Habitat fragmentation

Introduction

With this lecture we begin more concrete discussions of principles related to the design of conservation reserves or reserve systems and to conservation programs directed either at multiple species or at entire systems. We'll talk more about the history of reserve design and the purposes reseve systems serve in a couple of weeks. For now it's enough to know that there are four broad purposes such reserves may serve:

1. Conservation of large, intact, functioning ecosystems,
2. Conservation of areas with high biological diversity,
3. Conservation of species or groups of species of special interest, or
4. Conservation of significant natural communities.

Conservation reserves are needed because of the enormous impact that human beings have on this planet. As I've said repeatedly in this course, we cannot choose to have no impact. We can only choose the type of impact we will have. Of course, when we think of the impact we have, we tend to focus on the direct and obvious impacts:

- Pollution of air, streams, lakes, and groundwater,
- Depletion of the ozone layer,
- Global warming, and
- Habitat destruction.

As we saw early in this course, human activities dominate many of the earth's ecosystems. We manage them for agriculture or forest products, pave them for shopping malls, convert them to housing developments, and extract their resources for our consumption. Our activities fix more nitrogen than all biotic and abiotic sources, fertilizing the entire planet [9]. Not only

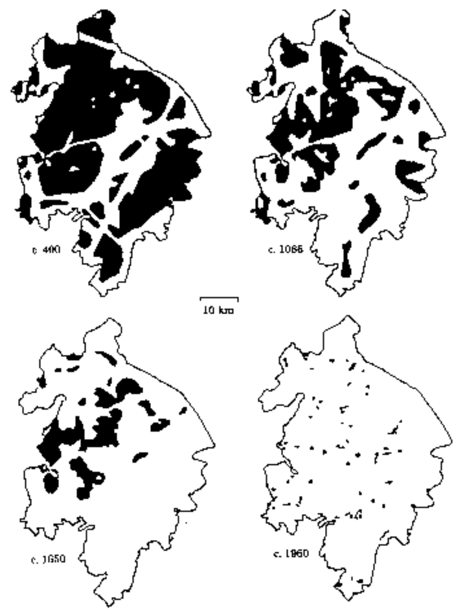

Figure 1: Forest fragmentation in Warwickshire, England

do our activities directly diminish the amount of relatively undisturbed habitat available to other species, not only do they modify the character even of remote habitats that never see a bulldozer or chain saw, in areas where bulldozers and chainsaws are common our actions create islands of undisturbed habitat in a sea of human-dominated ones.

When we think of habitat destruction, the tropical rainforest almost always leaps to mind. When we think of habitat fragmentation, however, we need look no further than our own backyard (Figure 1).[1]

As Figure 1 makes clear, habitat fragmentation has several related effects:

- The total area of available habitat decreases,
- The area of remaining habitat patches decreases,
- The number of remaining habitat patches increases, and
- The connectedness of remaining habitat decreases.

[1] The fragmentation here is the inverse of the reforestation we saw in Foster's analysis of Petersham, Massachusetts. But that's because we (or I) focused on the *forest* ecosystem in Petersham, not the grasslands.

What will be affected by fragmentation?

Before we can discuss the effects of fragmentation, we must identify the species likely to be affected.[2] That means identifying species in which fragmentation will alter

- the distribution of populations,
- the migration rates among populations, or
- the sizes of local populations.

Let's start with the last one first. For animals, the ones most severely affected are (obviously) those with large home ranges, because we expect these species to be entirely lost from small fragments.

- ivory-billed woodpeckers: ca. 7km^2 per breeding pair
- European goshawk: home range of 30-50km^2
- male mountain lion (puma): home range of 400km^2

  Suppose that 50 males are needed for a population to have a reasonable chance of persistence for a couple of centuries. This would require an area of about 20,000km^2, which is roughly equivalent to the area of Connecticut, Rhode Island, and Cape Cod combined. Fortunately, puma are learning to live in close proximity to development, so completely undeveloped habitat doesn't appear to be necessary to conserve them. Some of the habitat they use can be moderately altered, as in south Florida or southern California. You see occasional news reports of joggers being attacked by puma in southern California, and I've had people tell me that attacks also occur occasionally on trails near Boulder, Colorado.

- Forest birds — size of area needed for 50% probability of occurrence [7]
  - Great Crested Flycatcher: 0.3ha (a circle about 60m in diameter)
  - Cerulean Warbler: 1000ha (a circle about 3.5km in diameter)

[2] Did you notice how I slipped back into a species-centric focus here? That reflects the aspects of conservation that I tend to think about. Obviously, we could also concern ourselves with how fragmentation affects ecosystem processes or community structure/function, but that won't be my primary focus. They're important, but I know even less about them than I do about fragmentation effects on species. I am a population geneticist, after all.

Local population size	*Geographic range* Large *Habitat specificity* Wide	 Narrow	 Small *Habitat specificity* Wide	 Narrow
Large	locally abundant, large range, several habitats	locally abundant, large range, specific habitat	locally abundant, restricted range, several habitats	locally abundant, restricted range, specific habitat
Small	locally sparse, large range, several habitats	locally sparse, large range, specific habitat	locally sparse, restricted range, several habitats	locally sparse, restricted range, specific habitat

Table 1: Rabinowitz' typology of rarity

> Consequence: species composition of small fragments will differ from that of large fragments. The species remaining in small fragments will not be a random subset of those originally present. Species with large area requirements will be preferentially lost.

Some years ago Deborah Rabinowitz [6] developed a typology of rarity that is both interesting and useful in thinking about the possible impacts of fragmentation (Table 1). Notice that Rabinowitz identifies three axes of rarity:

1. limited geographic range,
2. specific habitat requirements, and
3. low population density.

Plants (or animals) that are rare in either of the first two senses seem unlikely to be greatly affected by habitat fragmentation, except to the extent that habitat fragmentation leaves them *outside* a fragment. To put it another way, they will be affected by habitat *destruction*, but habitat *fragmentation* may have little impact on either the migration rate among populations or the sizes of local populations.[3]

[3]Of course, this assertion depends on how fragmentation affects the character of the matrix in which fragments are embedded, a point that we'll return to in a bit.

Furthermore, not all plants or animals that are widely distributed will suffer the effects of fragmentation. Those that are patchily distributed are *already* fragmented. Unless fragmentation disrupts patterns of migration among the populations that remain, it will have fewer effects than it will on those that are continuously distributed.

Think about what this means, though. The plants[4] that are most likely to be affected by habitat fragmentation:

- are broadly and continuously distributed,
- have relatively non-specific habitat requirements, and
- are numerically abundant almost everywhere they occur.

These are roughly the characteristics we associate with plant species regarded as ecosystem dominants: douglas fir and hemlock in the Pacific northwest, mixed hardwoods in the Northeast. In short, whatever the effects of fragmentation are, they may be exhibited in a minority of species, but that minority of species will be the ones that have the largest impact on the structure and function of ecosystems in which they occur.

Dynamics and impacts of fragmentation

The first thing to realize about fragmentation is that there are some important differences between distributions that are naturally patchy and those that become patchy because of habitat fragmentation. Groom et al. [3, p. 219] mention four in particular:

1. Fragmentation reduces the extent and connectivity of remaining habitats, and species may or may not be able to persist as a result of those changes.
2. Natural patches have a rich internal patch structure *versus* relatively a simple, uniform patch structure in patches associated with human alteration of the environment.
3. Natural patches typically have a smaller contrast between interior and exterior of patch in natural patches (largely because of 2).
4. The matrix in which anthropogenically produced fragments are embedded may harbor activities and produce byproducts that are a direct threat to the patches that remain, while the threats from patch exteriors to natural fragments is less severe.

[4] Sorry for the plant-centric focus here, but it's what I know best and it's what I think is most scary.

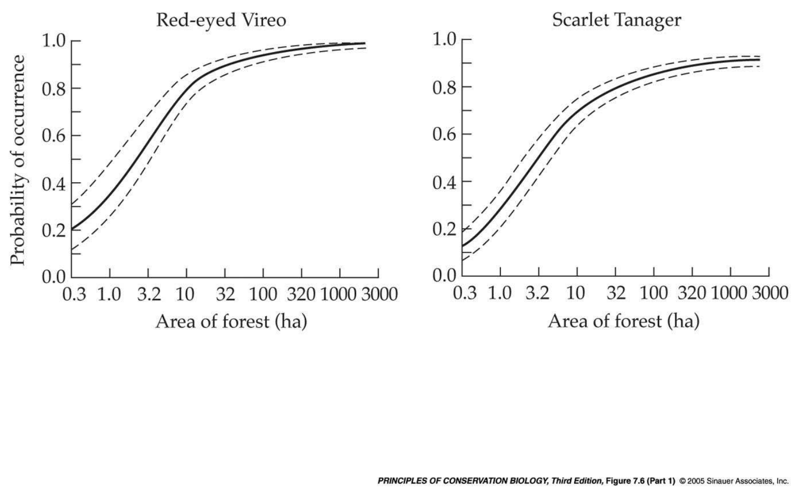

Figure 2: Relationship between size of forest fragment and probability of occupancy in red-eyed vireo and scarlet tanager (Figure 7.6 in [3]). Notice that the x-axis is on a logarithmic scale.

Another, less obvious, consequence of fragmentation is that typically the size of fragments becomes increasingly skewed as habitat destruction proceeds. Even if the total area of relatively undisturbed habitat remains fairly large, the size of remaining fragments may be quite small.

And remember what we said in one of the earliest lectures in this course. The number of species found in any place is related to its geographical area. Smaller fragments will contain a smaller number of species. Moreover, there are some "area-sensitive" species that require large areas to persist. They will be lost from *all* fragments. Consider the red-eyed vireo or the scarlet tanager, for example (Figure 2.) For either species fragments must be on the order of 10ha for a breeding pair to be found, and fragments must be on the order of 30-100ha to have a 90% chance of being occupied.

Wilcove et al. [10] use observations like these to predict how species diversity changes as a function of habitat loss and fragmentation(Figure 3). There are two very important facts to note in this figure:

1. Loss of species doesn't occur until a significant fraction of the habitat has been lost.

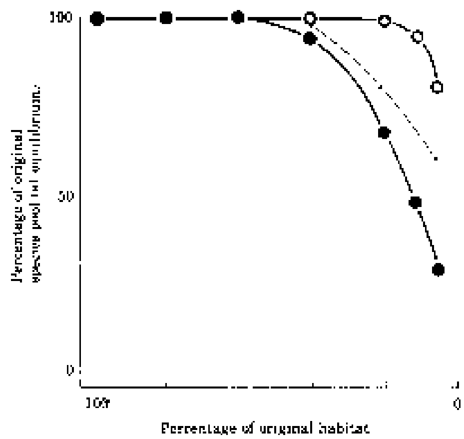

Figure 3: Loss of species diversity for species with large area requirements and low vagility (closed circles) and for species with less stringent area requirements and greater vagility (open circles).

2. Once species begin to be lost from the system, they are lost *very* rapidly (see 3).

Halting fragmentation is *always* worthwhile if it is feasible. Each additional increment of habitat fragmentation leads to loss of more species than did the last. Moreover, Seabloom et al. [8] illustrate that realistic scenarios of habitat loss, i.e., those in which habitat is aggregated into certain regions rather than spread randomly across a landscape, lead to even faster rates of species loss.

Edge effects

One of the problems with fragmentation is that the remaining fragments may be effectively much smaller than they seem.

- Vegetational changes are detectable for at least 10-30m from the forest edge in temperate zones and sometimes more.
- Edge-related increases in nest predation may extend as far as 300-600m into temperate forests (Figure 4). To take an extreme example, suppose that a single breeding pair of forest birds requires a patch of interior forest 10m in radius, where we define a patch of interior forest as the area not affected by increased nest predation. Then

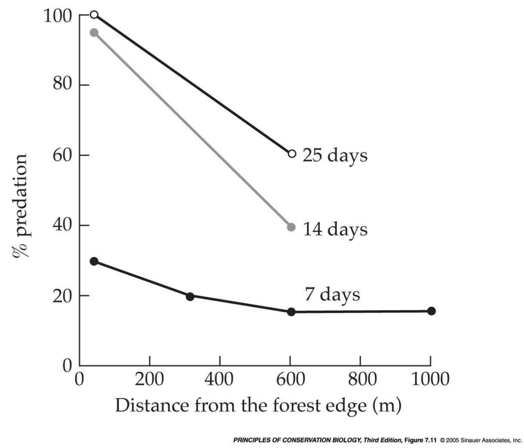

Figure 4: Fraction of quail eggs removed from experimental nests as a function of distance from forest edge (Figure 7.11 [3]).

  - With a 300m edge buffer, we need a circle 310m in radius, an area of 301,907m^2 or 30ha, about 75 acres.
  - With a 600m edge buffer, we need a circle 610m in radius, an area of almost 120ha.

  No wonder persistence of many forest interior songbirds requires areas of unfragmented forest *at least* several hundred hectares in extent.

- Laurance et al. [4] show that edge effects can have an unexpected and large effect on biomass accumulation in tropical forest trees.
  - Experiments begun between 1980 and 1986 with clearing to create replicate forest patches of 1, 10, and 100 ha in an area 80 km north of Manaus, Brazil.
  - Estimates of above-ground biomass assessed in 2-5 censuses through early 1997.
  - The regression of biomass change on distance to forest edge was significantly positive. Those plots that were the deepest in the interior of the remaining fragments showed no change in biomass. Those that were closest to the edge lost as much as 5 tons of biomass per hectare per year, a rate of about 1.3% per year.

Note: Circular areas minimize the edge to interior ratio, so if you have a choice in designing a reserve you may be better off to have one that's fairly round than one of equal area that's square or rectangular, unless your objective in designing the reserve is to provide habitat for "edge" species.

Corridors

The theory of island biogeography was the primary ecological theory from which conservation lessons were drawn in the 1980's. In the 1990s, island biogeography theory was replaced by metapopulation dynamics.[5]. Metapopulations, recall, are sets of interacting populations, populations connected by migration, extinction, recolonization. Not surprisingly, the degree of connectedness among populations within a metapopulation play an important role[6] in determining whether and how long a metapopulation is likely to persist. This has led to the widespread belief that it is important and desirable to provide corridors that connect remaining fragments. There are, however, several questions to be addressed (see [1] for a recent review and critique):

- Will the species of concern actually use the corridors? The evidence on this point is mixed.
- Will the presence of corridors enhance the transmission of disease among populations?
- Will invasive exotics use corridors to extend their influence more deeply into core areas than they otherwise could?

Unfortunately, it is very difficult to address these questions experimentally.

- It would be nice to have several replicates with the same (or at least similar)
  - distances among patches,
  - type of matrix habitat,[7] and
  - number and type of corridors.

  Moreover, you'd want to have a different set of replicates for each combination of distances, types of matrix habitat, and corridor arrangements that you thought you needed to investigate. In other words, you're going to need a *very* large experiment, assuming it's even possible to find a place where you can do that much manipulation.[8]

[5] Even though the concept dates back at least to 1970 [5]

[6] In theoretical models at least

[7] the habitat between patches

[8] Arguably, if you could, you'd be better off, for conservation purposes if not scientific ones, leaving it alone and managing it as a single, large reserve.

- In addition, models that suggest the utility of corridors typically assume that
  - the characteristics of each habitat patch are identical, with the possible exception of the size of the populations they will support,
  - the matrix is uniform, and
  - the fragments are not influenced by any large "mainland"-type populations, i.e., ones not subject to an extinction-recolonization dynamic.

  It's not obvious whether the theoretical advantages claimed for corridors will also apply in situations where one or more of these assumptions are violated. Of course, it's not obvious that the advantage *won't* apply either. We simply have to admit that the *a priori* evidence isn't particularly strong in either direction.

What to do? Well, I think that we don't trust our biological intuition as much as we should. Neither do we remember how severe are the constraints affecting those involved in conservation "on the ground", nor how different each situation is from the next. I suspect that in most circumstances it will be fairly easy to determine whether corridors are worthwhile based on the elements about which we are concerned in a particular place and what we know about their biology. And if we adopt an adaptive management approach, we can learn from our mistakes.

Fragmentation effects *versus* area effects

When discussing the effects of habitat fragmentation, we tend to lump together the effects of reduced habitat area and the effects of breaking a reduced area into smaller pieces. In a recent analysis of perennial flowering plants, darkling beetles, and predatory ground beetles Yaacobi et al. [11] showed that decreases in diversity associated with habitat fragmentation in a Mediterranean scrub landscape are the result of area loss, not degree of fragmentation. Their results are consistent with those reported by Fahrig [2] in a survey of 17 published studies that attempt to separate the effect.

What does this mean for conservation purposes? The results seem to contradict expectations implicit in the idea that some species are area-sensitive. How do we reconcile these claims?

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