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Hyperdynamism in fragmented habitats

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Abstract. Are the dynamics of most ecological processes fundamentally increased in frequency or magnitude in fragmented habitats? Hyperdynamism could alter a wide range of population, community, and landscape phenomena, and appears to be evident in fragmented tropical, temperate, and boreal communities. I suggest some potential causes and consequences of hyperdynamism, and argue that the responses of many species and ecological processes to habitat fragmentation can be understood in this context.

What is hyperdynamism?

Hyperdynamism is defined as an increase in the frequency and/or amplitude of population, community, and landscape dynamics in fragmented habitats. Examples of parameters that could be altered in habitat fragments include disturbance regimes, mortality and recruitment rates, the population fluctuations of individual species, species extinction and turnover rates, and the pace of biogeochemical cycling. Not all environmental processes will accelerate – some may remain stable or even decline – but I propose that the majority of ecological processes in fragmented landscapes will be hyperdynamic.

Following habitat fragmentation, the natural dynamics of a system could be altered in different ways (Fig. 1). The most obvious possibilities are that (1) fragments may invariably be more dynamic than intact habitat, or (2) fragments are initially more dynamic than intact habitat, then gradually stabilize and approximate the pre-fragmentation condition. Some might consider pattern 2 simply that of a perturbed system returning to a globally stable equilibrium point, but I include such effects in my definition of hyperdynamism because the return time to equilibrium may be lengthy (e.g. Diamond 1972; Tilman et al. 1994) and because these initial dynamics can have serious ecological repercussions (e.g. Terborgh et al. 2001). These are but two of an array of potential responses, and there is no compelling reason to assume that different ecological processes within the same habitat fragment will have similar dynamics.

What causes hyperdynamism?

The notion that habitat loss and fragmentation typically increase phenomena such as local extinction rates (MacArthur & Wilson 1967; Wahlberg et al. 1996; Fahrig 1997) and edge-related environmental changes (Lovejoy et al. 1986; Kapos 1989; Laurance et al. 1998a, 2000), and that such changes might alter the stability of ecosystem functioning (Naeem et al. 1994; Tilman et al. 1996; McGrady-Steed et al. 1997; but see Schwartz et al. 2000), is not new. The hyperdynamism premise differs from these earlier concepts in that it suggests that most environmental parameters are more dynamic in fragmented than intact habitats, and that these effects are frequently chronic in nature. In general, these changes occur because habitat fragments are more prone than large habitat tracts to environmental stochasticity, and are strongly affected by external dynamics and disturbances in the human-dominated lands that surround them.

Within any particular landscape, fragment size may often be important, with small isolates exhibiting greater dynamism than large isolates (cf. Kareiva 1987; Brown & Hutchings 1997; Hamer & Hill 2000). There are at least 8 potential causes of hyperdynamism in fragmented landscapes.

Disturbances during initial isolation

Landscape fragmentation occurs when surrounding habitats are destroyed or drastically modified. At the outset, this process of habitat conversion creates recurring disturbances that can destabilize plant and animal communities in fragments. In the tropics, for example, surface fires, loggers, hunters, miners, fuelwood gatherers, and livestock can all penetrate into forest remnants and cause a diversity of ecological changes (Schelhas & Greenberg 1996; Laurance & Bierregaard 1997). Smoke from nearby forest burning strongly disturbed butterfly communities in Amazonian
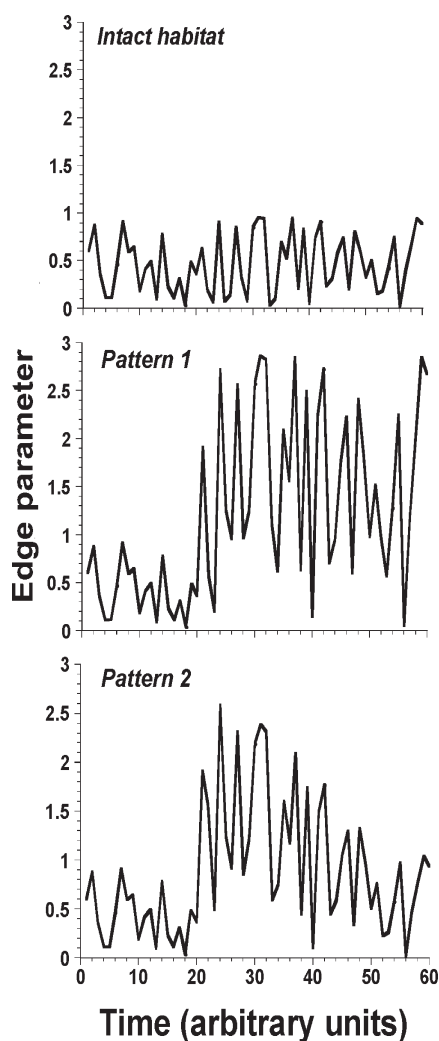
Fig. 1. Two potential patterns of hyperdynamism in fragmented habitats. In pattern 1, the dynamics of an environmental parameter increase after fragmentation (at time 20) and remain elevated indefinitely. In pattern 2, the dynamics increase after fragmentation but gradually decline to a level typical of intact habitat.

forest fragments, accelerating the loss of forest-interior species (Brown & Hutchings 1997). Similar trends were observed in Indonesian Borneo, where heat and smoke from forest burning stressed plants and inhibited insect pollinators in an adjoining national park, reducing mast seed production in large dipterocarp trees (Curran et al. 1999). Thus, disturbances associated with habitat destruction can alter ecological dynamics, even as fragments are being created.

Changing population dynamics

Landscape fragmentation can profoundly affect the dynamics of plant and animal populations. As habitat loss proceeds, displaced animals from surrounding degraded lands can flood into remaining habitat fragments, leading to sudden increases in local population densities (Lovejoy et al. 1986; Hagan et al. 1996; Schmiegelow et al. 1997; Curran et al. 1999). In the longer term, responses of animal species to fragmentation may depend on factors such as their mobility, territorial behaviour, and response to fragment size, habitat edges, and surrounding clearings (Stamps et al. 1987; Lidicker 1995, 1999; Hagan et al. 1996). For example, forest species that exploit edge or disturbed habitats often increase dramatically in fragmented landscapes (e.g. Margules & Milkovits 1994; Laurance et al. 2002).

Animal populations can be destabilized by reduced predation or parasitism in fragmented habitats. Populations of the California vole (*Microtus californicus*) introduced to a small island cycled more rapidly than did nearby mainland populations, apparently because of an absence of predators and frustrated dispersal (Lidicker 1973). Likewise, the common grassland vole (*M. arvalis*) exhibits higher-intensity fluctuations in areas with little native forest, probably because generalist forest predators that help stabilize its populations decline in such areas (Delattre et al. 1992). Population outbreaks by tent caterpillars (Roland & Taylor 1997) and aphids (Kareiva 1987) both increased in fragmented habitats, where predation or parasitism was reduced.

The dynamics of plant populations can also change in insular habitats, in response to edge effects, reduced dispersal, altered disturbance regimes, and changing herbivore pressure (Sork 1987; Quintana-Ascencio & Menges 1996). In an isolated national park in Uganda, for example, tree consumption and trampling by overpopulated elephants and altered fire regimes resulted in the rapid conversion of native woodlands and riparian forests to grasslands (Buechner & Dawkins 1961). A century after isolation, many shade-tolerant shrubs, rattans, and epiphytes had declined in a small forest fragment in Singapore, whereas some climbers and tree species increased sharply (Turner et al. 1996). These striking changes are consistent with the predictions of some theoretical models, which suggest that the relative abundances of species can fluctuate wildly in small communities, especially when immigration is low and disturbances are frequent (Hubbell 2001:95).

Increasing extinction rates

Ecological theory and numerous field studies suggest that local extinction rates of species will increase following habitat fragmentation as insular biotas 'relax' to a lower equilibrium species number (e.g. MacArthur & Wilson 1967; Diamond 1972; Lovejoy et al. 1986; Laurance 1991). Under classical Island Biogeography Theory, extinction rates are a simple function of isolate area (MacArthur & Wilson 1967; Pimm et al. 1988), with small fragments having smaller populations and thus higher extinction rates than large fragments. Fragment isolation, however, can also influence extinction rates by affecting the arrival of immigrants that can bolster small, dwindling populations in fragments, providing a buffer against extinction (Brown & Kodric-Brown 1977).

The most plausible models of extinction kinetics involve an exponential decline of species richness, with extinction rates peaking immediately after fragmentation and then gradually declining over time (Terborgh 1974; Wilcox 1978). Field studies appear to support the notion that many species will disappear rapidly from smaller (< 1000 ha) habitat fragments. For example, in rainforest fragments in tropical Queensland (1 - 600 ha in area), the most vulnerable species of non-flying mammals disappeared in the first 35 - 60 yr after fragmentation (Laurance 1990, 1991, 1994). Thus, extinction rates will almost certainly be elevated in fragmented habitats, especially in the initial decades after fragmentation, although long-lived species like trees could require centuries to disappear (Janzen 1986a).

Changes in trophic structure

In addition to species richness, the trophic organization of communities will change as habitats are fragmented (Mikkelson 1993; Terborgh et al. 2001). Studies of recently created land-bridge islands suggest that collapsing faunal assemblages pass through a series of unstable transitional states that do not otherwise occur in nature (Terborgh et al. 1997a). Such changes could lead to ecological distortions that may accelerate the process of species impoverishment. For example, generalist mammalian omnivores and seed predators increase markedly in some fragmented forests following the loss of large, dominating carnivores whose area requirements exceed fragment boundaries (Soulé et al. 1988; Crooks & Soulé 1999; Terborgh et al. 2001). This 'mesopredator release' can have major impacts on populations of nesting birds (Wilcove 1985; Sieving 1992) and large-seeded plant species (Sork 1987; Asquith et al. 1997). Ecological distortions also occur in Amazonian forest fragments, where the dominant insectivores

– understory insectivorous birds, insect-gleaning bats, and army ants – have all declined substantially; such losses might lead to increased insect herbivory in fragments (Laurance et al. 2002). By destabilizing food webs, habitat fragmentation may cause considerable fluctuations in species abundances and interactions over time.

Increasing species turnover

Recent evidence suggests that species turnover accelerates in fragmented habitats, at least for some groups of organisms (turnover is defined as the average of local extinction and colonization rates). On small (≤ 12 ha) man-made islands in Venezuela, species composition of birds was highly variable and unpredictable, with a very large proportion of transient individuals. Turnover of species was remarkably high, with many species disappearing rapidly and being replaced by individuals from a large pool of potential colonists (Terborgh et al. 1997b). A similar pattern was observed on natural boreal islands in the Gulf of Finland (Haila et al. 1993). Bat and butterfly communities in Amazonian forest fragments also seem to exhibit unusually rapid species turnover, apparently because of high rates of disappearance of forest-interior species coupled with an influx of opportunistic species that proliferate on forest edges and in nearby regrowth (Brown & Hutchings 1997; Sampaio 2000). Finally, rare tree species had very rapid turnover on small (< 1 ha) man-made islands in Panama (Leigh et al. 1993).

Abiotic ecosystem fluxes

Large-scale clearing of native vegetation can cause major changes in water and nutrient cycles, radiation balance, and wind regimes, which in turn affect communities in habitat remnants (Saunders et al. 1991). In western Australia, the removal of most native vegetation for wheat production has reduced evapotranspiration and altered soil water flows (Hobbs 1993). This has increased peak runoffs and local flooding and brought the water table with its dissolved salts closer to the soil surface. As a result, vegetation remnants in low-lying areas have suffered from chronic waterlogging and salinization. The clearing of native trees has also intensified wind speed near ground level, which increases windthrow in forest remnants and accelerates soil erosion in cleared areas. As a consequence, large fluxes in wind, moisture, nutrients, and radiation between the remaining native vegetation and surrounding agricultural lands (Hobbs 1993) may drive long-term changes in habitat remnants. Wind- or waterborne fluxes of agricultural chemicals (fertilizers, herbicides, pesticides)
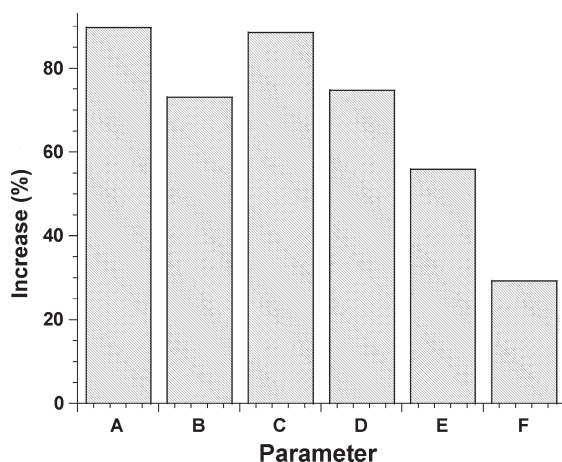
Fig. 2. Examples of accelerated population, community, and ecosystem dynamics in Amazonian forest fragments. Data shown are the mean percentage increase in each parameter near fragment edges (< 100 m from edge) relative to sites in forest interiors (> 100 m from edge). A = turnover of social spider colonies (after Venticinque et al. 1993); B = annualized rate of tree mortality; C = annualized tree damage; D = annualized tree recruitment (after Laurance et al. 1998a); E = production of coarse wood debris; F = turnover of coarse wood debris (after Nascimento & Laurance in press).

and other pollutants into habitat remnants (Cadenasso et al. 2000; Weathers et al. 2001) could also have long-term effects on fragment dynamics.

Edge effects

Perhaps the most important drivers of hyperdynamism are edge effects – diverse ecological changes associated with the abrupt, artificial boundaries of habitat fragments. In Amazonian forest fragments, edge effects cause a wide array of ecological changes. Edge-related desiccation (Kapos 1989) and wind turbulence lead to chronically elevated rates of tree mortality within 100 - 300 m of fragment margins (Laurance et al. 1998a, 2000). Large (≥ 60 cm diameter) trees are especially vulnerable (Laurance et al. 2000). This accelerates canopy-gap formation (Kapos et al. 1993), increases tree-recruitment rates (Laurance et al. 1998b), and promotes a proliferation of short-lived pioneer trees and lianas (Laurance et al. 2001a), all of which substantially accelerate turnover in tree communities (Fig. 2).

The rapid mortality of trees in Amazonian fragments has important impacts on ecosystem processes such as carbon cycling (Fig. 2). Tree biomass declines near forest edges (Laurance et al. 1997) while the production of wood debris and litter increase substantially (Nascimento & Laurance in press). Upon decay, the loss of living biomass in fragmented forests could be an important source of greenhouse gas emissions, potentially produc-

ing tens of millions of tons of emissions annually (Laurance et al. 1998c). The rate of carbon cycling probably increases markedly in fragmented forests as large, old-growth trees – some of which can live for more than a thousand years (Chambers et al. 1998) – are replaced by shorter-lived successional trees and vines (Nascimento & Laurance in press). Comparable trends have been observed in fragmented coniferous forests in western North America (Chen et al. 1992).

Because they are exposed to external vicissitudes and disturbances, fragment edges can be ecologically unstable. For example, population turnover of the social spider *Anelosimus eximius* was much higher near Amazonian forest edges than in forest interiors (Fig. 2), apparently because of frequent disturbances from falling branches and litter (Venticinque et al. 1993). In fragmented boreal forests in Sweden, recurring wind disturbance caused a reduction in the abundance of epiphytic lichens near forest edges (Esseen & Renhorn 1998). Insect activity near Amazonian forest edges is highly variable and is influenced more strongly than forest interiors by daily weather variation (Martins 1987; Fowler et al. 1993). Altered environmental conditions near edges significantly affected phenological patterns of flowering, fruiting, or leaf production in nearly a third (4/14) of the studied tree species in Amazonian forest fragments (W. F. Laurance pers. obs.).

Edge effects can be highly variable in space and time (Hagan et al. 1996; Didham 1997; Esseen & Renhorn 1998; Laurance et al. 1998a; Restrepo & Gomez 1998), further increasing fragment dynamics. Periodic droughts (Laurance et al. 2001b) and windstorms (Savill 1983) create a high degree of spatial and temporal variability in edge-related tree mortality. Edge age also influences the intensity of edge effects in most temperate and tropical forests; newly created edges tend to be structurally open and more permeable to fluxes of light, heat, and moisture than are older edges, which become buffered by dense second growth (Kapos et al. 1993; Matlack 1993; Young & Mitchell 1994; Didham & Lawton 1999). Varying edge conditions are probably key drivers of hyperdynamism.

Dynamics of the surrounding landscape

The altered landscapes surrounding habitat fragments are rarely static, but instead undergo continual changes in land use and succession. These dynamics can strongly influence habitat fragments. In the Amazon, dramatic irruptions of some Heliconine and Ithomiine butterflies occurred when their weedy food plants (*Passiflora* vines and *Solanum* bushes) proliferated near fragment margins (Brown & Hutchings 1997). In the same fragments, forest regeneration on abandoned
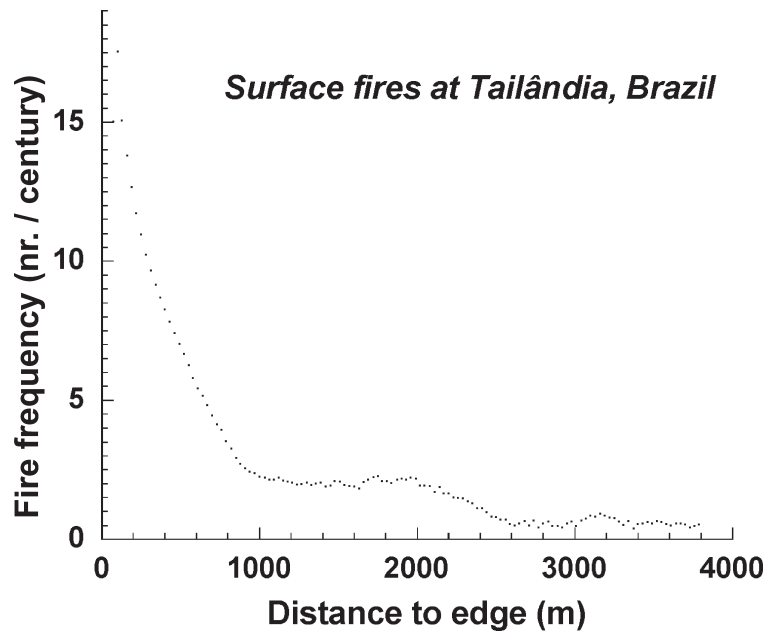
Fig. 3. Estimated frequency of surface fires in fragmented forests in eastern Amazonia, as a function of distance from forest edge (adapted from Cochrane & Laurance 2002).

cattle pastures reduced edge-related tree mortality (Mesquita et al. 1999) and allowed some vulnerable primates, understory birds, and euglossine bees to recolonize fragments from which they had previously disappeared (Becker et al. 1991; Stouffer & Bierregaard 1995; Gilbert & Setz 2001). Over longer time scales, regional or global climate change might affect vegetation dynamics in fragments by altering temperate, precipitation, or fire regimes (Nielson 1993; Díaz & Cabido 1997; Laurance & Williamson 2001).

Changes in surrounding modified lands affect the abundance and diversity of exotic species that invade habitat fragments. A proliferation of second growth, for example, could increase the seed rain from generalist plant species into fragments, potentially disrupting normal successional processes (Janzen 1986b). Likewise, the expansion of agricultural land around fragments can lead to a rise in generalist nest predators and brood parasites that have serious impacts on breeding birds and other fauna (Paton 1994; Bayne & Hobson 1997).

Finally, modified landscapes can be a major source of recurring disturbances. In seasonal areas of the Amazon, surface fires from the burning of adjoining pastures can penetrate up to 2 - 3 km into fragment interiors (Fig. 3), drastically increasing plant mortality (Cochrane & Laurance 2002). Over time, these recurring fires can cause a collapse of fragment boundaries and an 'implosion' of forest fragments (Cochrane et al. 1999; Gascon et al. 2000). In the tropics, human activities such as hunting, logging, and fuelwood gathering often have a destabilizing effect on fragmented forests (Cullen et al. 2001; Laurance & Cochrane 2001; Peres 2001).

Conclusion

The intent of this essay is to urge researchers to place greater emphasis on understanding the nature, causes, and consequences of dynamic changes in fragmented habitats. If fragmented landscapes are hyperdynamic, it could have key implications for conservation and fragmentation science. Field, experimental, and theoretical studies suggest that greater population variability can markedly increase extinction risk for insular populations (e.g. Leigh 1981; Karr 1982; Belovsky et al. 1999). Alterations in the dynamics of natural disturbance regimes can have potent impacts on fragmented systems and greatly increase invasibility (Hobbs & Huenneke 1992). Studies of non-linear dynamics suggest that recurring, long-term stresses can potentially cause sudden, catastrophic shifts in biodiversity and ecosystem functioning (Scheffer et al. 2001).

Understanding how and why the dynamics of fragmented landscapes are altered will improve our ability to predict and manage the deleterious consequences of landscape insularization. In my view, researchers should focus on at least four fundamental questions:
• Are fragmented ecosystems chronically hyperdynamic, or do they eventually tend toward an equilibrium state?
• What are the major drivers of hyperdynamism, and how do these change over time?
• Are community dynamics strongly influenced by fragment size?
• How does hyperdynamism affect plant and animal populations, communities, and ecosystem attributes in fragmented landscapes?

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