Comment

Scale and the Spatial Concept of Fragmentation

JANICE M. LORD
Department of Plant and Microbial Sciences
University of Canterbury
Christchurch, New Zealand

DAVID A. NORTON*
Conservation Research Group
School of Forestry
University of Canterbury
Christchurch, New Zealand

Introduction

In a recent issue of *Conservation Biology* (Vol. 2, No. 4), a special section was devoted to edge effects and fragmented landscapes. These papers and others (e.g., Lovejoy et al. 1986; Wilcove et al. 1986) typify the current view of fragmentation as a spatial phenomenon at the landscape scale. However, it needs to be recognized that fragmentation is not restricted to any particular scale, nor to the spatial domain as opposed to any other domain (e.g., temporal or functional). Fragmentation is simply the disruption of continuity. When defined in this manner, the concept of fragmentation can be applied to any domain in which continuity is important to the functioning of ecosystems. Because ecosystems function across a wide range of scales, fragmentation is not scale-limited. Here we discuss the effect of scale as applied to fragmentation in the spatial domain. In particular, we explore the conservation implications of scale in spatial fragmentation, since fragmentation is a major conservation issue.

Scale and Spatial Fragmentation

Spatial fragmentation of natural vegetation occurs across a range of scales independent of the total amount of vegetation. For any given area, since the amount of vegetation remaining is an absolute value, the vegetation must be at one particular stage along a continuum from intact natural vegetation to completely alien vegetation. However, this vegetation can be spatially arranged in many different ways. We call the variation in spatial arrangement "dispersion," a concept analogous to that of "grain size." Grain size has, however, been used in a variety of ways (e.g., MacArthur & Levins 1964; Wiens 1976, 1989); the usage applicable here is that from landscape ecology (Forman & Godron 1986) where grain size refers to the size of the landscape elements present. Dispersion is essentially a scalar phenomenon.

To adequately describe the dispersion of fragments in an area, a number of fragment attributes need to be considered. Fragments have many features in common with vegetation patches in terms of both their physical properties and the ways organisms respond to them (e.g., Wiens 1976; papers in Pickett & White 1985). However, fragments represent only one type of patch, the remnant patch of Forman and Godron (1986), in which the fragment has been created (or isolated) by disturbance of the surrounding area.

Important attributes of fragments include density, isolation, size, shape, aggregation, and boundary characteristics. Many of these attributes are related and all are affected by the scale of fragmentation. Harris (1984) showed that isolation increased geometrically as fragment density decreased. Density and mean fragment size are also geometrically related for a given amount of vegetation. Boundary characteristics and the degree of difference between the matrix and the fragment tend to

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* *Correspondence and requests for reprints should be addressed to this author.*

Paper submitted 7/6/89; revised manuscript received 12/3/89.

be influenced by fragment size and density. Small fragments are more affected by the nature of the matrix (Forman & Godron 1986), and closely located fragments may influence the nature of the intervening matrix. Finally, fragment isolation is influenced by fragment density and aggregation. For a fixed number of fragments, a clumped distribution will clearly reduce isolation as compared to a systematic distribution (Diamond 1975; Harris 1984). Perhaps more importantly, the nature of the surrounding matrix can have a significant impact on fragment isolation, because a steep ecological gradient at the boundary where fragment and matrix abut forms a greater barrier to movement between fragments than does a shallow gradient.

Extreme Types of Dispersion

To evaluate the importance of scale in the concept of spatial fragmentation, it is useful to typify the extreme conditions of fragment dispersion. The classical concept of fragmentation, where a large intact area is divided up into several smaller intact units (Fig. 1), is essentially one extreme type of dispersion. Here, the spatial scale of fragments is large compared to the scale of the physiognomically dominant plants. We have termed this "geographical fragmentation," which is analogous to a course-grained landscape. The extent of geographical fragmentation has been widely documented (e.g., Johnston 1969; Blackwood & Tubbs 1970; Burgess & Sharpe 1981; Harris 1984; Saunders et al. 1987) and has formed the cornerstone of much conservation biology research because it has been seen as a major threat to the preservation of biodiversity (Wilcox & Murphy 1985). This concept has been primarily developed from, and applied to, forest fragments occurring as obvious islands in a human-induced landscape.

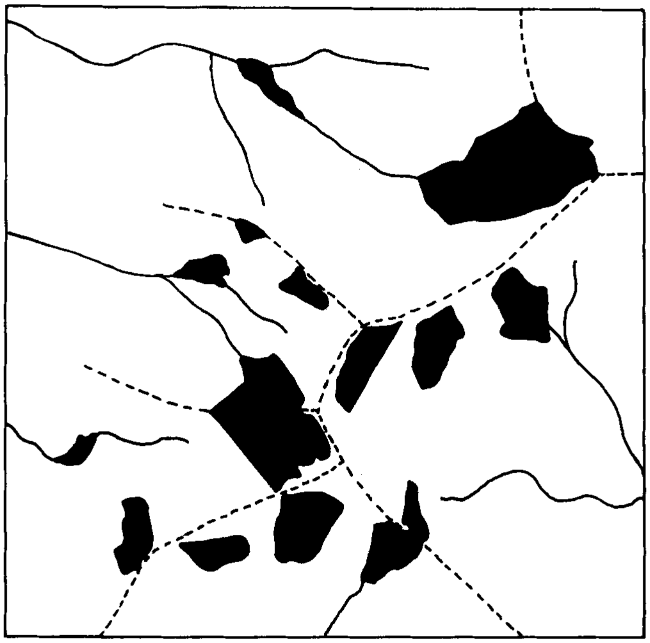

Figure 1. Geographical forest fragments, Banks Peninsula, eastern South Island, New Zealand. This 1200-ha area was completely forested 150 years ago and is now used predominantly for pastoral farming.

At the other extreme of dispersion, intact vegetation fragments are small, occurring at the scale of the physiognomically dominant plants. Here, "fragments" can simply be individual plants or small groups of plants embedded in an alien matrix (Fig. 2). We term this condition "structural fragmentation," which is analogous to a fine-grained landscape. One way that previously intact vegetation can become structurally fragmented is through the invasion of species alien to the vegetation. While geographical fragmentation has been primarily a forest concept, the concept of structural fragmentation first came to our attention in grassland vegetation, although it clearly also applies to other vegetation types.

This extreme scale of fragmentation can be seen in the short-tussock grasslands of eastern South Island, New Zealand. These grasslands are physiognomically dominated by tussocks (perennial bunchgrasses) of *Festuca novae-zelandiae* (Hack.) Cockayne, *Poa cita* Hook. f., and *Rytidosperma* Streudel, and would have

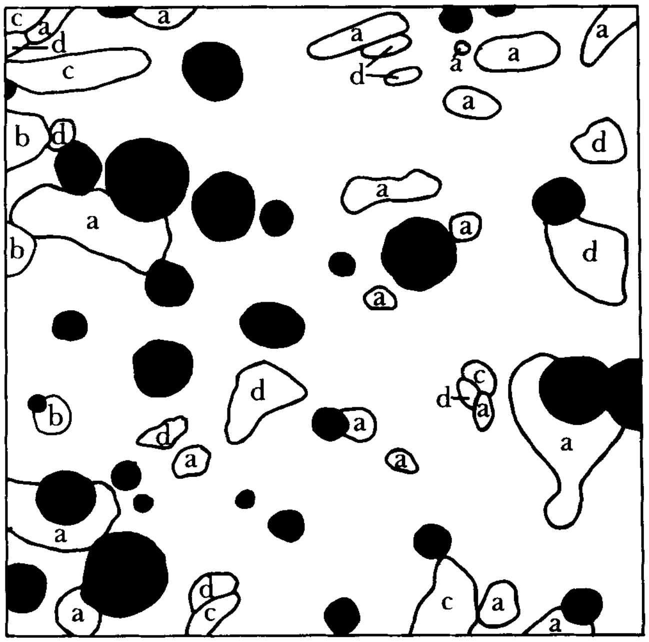

Figure 2. Map of 2m × 2m section of short-tussock grassland, Cass Basin, South Island, New Zealand. Indigenous species: a, Poa colensoi *Hook. f.; b,* Discaria toumatou *Raoul; c,* Raoulia subsericia *Hook. f.; d,* Coprosma petriei *Cheesm.; filled in areas are tussocks of* Festuca novae-zelandiae. *Blank areas between the indigenous plants are overwhelmingly dominated by the naturalized grasses* Agrostis capillaris *and* Anthoxanthum odoratum.

occurred naturally in periodically disturbed sites such as river flood plains (Cockayne 1928). Since the settlement of New Zealand by Polynesians some 1000–1200 years ago, these grasslands have expanded rapidly as a result of fire (Molloy et al. 1963; McGlone 1983), and when Europeans first settled in New Zealand in the mid-nineteenth century, the short-tussock grasslands had a well-developed indigenous herbaceous flora (Cockayne 1928). However, in the 100–150 years since European settlement, they have been severely modified by fire, grazing, and oversowing (O'Connor 1982), facilitating the invasion of naturalized plants and their subsequent domination in many areas (Lord 1990).

Despite this modification, the physiognomic dominants still remain (Fig. 3), although reduced in density and stature, and patches of the indigenous herbaceous substratum still occur throughout. However, in virtually all the remaining short-tussock grassland (approximately 2.5 million ha), the intertussock sward (matrix) contains naturalized grasses (e.g., *Agrostis capillaris* L., *Anthoxanthum odoratum* L., and *Dactylis glomerata* L.) and forbs (e.g., *Hieracium* L. species, *Hypochoeris radicata* L., and *Rumex acetosella* L.). The degree of dominance of naturalized species varies with site conditions and degree of disturbance (Rose 1983; Meurk et al. 1989). This vegetation has essentially been finely fragmented into many small patches of indigenous species embedded in an alien matrix (Fig. 2).

Implications for Conservation

Geographical fragmentation has been the traditional concept of fragmentation, and its implications for conservation have been extensively discussed. Since we now view geographical fragmentation as one extreme of a continuum of fragment dispersion, these implications can be applied to the whole continuum, although their relative importances may vary. Four major aspects of fragmentation have been postulated as important for conservation (Table 1): small fragment size, isolation, edge effects, and increased vulnerability to extrinsic disturbances. These factors are not independent, however, and interact with each other (e.g., fragment size becomes more crucial with increasing isolation).

Figure 3. Structurally fragmented short-tussock grassland, MacKenzie Basin, South Island, New Zealand. (Photo by D. A. Norton.)

The primary impact of fragmentation is through loss of habitat continuity, because any disruption of previously intact vegetation has some effect on the population size of species dependent on that habitat (Soulé 1987). Numerous examples of the importance of fragment size in determining species diversity occur in the literature (e.g., papers in Saunders et al. 1987).

Habitat reduction per se has equal impacts at any scale of fragmentation when assessed for organisms that operate at that scale. The division of a small area of forest by a concrete path, for example, is just as important to a ground-dwelling invertebrate as the division of a large forest tract is to a forest raptor. However, different organisms will perceive the *same* scale of fragmentation as affecting the continuity of their habitat in different ways. For organisms operating at the same scale, generalists tend to be less affected by fine scales of fragmentation than specialists, because the tendency for fragments to be close together and for the gradient between matrix and fragment to be shallow produces a pseudocontinuous usable area. Specialist species requiring "interior" habitat, however, will not be sustained in finely fragmented vegetation no matter how close the fragments are, and they will be less likely to utilize areas of finely fragmented vegetation as corridors between intact vegetation fragments. Thus the degree of isolation experienced by an organism subsequent to fragmentation depends on how it reacts to the scale of fragmentation that has occurred.

The impact of habitat loss and isolation at a given scale of fragmentation can be considered organism-specific, but the physical impacts of edge effects and increased vulnerability to disturbance are much more

Table 1. Implications of different scales of habitat dispersion to various attributes of fragments and fragmented landscapes.

	Dispersion	
	Geographical < - - - >	*Structural*
Size (m^2):	large: >1000	small: <10
Isolation:	usually medium to large	usually small
Boundary gradient:	steep	shallow
Impact of extrinsic disturbance:	confined to edge and up to a few hundred metres in	throughout
Vulnerability to functional disruption:	medium to small	medium to large
Scale of organism affected:	large generalist to medium specialist	medium specialist to small specialist
Advantages for conservation:	usually has intact interior	usually of greater total extent

dependent on the nature of fragmentation itself, even though their ultimate effects are also likely to be organism-specific. The significance of edge effects in geographical fragments has been well documented (e.g., Whitney & Runkle 1981; Lovejoy et al. 1986; Yahner 1988), with some studies suggesting that edge effects may penetrate for several hundred meters into fragments (Wilcove et al. 1986). However, because of the substantial internal modifications associated with finer scales of fragmentation and the lack of intact "core" areas, structurally fragmented vegetation can be regarded as having similar properties to edges throughout. Thus many of the problems associated with edges in geographical fragments are likely to increase as the scale of dispersion becomes finer (i.e., moves toward structural fragmentation).

The reduction in spatial continuity, together with edge effects, increases the vulnerability of fragmented vegetation to extrinsic disturbances such as windstorm, fire, and flooding. The importance of this increased vulnerability has perhaps been less widely recognized than, for example, edge effects, but also has significant implications for the long-term viability of fragmented vegetation (Pickett & Thompson 1978; Norton 1989). The impacts of extrinsic disturbances vary with the nature of fragment dispersion. In geographical fragments, disturbance impacts are largely confined to edges, but they occur throughout structurally fragmented vegetation. Finer scales of fragmentation may not only increase the vulnerability of vegetation to disturbance but may also lead to the occurrence of disturbance regimes that would not occur in equivalent intact vegetation. Frost-heave, for example, is likely to have been of little importance in dense undisturbed New Zealand tussock grassland, but with reduction in tussock density, this disturbance has become considerably more prevalent (Simpson & Moore 1955; Gradwell 1960). At larger scales of fragmentation, the impact of extrinsic disturbance can be minimized if appropriate buffer zones are present.

The scale at which previously intact vegetation has been fragmented also has important implications for functional interactions between organisms. At larger scales of fragmentation, fragments are more likely to retain a greater complement of the original species and some intact interior, so organism interactions such as pollination, seed dispersal, and predation and ecosystem processes such as nutrient cycling are more likely to remain functional. At finer scales of fragmentation, those interactions reliant on, for example, microclimate may be more easily disrupted. More complex ecosystems (e.g., tropical systems) involving interactions between many species and containing many specialist species are more likely to be adversely affected by finer scales of fragmentation than less complex ecosystems (e.g., temperate systems) comprised of fewer, more generalist species. In the latter case, the wide ecological amplitudes of the species present may buffer the changes occurring with finer scales of fragmentation.

In the sense that any landscape is a heterogeneous mosaic at some scale (Forman & Godron 1986), finer scales of fragmentation can occur concurrently with coarser scales. A large geographical grassland fragment, for example, may itself be structurally fragmented to various degrees over most, if not all, of its area (e.g., Meurk et al. 1989). This nesting of scales is likely to be the norm in fragmented landscapes simply because the usual agent for disruption, human activity, also exerts its influence at a range of scales.

Conclusions

Finer scales of fragmentation are widespread in the landscape and have, in the past, been grouped under the ubiquitous but unspecific term "modified." This is unsatisfactory, since modification is an unidimensional concept providing, at best, information only on the question of "how much" (e.g. slightly versus highly modified) and leaving totally unanswered the question of "in what manner." In introducing the concept of scales of fragmentation and of fragment dispersion, we are trying to improve the information content of the terminology associated with "modified" vegetation. Once it is recognized that fragmentation can occur at any scale with varying impacts on organisms, it follows that the conservation value of a fragmented landscape is not an absolute property of how much habitat remains; the degree of dispersion is of equal importance.

Some general statements can be made about the effects of scale on the impacts of spatial fragmentation.

1. At finer scales of fragmentation, ecosystem functioning is more likely to be disrupted, either through extrinsic abiotic disturbances or invasion, or through intrinsic breakdown of functional interactions.
2. Complex systems such as those that occur in the tropics are more likely to be disrupted at a given scale of fragmentation than are simpler systems.
3. The finer the scale of fragmentation, the smaller the organism adversely affected, although there could be increasing positive effects for larger generalist organisms as scale decreases.
4. Specialists are more likely to be affected by finer scales of fragmentation than generalists.
5. Finer scales of fragmentation may be used as continuous habitat by organisms with a wide range of mobility, whereas coarser scales are more likely to be used as continuous habitat by very mobile organisms only.

Of course in all cases, intact is better than fragmented. In the real world, however, we are more and more being left with a fragmented landscape in which to salvage functional ecosystems. By recognizing the scales of fragmentation present within a particular landscape, we can make management decisions about the types of organisms most likely to be affected and take appropriate remedial measures.

By ignoring difference scales of fragmentation we could be ignoring potentially valuable refugia for biodiversity and opportunities for restoration, particularly in tropical ecosystems (e.g., Janzen 1988). Furthermore, any vegetation that has a greater spatial continuity, whether structurally fragmented or essentially intact, may be better able than isolated (geographical) fragments to cope with the major environmental changes predicted as a result of global climate change (Peters & Darling 1985).

Acknowledgments

We thank Richard Duncan, Colin Meurk, Ian Spellerberg, Chris Thomas, and two anonymous referees for helpful comments on earlier drafts of this paper.

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