Habitat loss: ecological, evolutionary and genetic consequences

Habitat loss is probably the most important factor causing species declines worldwide. Thus, it is crucial to understand mechanisms underlying the effects of habitat loss. Because it often involves habitat fragmentation, metapopulation and landscape concepts that focus on spatial effects play a major role in studies of habitat loss. To understand habitat loss better, the Spatial Ecology Research Programme at the University of Helsinki, Finland recently organized a conference featuring >100 talks and 26 posters presented by participants from 19 nations*.

How severe is habitat loss? Stuart Pimm (Columbia University, NY, USA) used species–area relationships to estimate that habitat loss could cause the Earth to lose 50% of its species in the next 50 years. To prevent this catastrophe, we need to protect land, such as national parks; however, many national parks are in cold, mountainous areas with relatively few species. On a positive note, Pimm suggested that by conserving 'hot spots' of high species diversity, such as Brazilian coastal forests, a large percentage of the world's biodiversity could be saved by protecting a relatively small percentage of land.

To do this well, we must understand how habitat loss causes reduced biodiversity. As Per Lundberg (Lund University, Sweden) and others noted, habitat loss involves at least four phenomena: reduction in habitat area, habitat fragmentation, habitat deterioration within patches and deterioration of the habitat (matrix) between patches. Dan Simberloff (University of Tennessee, USA) generated considerable controversy by reviewing evidence suggesting that loss of habitat area *per se* is more important than fragmentation in explaining reduced abundance and diversity. He moderated this view by noting that habitat fragmentation can have important effects, independent of habitat loss, if predation, herbivory or negative impacts of exotics are enhanced along habitat edges that are associated with fragmentation. Generalities on when each of these mechanisms is likely to be important can help to focus further study and conservation efforts.

Spatial ecology and habitat loss

A major paradigm for studying the ecology of habitat loss and fragmentation is the metapopulation view[1,2], which posits that metapopulation persistence depends on the interplay between extinction from occupied patches and recolonization of empty patches. Habitat degradation can increase patch extinction rates, and habitat fragmentation and reductions in matrix quality can decrease recolonization rates. However, the original Levins metapopulation model included major oversimplifications that need to be addressed to understand habitat loss effects.

Simple metapopulation models treated patches as either occupied or unoccupied, but they ignored within-population dynamics. To better understand within-patch effects of habitat loss, Bill Sutherland (University of East Anglia, Norwich, UK) showed that relatively simple models that include resources, major sources of mortality, density-dependence and adaptive behavior can accurately predict the magnitude of within-patch population decline owing to a given amount of habitat degradation. He illustrated his approach with examples involving birds and fish. Accurate within-patch predictions are obviously important both for scientific and management purposes.

Simple metapopulation models also assumed that all occupied patches are equally likely to supply colonists to all empty patches. However, in reality, most successful dispersal and recolonization comes from nearby patches – patch locations in a landscape matter. Kimberly With (Bowling Green University, OH, USA) addressed landscape effects by using grid-based models, which potentially can include many aspects of reality. At the other extreme, Jordi Bascompte (NCEAS, Santa Barbara, CA, USA) showed that for some issues, the essence of distance and neighborhood effects can be captured by simply adding a spatial autocorrelation factor to analytical models. At an intermediate level of complexity, Ilkka Hanski (University of Helsinki, Finland) analysed incidence function models parameterized by real data sets that account for both area and distance effects on connectivity among all patches. Using these different types of models, Hanski, With, Mark Hill (with Hal Caswell, Woods Hole, MA, USA) and others found that habitat loss should cause less extinction if suitable habitat is left in clusters rather than in an equal area of isolated habitat patches. The rationale is that if dispersal success depends on distance, then isolated patches that become extinct are unlikely to be recolonized. A set of isolated patches will gradually, but inexorably, wink out of existence.

For a more mechanistic view of dispersal, Lenore Fahrig (Carleton University, Ontario, Canada) emphasized that variation in successful dispersal depends on the tendency to leave patches, the ability to move among patches (which depends also on matrix quality) and the ability to successfully colonize patches. However, relatively few studies have examined details of dispersal behavior and success. In a notable exception, Philip Taylor (Acadia University, Nova Scotia, Canada) showed that effects of habitat loss on damselfly dispersal can be analysed using simulation models that blend information across spatial scales, from short-term observation of flight behavior to larger-scale landscape effects.

Finally, simple metapopulation models were deterministic, although nature is stochastic. Russ Lande (University of California, San Diego, USA) found that with stochastic local population dynamics, metapopulation persistence depends crucially on the rescue effect and on positive feedback in colonization rates. These effects can increase the time to extinction and produce complex dynamics. Spatio-temporal patterns of stochasticity also influence spatial synchrony in population fluctuations – greater synchrony tends to increase the risk of extinction. This effect goes against the earlier suggestion that clustered habitats should enhance species persistence. In a stochastic world, clustered patches can have synchronous local dynamics (relative to isolated patches) and thus enhanced risk of extinction.

Expanding the metapopulation paradigm

One 'new horizon' outside the main, single-species, metapopulation ecology view looked at how adaptive responses to habitat loss might influence species persistence. Bob Holt (University of Kansas, USA) addressed limits to adaptive evolution in declining habitats, that might often be 'sinks' in a source–sink system[3]. He suggested that adaptive evolution would be more likely if habitat deterioration is gradual and if populations show moderate immigration from source to sink – enough to provide the sink with genetic variation while continually rescuing it from local extinction. Sinks might then be important sites of evolutionary innovation. Other papers focused on the evolution of dispersal in response to habitat loss. Mikko Heino (University of Helsinki, Finland) and

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Régis Ferrière (Ecole Normale Supérieure, France) used different modeling approaches to show that natural selection can provide an 'evolutionary rescue' via the evolution of enhanced dispersal, which increases metapopulation persistence. Fascinatingly, both also revealed the possibility of 'evolutionary suicide' leading to population extinction; for example, if habitat loss results in higher mortality during dispersal.

A second 'new horizon' examined effects of habitat loss on multispecies interactions. Bascompte and Holt suggested that because predators tend to be more sensitive than prey to habitat loss, some prey species might benefit (via release from predation) from moderate habitat loss. Other less competitive prey can be impacted negatively if habitat loss removes a keystone predator. Holt also noted that habitat loss might produce the transient effect of creating 'habitat dumps' where 'refugees' from lost habitats collect in unusually high densities. During temporary periods of high density intense species interactions could result in local extinctions. Esa Ranta (University of Helsinki, Finland) found that a refugee effect could produce complex dynamics at a metapopulation scale.

Understanding transient dynamics is crucial for understanding extinction debts – the notion that extant habitat loss dooms many rare, but still surviving, species to extinction in the near future, but that these extinctions (the debt) take time to unfold. Hanski suggested that regional species extinctions in areas that suffered habitat loss in the past might provide useful estimates of ultimate extinction debts to be paid in more recently disturbed habitats.

Genetics and habitat loss

The genetics sessions began with an overview by Pekka Pamilo (Uppsala University, Sweden) who reviewed equilibrium models in population genetics and introduced new, nonequilibrium approaches (e.g. genetic 'assignment' tests).

Several presentations assessed the effects of physical landscape structures (e.g. streams, hills, valleys and roads) on gene flow and genetic structure; thus, a new discipline 'landscape genetics' is emerging. For example, Michael Antolin (Colorado State University, USA) showed that for black-tailed prairie dogs (*Cynomys ludovicianus*), geographic distance between populations does not correlate with genetic distance between populations as well as does distance along gullies that connect populations. Similar studies correlating genetic distance and 'ecological distance' were presented for plants (e.g. *Carex* spp.), amphibians (*Rana arvalis*) and bush-crickets (*Metriotera brachyptera*) in The Netherlands, and island populations of mice (*Peromyscus maniculatus*) in Quebec.

A common theme was the promise of molecular markers and new statistical methods for detecting 'realized' population fragmentation (i.e. reduced dispersal among populations). The effects of habitat fragmentation on interpopulation dispersal can be unpredictable and difficult to quantify. For example, theoretical models suggested that habitat fragmentation might actually increase dispersal rates under some demographic scenarios. Conversely, Phillip England (Wollongong University, NSW, Australia) showed that plant populations (e.g. the rare shrub *Grevillea* spp.) effectively can become fragmented (and suffer reduced gene flow) in the absence of habitat fragmentation if, for example, a pollinator is lost. These studies demonstrated that 'realized' population fragmentation will often be detectable only by using molecular markers. Interestingly, new genetic 'assignment tests' were introduced that can help detect realized fragmentation via detection of dispersal or population isolation (i.e. by identifying immigrants or by detecting a lack of immigrants).

Other presentations introduced innovative approaches for assessing the interactive role of gene flow and selection in local adaptation, and in the spread of adaptations in diverse organisms from rainforest *Drosophila* to boreal forest trees. Finally, several studies assessed the (sometimes controversial) role of genetic variation in population persistence. For example, it was shown that inbreeding can increase extinction risk in butterfly populations (*Melitaea cinxia* and *Coenonympha hero*), and that inbreeding depression can be more severe under food stress – consistent with a growing number of studies linking inbreeding depression, stress and reduced population persistence.

Overall, the genetics presentations provided a good balance of theory, models and empirical studies, and suggested an increasing role for genetics in understanding the effects of habitat fragmentation on population persistence and evolution.

Other focal issues

Several papers emphasized that habitat loss is a temporal phenomenon; thus, historical knowledge might be crucial for understanding current patterns. History can be traced through old maps, written accounts and interviews, as well as with modern tools like remote sensing and geographical information systems. A notable example examined change in the distribution of farmland birds in southern Finland.

Research on habitat loss in boreal forests focused on the importance of landscape contexts, the consequences of structural changes and the temporal aspects of habitat loss. Research has moved from previous snapshots of local-scale patterns (i.e. stand level) to a wider concern for the landscape context and the temporal dimension of change.

The notion that one can 'travel in time' by moving from heavily utilized western European boreal forests to Russian areas was emphasized by Per Angelstam (Swedish University of Agricultural Sciences, Sweden). This approach is being utilized successfully to compare Finnish forests with biogeographically similar areas in the Russian Karelia. Baseline information on the changes that boreal areas have experienced as a result of human activities emphasize that 'habitat loss' in boreal areas mainly involves the loss of structural elements associated with old-growth forests and not the conversion of forested areas to other vegetation types. To date, research on habitat loss in boreal areas largely is empirical. However, this conference might have provided the stimulus for blending theory and modeling with empiricism.

Finally, relatively few presentations focused on habitat loss and population management; exceptions included management of sand lizards (*Lacerta agilis* L.) and breeding programs for salmon.

Prospects

Habitat loss presents perhaps the ultimate challenge to ecologists and evolutionary biologists from both a scientific and management perspective. However, many integrative bridges remain to be built. Although theory and small-scale experimental studies have been reasonably well integrated, these approaches remain largely uncoupled from larger-scale empirical work that applies most directly to conservation and management policy. An exception involves work by Hanski and colleagues using practical incidence function models. Similarly, although there are exciting new developments in ecology and genetics, only a small but growing number of studies blend the two. Future work that bridges these gaps will move us yet closer to an integrative understanding of habitat loss.

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Do edge effects occur over large spatial scales?

In recent years, biologists have come to realize that one of the most important consequences of forest fragmentation is a dramatic increase in the amount of habitat edge[1,2]. Although certain game species benefit from habitat ecotones, mounting evidence reveals that the abrupt, artificial edges created by forest fragmentation negatively affect many forest species and ecological processes[1–11].

Edge effects in fragmented landscapes are remarkably diverse. They include microclimatic changes, such as increased desiccation and temperature variability near forest edges[3], which, in turn, affect many plants and animals. Greater wind turbulence near edges leads to elevated rates of wind-throw and forest structural damage[4]. Predation on bird nests often is increased near edges because of an influx of generalist predators and brood parasites from surrounding modified habitats[5]. Understory insectivorous birds[6], certain mammals[7] and a variety of invertebrate taxa[8] avoid forest edges and thus are especially vulnerable to habitat fragmentation. Ecological processes, such as pollination, seed dispersal, nutrient cycling and carbon storage, can also be altered by edge effects[4,7,8].

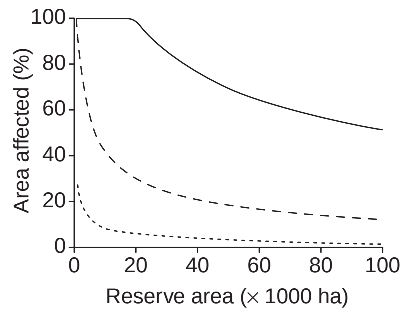

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Fig. 1. A mathematical core-area model illustrating the impacts of edge effects on nature reserves ranging from 1000 to 100 000 ha in area [this example was generated for reserves with a realistic shape-index value of 2.5 (see Ref. 11 for details)]. The curves show the percentage of the reserve's total area that is influenced by edge effects that penetrate to distances of 100 m (dotted line), 500 m (dashed line) or 2 km (solid line) inside the reserve. For an edge effect that penetrates to 5 km (not shown), the reserve would need to be approximately 650 000 ha in size to ensure that half of its area is free from edge effects.

Most empirical studies have found that edge effects penetrate less than 150 m into fragmented forests[5,7,8,10], although one study suggested that increased disturbance and exotic weeds could be detected up to 500 m from edges in Australian tropical rainforest fragments[11]. A few authors have hypothesized that edge effects potentially could occur over larger spatial scales, on the order of 1–5 km (Refs 1,9), but compelling evidence has so far been lacking – possibly because such large-scale phenomena are inherently difficult to study. However, new results from several independent investigations suggest that habitat edges may be having far more pervasive and wide-ranging effects on forest ecosystems than suspected previously. If so, it would be difficult to overstate the implications for biodiversity conservation.

Fragmentation and tree regeneration

One of the most striking examples of apparent, large-scale edge effects is provided by Lisa Curran *et al.*[12], who found that recruitment of canopy trees has collapsed in the 90 000 ha (hectare) Gunung Palung National Park in western Borneo. This is mainly because vertebrate seed predators have flooded into the park from surrounding degraded areas. Canopy trees in these forests are dominated by the Dipterocarpaceae, a diverse family exhibiting mast fruiting – in which massive seed crops are produced for brief periods of a few weeks, followed by several years with little or no fruit production. Dipterocarps are dispersed by wind, water or gravity, and the masting strategy apparently has evolved as a mechanism to swamp seed predators (nomadic vertebrates and many insects) and thus ensure successful recruitment. During successful mast years, densities of new dipterocarp seedlings can exceed 100 000 individuals per ha (Ref. 12).

Curran *et al.* showed that masting episodes across large areas of Borneo over the past three decades were correlated strongly with potent El Niño droughts, which act as a cue to trigger synchronized regional fruiting. However, in areas that have been selectively logged masting is reduced greatly because loggers harvest or severely damage most large dipterocarps. Near Gunung Palung National Park, uncontrolled logging, exotic tree plantations and human-caused wildfires have rapidly fragmented much of the landscape outside the park. This has disrupted regional seed production and led to increased desiccation of degraded forests during droughts.

Gunung Palung is now an island of mostly intact forest surrounded by a sea of degraded land. During the masting event associated with the 1998 El Niño drought, Curran *et al.* found that dipterocarp recruitment in the park fell drastically because of a dramatic increase in seed predation by vertebrates. Smoke and heat from nearby forest fires could also have contributed to this decrease in recruitment by stressing trees and inhibiting insect pollinators. The net result was that dipterocarp reproduction in the park collapsed completely; the investigators could find no new dipterocarp seedlings in 1998, compared with average densities of over 150 000 seedlings per ha after the 1991 masting event.

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