real landscapes function in a manner more complex than that of metapopulations (172). Landscapes are ensembles of many habitat types. Hence, the processes in a particular patch are influenced not only by the other patches of the same type around the focal patch, but also by the other patch types. The matrix may facilitate (Figure 1d) or inhibit dispersal (Figure 1e). Some habitat types of the matrix may have no effect on dispersal (Figure 1f) (note that for a neutral matrix one can approach the system as a metapopulation; compare Figure 1c with Figure 1f). One way to approach real landscapes within the frame of the Levins model is to consider several types of habitat patches...
Such models enrich the predictions of the metapopulation models outlined above. For example, (habitat) generalists may persist in one habitat simply because they exploit a range of habitats. Hence, species that persist in one habitat may increase species richness in other habitats (spillover effect). Two habitat specialists, both attacked by a predator that is a habitat generalist, will influence each other via the predator (so-called apparent competition). Hence, a species in a common habitat may force other species to extinction by providing a reservoir for predators (72).

More complex landscapes may be modeled by spatially realistic metapopulation models or grid-based models (22). The latter divide the landscape into an array of equal-sized grids. Grids may have different attributes that influence a population or individual during dispersal. Grid-based models have been used to test certain metrics or to analyze the importance of habitat destruction and fragmentation on the threshold of population persistence or animal movement (7, 38–40). The simplest version of such models considers grids only as habitats or nonhabitats (5). Analyzing such models with habitat reduction shows a nonlinear response: With increasing habitat reduction, the suitable habitat becomes suddenly fragmented; when around 40%, the suitable habitat has become destroyed.

Kareiva & Wennergren (82) argue that the spatial arrangement of habitat fragments may compensate for overall habitat loss and mitigate extinction risks, whereas Fahrig (38) and Harrison & Bruna (63) argue that only habitat loss is of major importance. This difference in conclusion comes from the fact that in landscape models the matrix is not always hostile. If the matrix allows some survival, habitat fragmentation is of less importance than habitat destruction. Fragmentation will have large effects in landscapes with little suitable habitat (3).

**CONCLUSIONS AND OUTLOOK**

Empirical data and models show that we can understand local plant-insect interactions only if we incorporate a landscape perspective. The several variants of the metapopulation models provide a conceptual framework to evaluate the dynamics of populations and communities in fragmented landscapes, especially in the context of habitat destruction and fragmentation. However, the processes in real landscapes are more complex than envisaged by metapopulation models, so the study of plant-insect patterns needs to include characteristics of the surrounding landscape as well as the scale of foraging and dispersal. Plant-insect patterns and processes are contingent on species and landscape (173). Communities of insects within a patch are a complex mixture of species that function as a metapopulation, from species that function as a system of source-sink population to species where all individuals across a landscape form a patchy population.

Despite considerable theoretical progress, there are still some areas where predictions (Table 3) have not been convincingly validated in nature (55). Examples are the complex spatial patterns of spatial predator-prey models (78, 101), the
existence of multiple equilibria, and the constraints for the length of food webs. The local-regional interplay, the many specific spatial strategies of all the species in food web interactions, and the slow temporal dynamics of metapopulations call for more large-scale and long-term investigations in the field. In fact, many of the models are far ahead of the empirical results. Without data across large spatial and temporal scales, we will never grasp the complexities of plant-insect interactions in fragmented landscapes.

ACKNOWLEDGMENTS

Martin Brändle and two anonymous reviewers provided valuable comments on the manuscript. Financial support came from the Deutsche Forschungsgemeinschaft (DFG; German Science Foundation) and the German Ministry for Research and Education (BMBF).

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