Habitat Loss and Fragmentation

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Glossary

Cover type A term used by the geographers for a type of mapped feature (e.g., forest, freshwater, or grassland). The dominant natural cover type in a landscape is often used to approximate habitat.
Fragmentation per se The breaking apart of habitat while keeping habitat amount constant.
Habitat The place where an organism normally lives.
Habitat fragmentation The breaking apart of habitat into several smaller pieces. Habitat fragmentation results in both habitat loss and fragmentation per se.
Habitat loss A change to an area that prevents a species from living there (e.g., conversion of forest to crop field).
Human landscape modification An umbrella term used to describe the many complex and related features and processes correlated with human-caused habitat loss and fragmentation.
Landscape complementation The degree to which a landscape provides all necessary cover types for a species that requires multiple cover types to complete its life cycle.
Matrix An area where an organism does not usually live.
Scale of effect The spatial extent over which the habitat and the matrix characteristics in the surrounding landscape influence individual, population, or community processes in a focal area.

Introduction

Habitat loss is occurring at an alarming rate. Agriculture, the major cause of habitat loss (FAO, 2010; **Figure 1**), covers 36% of Earth's potentially suitable land (FAO, 2003). The cover type for which loss is best documented globally is forest (Balmford *et al.*, 2002). Earth's forests underwent a net decrease of 5.2 million hectares per year between 2000 and 2010 with the greatest losses occurring in tropical and subtropical woodlands (FAO, 2010). Although some forest loss has natural causes (e.g., fire, Harrod *et al.*, 1999), most of the current forest loss results from human land use (FAO, 2010). The impact of forest loss on the biodiversity is even larger than expected from the raw number of hectares because forest loss is greatest in the species-rich regions of the tropics and subtropics (Pereira *et al.*, 2010). Furthermore, it is in these areas that the most agricultural growth is expected in the future (FAO, 2003).

Habitat loss has consistent, strong, negative effects on biodiversity. Habitat loss has negative impacts on species richness (Laurance *et al.*, 2002), population abundance (Laurance *et al.*, 2002), and genetic diversity (Aguilar *et al.*, 2008). In addition, habitat loss can shorten trophic chain length; alter species interactions; and reduce successful foraging, breeding, and dispersal (reviewed in Fahrig, 2003). A combination of agriculture and hunting is the greatest perceived threat to mammal, bird, and amphibian populations (Laurance and Useche, 2009). Habitat loss is commonly cited as the greatest threat to wild bee populations (Brown and Paxton, 2009) and is second only to hunting as the major threat to marine fish populations (Dulvy *et al.*, 2003).

Habitat loss affects not only biodiversity but also impacts humans directly by decreasing production of ecosystem goods and services such as pollination (Potts *et al.*, 2010; Ricketts *et al.*, 2008), soil and water management (Bruijnzeel, 2004), and carbon storage (Fargione *et al.*, 2008). After accounting for the potential economic benefits of habitat loss (e.g., agricultural and mineral products), a conservative estimate of the global net economic cost of habitat loss is US$ 250 billion per year (Balmford *et al.*, 2002).

Habitat fragmentation, or the breaking up of habitat into smaller pieces (**Figure 2**), is a second major effect of human land use. Its prevalence is difficult to summarize because it is confounded with habitat loss and can be measured in many different ways. Understanding of the effects of habitat loss and fragmentation on populations has been hampered by a vague conceptualization of habitat fragmentation, but some broad generalizations can be made. The strongest finding from decades of research on this topic is a consistent negative effect of habitat loss on biodiversity, although the strength of this effect depends on species traits and environmental factors.

Problems with the Concept of Habitat Fragmentation

Habitat Fragmentation is a Vague Concept Because it Encompasses Multiple Concepts

The term "habitat fragmentation" has been criticized as "broadly conceived and therefore oversimplified" (Bunnell, 1999); "a conceptually ambiguous and empirically multifaceted term" (Haila, 2002); a "catchall for human-caused habitat changes that have negative effects on biodiversity" (Fahrig, 2003); and a "generic umbrella term" that is "vague and ambiguous, thereby limiting its practical value for conservation managers" (Lindenmayer and Fischer, 2007). Despite these criticisms, the term habitat fragmentation continues to be used to refer to the general effects of human landscape modification, a practice defended by researchers who credit the term with "real heuristic value in explicit recognition of an overarching domain" (Ewers and Didham, 2007).

Habitat fragmentation refers to the subdivision of habitat into smaller pieces (Andrén, 1994; Ewers and Didham, 2006; Fahrig, 2003) and as such can refer to many potentially

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Figure 1 An aerial photo depicting a typical agricultural area near Ottawa, Ontario, Canada (OMNR, 2010). To meet the growing demand for human food, forested land (shown in dark green) has been replaced by agricultural crops (usually corn, soy, wheat, or alfalfa in this region). Photo provided by Carleton University under licence from Ontario Ministry of Natural Resources. Reproduced from OMNR (2010) DRAPE: Orthoimagery (computer file). Ontario Ministry of Natural Resources.

confounded processes and concepts. This definition can refer to both habitat loss and fragmentation per se (i.e., a change in habitat configuration), can be measured at the patch scale or the landscape scale, is used to refer to either the loss of habitat or the loss of a cover type, does not require that the multiple cover types that some species require are accounted for, may not account for the scale at which a species interacts with the landscape, and does not usually distinguish between human-caused fragmentation or natural fragmentation. Each of these areas of confusion is described in further detail.

Habitat Loss versus Habitat Fragmentation

Habitat fragmentation involves both habitat loss and a change in the configuration of habitat (Andrén, 1994; Fahrig, 2003). Use of "habitat fragmentation" to describe both processes obscures the fact that the habitat loss has a much stronger negative impact on biodiversity than fragmentation per se, which generally has weak effects that can be both positive and negative for the biodiversity (Fahrig, 2003, *see* Effects of Habitat Loss and Fragmentation: Habitat Loss is More Devastating than Fragmentation per se). The correct emphasis on habitat loss can be particularly important when management decisions (e.g., whether to increase habitat amount or reduce subdivision) are being made (Lindenmayer and Fischer, 2007).

Landscape Scale versus Patch Scale

Island biogeographic theory (MacArthur and Wilson, 1967) greatly increased interest not only in the consequences of habitat fragmentation but also led to an overemphasis on patch-level ("island") measurements rather than landscape-level measurements (Laurance, 2008). Many habitat fragmentation studies (possibly more than 50%, Fahrig, 2003; McGarigal and Cushman, 2002) measure fragmentation using patches as the unit of replication (e.g., they measure isolation and size of individual patches rather than habitat loss over the entire landscape), which can create confusion when making inferences at the landscape scale. If all patches are in the same landscape, then inference regarding the landscape scale effects of fragmentation is impaired by the lack of replication at the landscape scale (Delin and Andrén, 1999). Inferences at the patch scale cannot necessarily be scaled up to inferences at the landscape scale without explicit consideration of landscape scale measurements because qualitatively different patch characteristics can result from the same amount of habitat loss (**Figure 3**; Fahrig, 2003).

Habitat Loss versus Loss of a Cover Type

The term "habitat" is defined as the place where an organism normally lives (Ricklefs, 2008), but is often used to refer to a natural cover type (e.g., forest) whether or not the taxon of interest normally lives there. For example, some species thrive

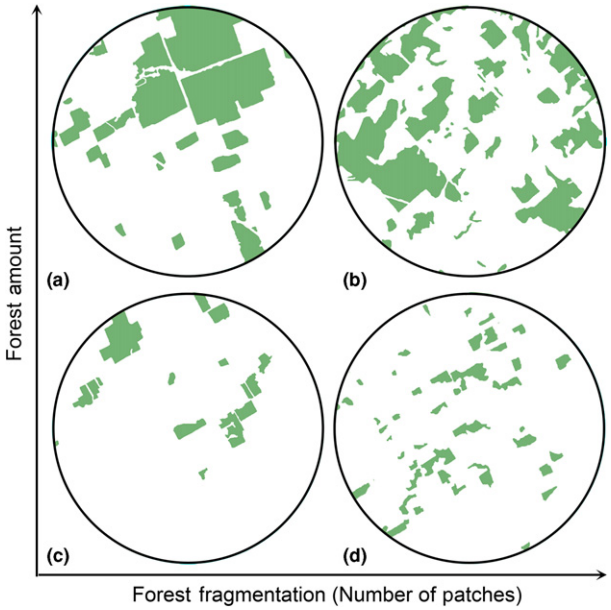

Figure 2 Landscapes near Ottawa, Ontario, Canada, which differ in the amount and fragmentation of forested habitat. Green areas indicate forest. Other habitats (agriculture, roads, and water) are shaded in white. Although most habitat loss involves both reduced amount and increased fragmentation (breaking up into pieces), these landscapes were selected to have independent variation in habitat amount and fragmentation: (a) high amount, low fragmentation; (b) high amount, high fragmentation; (c) low amount, low fragmentation; (d) low amount, high fragmentation. Adapted from Ethier K and Fahrig L (2011) Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada. *Landscape Ecology* 26: 865–876.

in human-dominated cover such that it constitutes habitat from the species' perspective. When measuring natural cover (e.g. forest amount) to estimate habitat amount one might erroneously conclude that species abundance is improved by "habitat" loss, when that species' habitat is actually the cover type (e.g., agriculture) that increased with human landscape modification.

The use of natural cover types as an approximation for habitat is common because most species decline with decreased natural cover, but the exceptions to this rule can make the use of "habitat" to mean "natural cover" misleading. Species richness declines with loss of natural cover for most groups (bacteria, Gans *et al.*, 2005; birds, butterflies, canopy beetles, canopy ants, and termites, Lawton *et al.*, 1998; forest birds, molluscs, and lichens, Moning and Müller, 2009; and spiders, Prieto-Benítez and Méndez, 2011). However, a significant number of species benefit from human-dominated cover. Edge- and matrix-favoring groups in the Amazon benefit from forest loss (Laurance *et al.*, 2002), and some prey species can increase in abundance following habitat loss, if the habitat loss has a larger negative effect on the predators than on the prey (Ryall and Fahrig, 2005; Ryall and Fahrig, 2006). Measurement of a cover type without reference to a species use of it can lead to confusing conclusions about the effect of habitat loss (Lindenmayer and Fischer, 2007).

Even if a cover type reflects an accurate measure of habitat, it may be insufficiently precise. Holland *et al.* (2005) found that the amount of forest in the surrounding habitat was more strongly related to the abundance of beetles that relied on multiple food sources than the abundance of beetles that relied on a single food source. They hypothesized that this occurred because the specialist feeders were each limited to specific stand types within a forest and the generalist feeders were more tightly associated with forest cover in general.

Landscape Complementation

For some species, measurement of a single cover type may be inadequate because their habitat includes multiple cover types. Leopard frogs, for example, require spring breeding habitat (ponds), summer foraging habitat (grassy meadows), and overwintering habitat (streams or lakes). In a study of landscape effects on local leopard frog abundance, researchers were unable to detect an effect of breeding habitat amount on abundance in focal ponds unless the amount of summer foraging habitat was also included in their model (Pope *et al.*, 2000).

Scale of Effect

The spatial extent at which cover is measured influences the ability to accurately identify the relationship between landscape structure and population or community outcomes. Numerous studies show that the spatial extent over which habitat is measured influences the strength of the relationship between habitat and the response of interest (e.g., abundance), and that this "scale of effect" is species specific (Carr and Fahrig, 2001; Holland *et al.*, 2004; Roland and Taylor, 1997; Steffan-Dewenter *et al.*, 2002). Failure to measure habitat at the scale of effect can lead to the erroneous conclusion that habitat amount is not associated with biodiversity (Holland *et al.*, 2004). When researchers are unsure of the scale at which a species responds to the landscape, a common solution is to measure landscape features at multiple spatial scales to find the one that best correlates with the response of interest (Holland *et al.*, 2004). A simulation study indicates that the maximum dispersal distance recorded for a species is likely to be a good estimate of the scale of effect (measured as the diameter of a circular landscape surrounding a focal area, Jackson and Fahrig, in preparation).

Grain, or the resolution at which landscape structure is defined, may also influence the ability to detect relationships between species and landscape structure. Animals are expected to have a "functional grain" or the smallest spatial scale at which they recognize spatial heterogeneity (Baguette and Van Dyck, 2007). If the grain of a landscape is defined too coarsely (e.g., the finest resolution is larger than a species' average dispersal distance), important relationships between a species and landscape structure may be overlooked.

Human-Caused Fragmentation versus Natural Fragmentation

Habitat fragmentation is sometimes used to refer to both natural fragmentation (e.g., forest patches separated by fire-maintained savannah) and human-caused fragmentation (e.g., forest patches separated by agricultural land). Species in

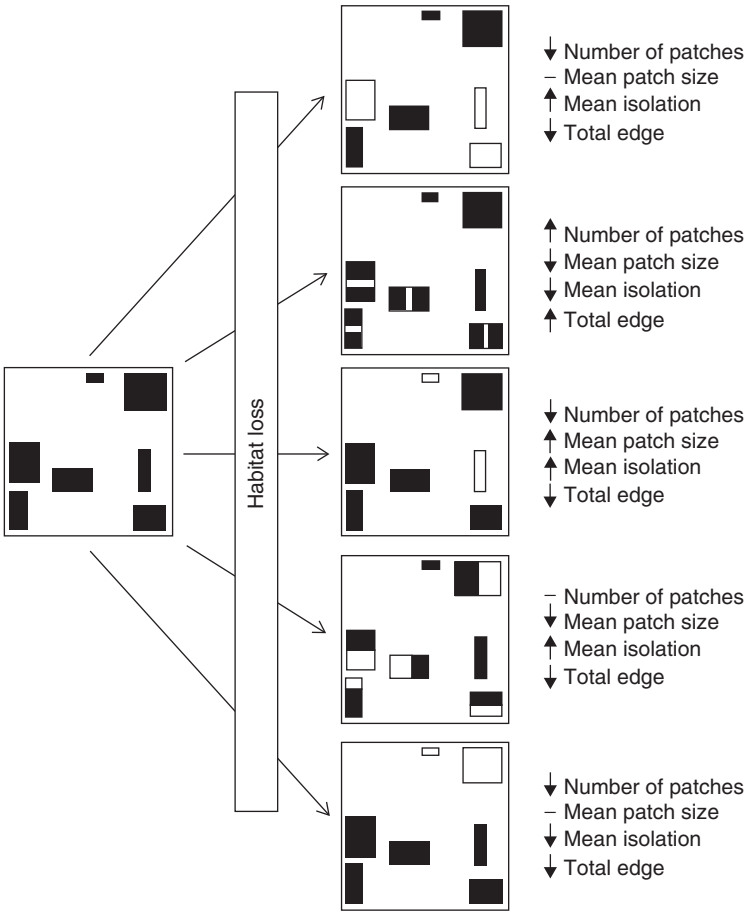

Figure 3 Illustration of how potential effects of habitat loss on measures of habitat fragmentation can be contrary to commonly expected effects. The commonly expected effects of habitat loss are an increase in the number of patches, an increase in mean isolation (here measured as nearest neighbor distance), a decrease in mean patch size, and an increase in total edge. Effects which are contrary to these expectations are italicized. Empty rectangles indicate areas of habitat loss. Adapted from Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487–515.

naturally fragmented habitats have presumably adapted to natural fragmentation such that their movement behavior (Fahrig, 2007) and population response (Bunnell, 1999; Haila, 2002) to fragmentation will be qualitatively different from species confronted with fragmentation in formerly contiguous habitats.

Precise Language Facilitates Informative Science and Clear Management Directives

A vague conceptualization of habitat fragmentation can lead to several problems. Inadequate separation of the processes involved in habitat fragmentation can lead to the false impression that the effects of fragmentation cannot be generalized (Fahrig, 2003). The effects of fragmentation can be generalized when the aspect of fragmentation that is measured is explicitly defined and the other aspects of fragmentation are held constant. In addition, the illusion of a single process of habitat fragmentation has led to the misconception that one measure of the habitat fragmentation is equivalent to another (Fahrig, 2003). Without carefully delineating terms, one might be led to believe that any measure of fragmentation refers in the same way to the broader concept when in fact different metrics measure different processes. Finally, linguistic uncertainty can make management decisions more difficult (Regan *et al.*, 2002).

The main remedy for confusion surrounding the broad conceptualization of fragmentation is precise communication concerning what aspect of human landscape modification is being measured. Fahrig (2003) recommends that "fragmentation" be reserved for the breaking apart of habitat after accounting for habitat loss – fragmentation per se. Fischer and Lindenmayer (2007) also warn against "double-booking" for the term "habitat fragmentation" which can refer to both the broad concept (that includes everything discussed in this section) and the narrow definition of change in configuration after accounting for loss. They recommend that the broad concept be termed "human landscape modification" and accept Fahrig's suggestion that the narrow concept be called fragmentation per se. Ewers and Didham (2007) defend the use of "habitat fragmentation" for the broad

concept as an aid to communicating ideas across related studies but support other authors in their insistence that the specific way in which habitat fragmentation is measured should be clearly defined.

Careful language will improve the communication of ideas, but definitive separation of the various mechanisms conceptualized in the term habitat fragmentation also requires improved study design. Fahrig (2003) recommends that habitat loss and fragmentation per se be controlled, experimentally if possible, but statistically if necessary.

Effects of Habitat Loss and Fragmentation

Habitat Loss is More Devastating than Fragmentation per se

Measures of habitat configuration are almost always strongly correlated with habitat amount (**Figure 4**; Fahrig, 2003; Hargis *et al.*, 1998) making it difficult to discern whether the effects of human landscape modification are due to habitat loss or fragmentation per se. When the effect of fragmentation per se is measured independently from habitat amount (either by statistically or experimentally controlling for habitat amount), the effect size of habitat loss on biodiversity is usually much larger than that of habitat fragmentation per se. When fragmentation per se does have an effect, it is just as likely to be positive as negative (reviewed in Fahrig, 2003).

Habitat Loss is Associated with Greater Extinction Probability and Reduced Species Richness

Large amounts of habitat are expected to result in positive effects for populations and communities for a number of reasons. At the population level, greater amounts of habitat sustain larger population sizes, which are less susceptible to stochastic extinction (MacArthur and Wilson, 1967) and genetic drift (Wright, 1931). At the community level, lower extinction rates in areas with more habitat are expected to lead to greater species richness (MacArthur and Wilson, 1967). In addition, large areas of natural cover are more likely to include a larger variety of habitat types with their associated species (Williams, 1964). Greater species richness may also occur in larger areas simply because larger areas allow for a larger sample of species from a regional species pool, resulting in a greater number of rare species (Connor and McCoy, 1979).

Fragmentation per se Can Have Both Positive and Negative Results

Fragmentation per se is expected to lead to negative effects if it results in smaller, less viable populations or if the increased exposure to edge is detrimental (Bender *et al.*, 1998). Although the negative effects of habitat loss are expected to result from a reduced number of individuals, cover types, and species, fragmentation per se is generally assumed to reduce the probability of successful movement. This is likely a false

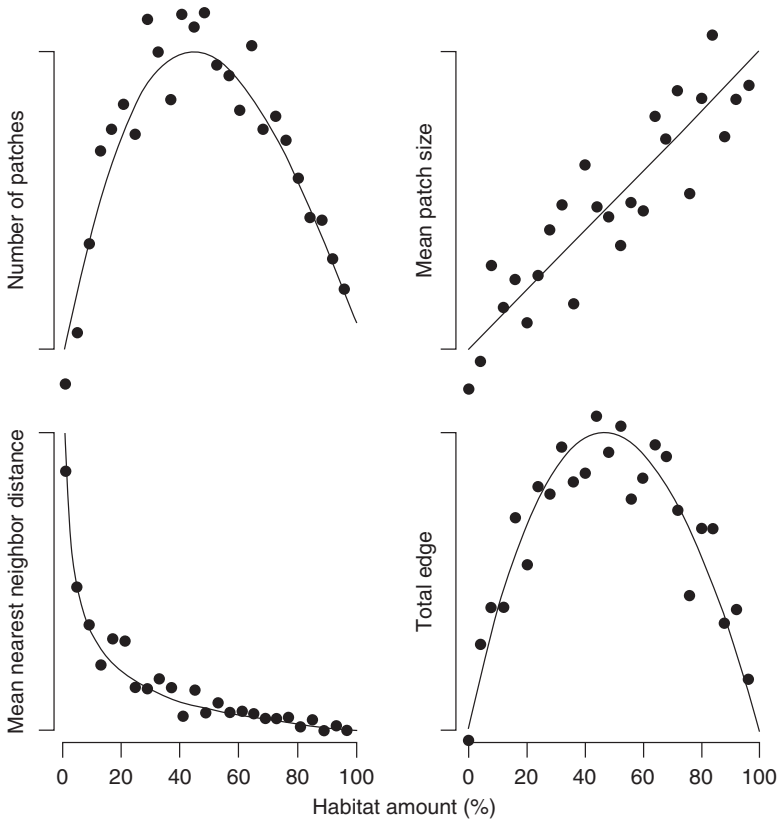

Figure 4 Illustration of typical relationships between habitat amount and four measures of fragmentation. Each data point corresponds to an individual landscape. Adapted from Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487–515.

dichotomy, however, because habitat loss itself reduces dispersal success by increasing the distances among patches (Fahrig, 2007).

Fragmentation per se implies a greater number of smaller patches. If the cost of crossing matrix is too high to allow for regular movement among patches, then individual subpopulations operate more or less independently. As in classic metapopulations (Hanski, 1994), the resulting small, isolated subpopulations are more susceptible to extinction.

A greater number of smaller patches also results in a higher perimeter to area ratio over the landscape. More frequent encounters with edges often increases emigration rates (Kareiva, 1985), thereby increasing the probability of dispersal mortality (Fahrig, 2001). Some matrix types are particularly risky and can have strong effects on population density (e.g., roads, Fahrig *et al.*, 1995).

Edges themselves can represent areas of decreased habitat quality. The Biological Dynamics of Forest Fragments Project documented strong effects of edges in a tropical forest, including the following: enhanced wind disturbance, increased tree mortality, invasion of disturbance-adapted species, altered species composition, lower relative humidity, decreased soil moisture, lower canopy height, decreased canopy foliage, increased temperature, and increased litter (reviewed in Laurance *et al.*, 2002). Negative edge effects are not as well-documented in temperate areas and may be less common (Fahrig, 2003).

Receiving less attention in the habitat fragmentation literature is the fact that fragmentation per se is just as likely to result in positive population responses as negative ones. Fragmentation per se may lead to positive population responses if subdivision of habitat results in (1) greater coexistence of competitors (Chesson, 1985), (2) greater coexistence of predators and their prey (Huffaker, 1958), (3) lower probability of simultaneous extinction of an entire population (Heino *et al.*, 1997), (4) greater immigration into habitat due to larger perimeter to area ratio (Bowman *et al.*, 2002), (5) greater dispersal success due to shorter interpatch distances (Grez *et al.*, 2004), (6) greater landscape complementation (e.g., providing access between foraging and nesting sites for bats, Ethier and Fahrig, 2011), or (7) positive edge effects (e.g., increasing abundance of edge-favored species, Laurance *et al.*, 2002).

Increased Reproductive Rate Decreases Sensitivity to Habitat Loss and Fragmentation

Reproductive rate may be the most important factor influencing the amount of habitat required to sustain a population. Theory predicts the existence of a threshold amount of habitat at which a small loss of habitat propels the probability of population extinction from 0 to 1 (Fahrig, 2001; Lande, 1987; With and King, 1999). The minimum habitat requirement likely depends on the attributes of the species and the landscape. A simulation testing the relative importance of reproductive rate, emigration rate, matrix quality, and fragmentation (randomly distributed vs. clumps of habitat) showed that the most drastic differences in extinction threshold occurred when the reproductive rate was varied (Fahrig, 2001).

Empirical evidence supports the importance of reproductive rate. Among 41 breeding bird species, higher reproductive rate is associated with lower minimum habitat requirements (Vance *et al.*, 2003). Likewise, for 17 mammal species, the sensitivity of abundance to road density declined with reproductive rate independently of body size (Rytwinski and Fahrig, 2011).

Mobility, Habitat Specialization, and Matrix Quality Interact to Alter the Effects of Habitat Loss and Fragmentation

Habitat loss may have particularly severe effects for species that do not avoid matrix. The negative effect is expected to be even stronger if the matrix is dangerous. This is likely because matrix avoidance and/or low mobility (low probability of moving and/or short dispersal distances) is expected to be common among species originating from naturally fragmented habitats surrounded by high-risk matrix (Fahrig, 2007). Species from naturally continuous habitat or with little exposure to high-risk matrix may not have evolved matrix avoidance and may therefore suffer greater mortality than matrix-avoiding species when encountering high-risk matrix resulting from habitat loss (Fahrig, 2007).

Theoretical and empirical studies support the important interaction between dispersal traits and matrix quality. Two studies of variation in matrix avoidance among butterfly subpopulations support the hypothesis that matrix avoidance is selected for when interpatch distances are high and probability of successful dispersal through matrix is low (Hanski *et al.*, 2004; Schtickzelle and Baguette, 2003). A simulation model testing the relative impact of the number of patches, the distance between patches, and matrix avoidance on population density found that matrix avoidance was the most important factor preventing population decline (Tischendorf *et al.*, 2005). A model by Fahrig (2001) showed that populations with increased movement probability (matrix avoidance was not modeled) required more habitat to persist. This result depended on the mortality risk in the matrix – when the risk of mortality in the matrix was low, the effect of movement on minimal habitat requirements was greatly decreased.

Low-contrast matrix (matrix similar in structure to habitat) is generally thought to be better tolerated by native species than high-contrast matrix, but this conclusion may depend on how "matrix" is defined – for habitat generalists, "matrix" may actually provide habitat. Matrix type was more important than fragment size when predicting the recolonization of many Amazonian insectivorous birds after deforestation, probably because the "matrix" in which forest regrowth was more rapid and was most likely to provide birds with foraging and breeding opportunities (Stouffer and Bierregaard, 1995). In other words, the secondary growth served as habitat (technically not matrix). Likewise, dung beetle assemblages largely returned to their pretreatment state 15 years after deforestation when fragments were surrounded by secondary growth forest. Again, this recovery was due to the ability of dung beetles to use resources in secondary growth forest (Quintero and Roslin, 2005).

Low-contrast matrix may be detrimental to populations if it fails to evoke matrix avoidance and provides no resources on its own. A planthopper specialized on cordgrass avoids crossing into natural mudflat matrix but crosses easily into inedible, nonnative brome, which is similar in height to

cordgrass (Haynes and Cronin, 2006). Higher emigration into nonnative brome is associated with decreased density of planthoppers within cordgrass patches (Haynes *et al.*, 2007) and increased probability of planthopper extinction in cordgrass patches (Cronin, 2007).

Matrix heterogeneity can obscure the relationship between habitat loss and dispersal success. In both a simulation study and a field study of two mammal species, large patch size and short isolation distances were strong positive predictors of dispersal success when matrix was homogeneous, but the predictive value of these metrics was greatly reduced when matrix consisted of multiple cover types (Bender and Fahrig, 2005).

The interaction between matrix quality and mobility emphasizes that the important dispersal characteristic for populations is not so much low or high mobility, but high probability of success when dispersal is attempted (Callens *et al.*, 2011; Fahrig, 2007; Van Houtan *et al.*, 2007). For example, a simulation study suggests that high dispersal mortality can deplete genetic diversity more rapidly than complete dispersal avoidance (Jackson and Fahrig, in review). Simulation studies indicate that successful dispersal in patchily distributed habitats is likely to rely on matrix avoidance (Tischendorf *et al.*, 2005), linear movements in matrix (Zollner and Lima, 1999), strong ability to perceive habitat from a distance (Zollner and Lima, 2005), and adequate energy storage (Zollner and Lima, 2005). Species with high rates of successful dispersal may have been less vulnerable during past mass extinction events (Stork *et al.*, 2009), potentially because of their ability to spread the risks of environmental and demographic stochasticity over a large area and to avoid inbreeding depression (reviewed in Bowler and Benton, 2005).

In summary, population health after human landscape modification depends strongly on the interactions among matrix quality, habitat specialization, and the response of species to matrix during dispersal.

The Effects of Habitat Loss are Often Exacerbated by Additional Environmental Threats

Habitat loss usually cooccurs with other environmental threats (Laurance and Useche, 2009). In a study of vertebrate species listed under International Union for Conservation of Nature (IUCN), the most common pair of threats was agriculture (the most common reason for habitat loss) and hunting (Laurance and Useche, 2009). Human landscape modification results in more edge, providing easier access for hunters than is available in continuous forest. In the Amazon, for example, small forest fragments tend to experience much greater hunting pressure than large forest fragments (Peres, 2001), which can result in local extirpation of game species (Cullen *et al.*, 2000).

Habitat loss can lead to increased fire frequency in the tropics. Forested edges tend to be significantly drier than forest interiors (Kapos, 1989) and often abut slash and burn agriculture in the tropics (Cochrane and Laurance, 2002). In one such region, forest fires on forest/agriculture edges occurred every 5 years, whereas the fire interval averaged 120 years in core forest areas (Cochrane and Laurance, 2002).

Habitat loss is also expected to exacerbate the effects of climate change on species. Poleward range expansion is hypothesized to be impaired if human landscape modification limits poleward movement or decreases population growth rate (Opdam and Wascher, 2004). One area of active research is the identification of areas of habitat conservation priority based not only on current habitat use but also on projected future distributions of species under various climate change scenarios (Olson and Lindsay, 2009).

Summary

The global scale of human landscape modification is staggering. Amelioration of its effects depends in part on clear communication. To enable understanding of the effects of habitat loss and fragmentation, practitioners must (1) clearly define which aspect of human landscape modification (habitat loss or some metric of fragmentation per se) they are discussing, (2) make measurements at the scale (patch or landscape) that will yield the most interpretable results (usually landscape scale with replication), (3) clearly define what constitutes habitat to the taxon of interest, (4) measure habitat at the spatial extent appropriate for the taxon of interest, and (5) delineate between natural and human-caused fragmentation. Habitat loss is a bigger problem than habitat fragmentation per se and should be the main focus of study and management. Fragmentation per se is expected to be a problem when it leads to smaller, isolated populations or when negative edge effects are expected to be prominent (e.g., in tropical systems). The effect of habitat loss is modified by species and landscape characteristics. An increase in reproductive rate decreases the amount of habitat required to sustain a population. High mobility is associated with high sensitivity to habitat loss if dispersal mortality is high, but some successful dispersal may be required for long-term persistence. Habitat loss and fragmentation are seldom the only threats in an area – they are often coupled with hunting, fire, and other threats, which should be taken into account.

See also: Deforestation and Land Clearing. Extinction, Causes of. Loss of Biodiversity, Overview. Metapopulations. Population Viability Analysis. Restoration of Biodiversity, Overview. Species–Area Relationships

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