

REVIEW

What do human economies, large islands and forest fragments reveal about the factors limiting ecosystem evolution?

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Abstract

What factors limit ecosystem evolution? Like human economies, ecosystems are arenas where agents compete for locally limiting resources. Like economies, but unlike genes, ecosystems are not units of selection. In both economies and ecosystems, productivity, diversity of occupations or species and intensity of competition presuppose interdependence among many different agents. In both, competitive dominants need abundant, varied resources, and many agents' products or services, to support the activity and responsiveness needed to maintain dominance. Comparing different-sized land masses suggests that productivity is lower on islands whose area is too small to maintain some of the interdependences that maintain diversity, productivity and competitiveness in mainland ecosystems. Islands lacking the rare, metabolically active dominants that make competition so intense in mainland ecosystems are more easily invaded by introduced exotics. Studies of islets in reservoirs identify mechanisms generating these phenomena. These phenomena suggest how continued fragmentation will affect future 'natural' ecosystems.

Introduction

What conditions constrain ecosystem evolution? We begin our answer by comparing natural ecosystems with human economies. Both evolve, in the sense of descent with cultural or genetic modification of their members, whether endogenous or driven by ideas or immigrants from outside. Unlike genes, ecosystems or economies rarely die or replicate: they are not units of selection. Both are shaped by competition among members for locally limiting resources needed to survive and grow or reproduce. For both economies and ecosystems, we show how interdependence underpins productivity, diversity of species or occupations and intensity of competition. Next, we show that island ecosystems are less productive as well as less diverse than their mainland counterparts because the small area of an island offers less opportunity for speciation *in situ*, specialization, and the relationships of interdependence that make possible the productivity

and diversity of mainland ecosystems. Darwin (1859) had already predicted that the intensity of competition was lower on islands, making them susceptible to invasion by mainland exotics, because island species are tested by fewer encounters with other species of competitors and predators. We also show that, absent human introductions, islands, especially smaller ones, lack rare, metabolically active dominant predators like those ensuring the rapid resource turnover that enhances productivity and intensity of competition in mainland ecosystems. Study of forest fragments isolated by reservoirs confirms these conclusions and identifies some of their underlying causes. As human activity is fragmenting natural ecosystems at an ever-increasing rate (Laurance & Bierregaard, 1997), we will use our conclusions to predict how fragmentation will shape the 'natural' ecosystems of the future.

Competition, economies and ecosystems

In human economies, individuals and families compete for the means to live. They often form coalitions such as tribes, businesses, city-states or republics, whose

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members cooperate to compete more effectively with others. Competitive success can be enhanced by finding new ways to make a living, specializing to exploit a narrower range of resources more effectively, specializing to particular techniques for procuring resources, or to particular locales for finding certain resources, or finding better ways to manage resources. Competition is most likely to enhance an economy's range of resource use, and its effectiveness in using them, if improvements differentially benefit their inventors, and if market-distorting monopolies do not restrict innovation (Smith, 1776; Netting, 1993). Thus competition favours innovation, specialization and diversification of occupations. For example, the invention and progressive improvement of agriculture enabled higher production by fewer people of more easily stored food, freeing people for other occupations. Effective agriculture made possible greater division of labour – a greater diversity of more specialized occupations, with greater efficiency in each specialty – thereby increasing interdependence among individuals with different specialties (Smith, 1776). The usefulness or attractiveness of products of other specialists or different lands made it possible to live by trade, an occupation based on interdependence.

Larger economies offer greater scope for interdependence and innovation, and more opportunity for the evolution of competitively dominant individuals, families or businesses. Stratified societies where cities with monumental buildings depended on extensive surrounding agriculture first developed on continents: the north China plain, the Indus valley, the 'Fertile Crescent' stretching from Mesopotamia to Palestine, Egypt, Mexico and Peru. Occupations connected with trade favoured, and were favoured by, innovations enhancing mobility, and multiplying the power of human work, such as domesticating carriage animals and developing water and road transport. The invention of machines for manufacture and transport gave rise to vehicles such as steamships, trains, trucks and airplanes. Inventing machines to produce these objects, and manufacturing them in the quantities needed, however, required the assembly of resources from a great many people and the coordination of work by specialists of many different types. These achievements are far easier in large economies, with the resources to support competitively dominant business firms that respond to more different stimuli and depend on a wider variety of resources and markets. In turn, manufacture and transport favoured further specialization and diversity of occupations and faster turnover of a greater variety of resources. Manufacture and transport also increased productivity by providing a greater variety of useful or desirable products, and allowing increased trade, greater exchange of talent and ideas, and a better match of people to opportunities. These developments enhanced interdependence and widened its range, linking formerly separated economies (Smith, 1776; Vermeij, 2004). The

invention, improvement and greatly reduced cost of various modes of long-distance communication amplified these developments. Larger economies support more occupations (Bonner, 2004) and greater specialization of occupations (Smith, 1776). They provide more opportunity for the origin of competitive dominants, enhance the intensity of competition, and provide more opportunities for different specialists to pool complementary abilities to compete better with third parties (Smith, 1776). These phenomena jointly increased the gross product, diversity of occupations and levels of interdependence in the world economy during historic time (Smith, 1776; Leigh & Vermeij, 2002; Vermeij, 2004).

Although these principles are most obvious and best known for human economies, they apply equally to ecosystems comprised of organisms of other species. Other organisms also need resources to survive and reproduce: they must also find ways to 'make a living.' As in human economies, competition among individuals, coalitions of cooperating individuals, and species, for resources needed to survive and reproduce has driven an increase of productivity, diversity and intensity of competition in the world's ecosystems over evolutionary time (Vermeij, 1987, 2004). In natural ecosystems, competition quickly breaks down most monopolies that 'distort the market' by defending poorly used resources: poorly used resources soon find better users.

Species diversify because organisms face trade-offs in the ability to exploit different resources or habitats, where adaptations enabling better use of one diminish the capacity to use another. Speciation normally begins with genetic divergence of different parts of a population in response to a trade-off (Fisher, 1930: 125–129). Experiments and careful monitoring show that, where there are trade-offs between the capacity to use different resources, 'divergence of character' (Darwin, 1859: 111), now called character displacement (Brown & Wilson, 1956), reduces competition for shared resources, promoting coexistence among the species involved (Schluter, 1994, 2005; Grant & Grant, 2007). As in human economies, where the specialization involved in division of labour allows great increases in efficiency (Smith, 1776), the specialization resulting from adaptive divergence leads to more thorough exploitation of resources. Moreover, enhanced sensory capacities permit more refined choice of mates, allowing more opportunity for divergent sexual selection, which promotes speciation and diversification (Fisher, 1930; Losos, 1994: 486; Jiggins *et al.*, 2001; Grant & Grant, 2007; Puebla *et al.*, 2007). Diversity therefore increases over evolutionary time.

Innovation opens up new specialties and enhances interdependence. Photosynthesis provided good livings for its inventors and for whole ecosystems of herbivores, carnivores and decomposers. Aerobic respiration enabled its inventors to use the 'waste' oxygen produced by photosynthesis to extract far more energy from a food

item (Knoll, 2003), increasing productivity by speeding up resource turnover. Novel growth forms, such as trees, corals, grasses, mangroves and seagrasses created new habitats – coral reefs, forests, mangrove, grasslands and turtlegrass beds (Corner, 1964; Goreau *et al.*, 1979; Jackson, 1997: S26; Retallack, 2001) – each leading to increased local productivity and providing livings for many new species. Innovations that enhance sensory and motor capacities can make a predator more effective. Indeed, dominants tend to be replaced by more powerful successors with higher metabolism and greater activity, that use a greater variety of resources, respond to more stimuli, and interact with, and benefit from the services of, more different species (Vermeij, 1999). Increased mobility, in particular, increases interdependence. For example, different life stages of a mobile species can exploit different habitats. Mangroves, for example, provide ideal ‘nurseries’ for many marine animals whose adults live elsewhere (Robertson & Blaber, 1992). Similarly, increased mobility allowed animals ranging from locusts and butterflies to birds and wildebeest to move seasonally from region to region, according to where food is most abundant (McNaughton, 1985; Loiselle & Blake, 1991; Dingle, 1996). Such animals depend on many different habitats.

Evolving certain types of cooperation among members of the same species, and among members of different species, often from different kingdoms, with complementary abilities, were major transitions in evolution (Leigh & Rowell, 1995; Maynard Smith & Szathmáry, 1995). Such transitions included: (1) members of the same species cooperating in sexual reproduction to produce more varied offspring; (2) independent prokaryotes invading other kinds of prokaryotes as parasites or symbionts and being transformed into intracellular organelles, such as mitochondria and chloroplasts, essential for their hosts’ function; (3) evolving multicellular organisms and (4) evolving insect societies, where exchanging information and partitioning tasks among members, and working together to accomplish tasks, allowed societies to do things far beyond the abilities of any one insect (Margulis, 1993; Maynard Smith & Szathmáry, 1995). The evolution of societies of ants and termites, and partnerships between cells and endosymbionts and between corals and zooxanthellae, transformed their ecosystems (Wilson, 1971; Goreau *et al.*, 1979).

The evolution of cooperation between flowering plants and animal pollinators eventually transformed forest ecosystems. Wide-ranging animal pollinators enable rare plant species to maintain adequate genetic variation. Therefore plants that germinate far enough from adult conspecifics to escape their specialist pests (Janzen, 1970) will still be pollinated (Regal, 1977). Escaping specialist pests (at least until big enough to survive their attention) therefore becomes a viable strategy, whose practitioners can shift resources from anti-herbivore defense to fast

growth. Animal pollinators eventually enabled a diverse set of rare, fast-growing, animal-pollinated flowering plants to replace a less diverse set of slower-growing, better-defended, wind-pollinated gymnosperms (Corner, 1964; Regal, 1977; Leigh, 1999). Flowering plants, however, are far less ‘self-sufficient’ than their gymnosperm counterparts. A flowering plant depends, not only on pollinators, and perhaps seed dispersers, but also on other plants, or even other forests, to support these animals when it is not bearing flowers or fruit.

How an island’s size affects its ecosystem’s features

The area of a long-isolated land mass limits its ecosystem’s diversity, productivity, pace of life and intensity of competition, and enhances its invasibility (Darwin, 1859; MacArthur & Wilson, 1967; Leigh *et al.*, 2007). How does an isolated island’s limited area restrict the capacity of competition to ‘develop’ its ecosystem?

Diversity

As MacArthur & Wilson (1967) showed, species diversity, total and local, is generally lower on smaller islands (Table 1). Competition drives diversification (Darwin, 1859): indeed, the role of competition in promoting diversification has been demonstrated most clearly in island ecosystems (Lack, 1947; Losos, 1994; Grant & Grant, 2007). As the ‘jack of all trades is master of none’ (MacArthur, 1961), specializing as far as environmental conditions allow normally reduces the likelihood of extinction by competitors. Populations on very small, isolated islands, however, are small and local enough to be in great peril of extinction, these islands receive few immigrants, and they are too small to support allopatric speciation *in situ*, so smaller islands support fewer species (MacArthur & Wilson, 1967). To persist on such small islands, populations must be as large, and as insensitive to environmental variation, as possible (McNab, 2002):

Table 1 Total plant diversity and local tree diversity on land masses of different size.

Land mass	Area (km ²)	<i>T</i>	<i>S</i>
Réunion	2510	660	40
New Caledonia	16 700	3061	97
Madagascar	587 000	11 000	146
New Guinea	808 000	15 000	228
South America	17 800 000	> 80 000	283

Total number *T* of indigenous species of flowering plants, and number of species *S* among the trees ≥ 10 cm trunk diameter on a hectare of everwet forest, in selected land masses.

Total plant diversity of Réunion is from Tassin *et al.* (2006); total plant diversity of South America is from Colinvaux (1997: 9); local tree diversity for South America is from Gentry (1988), and other data are from Leigh *et al.* (2007), Résumé and Table VIII.

they cannot afford to specialize. On larger islands, successful populations can grow larger and spread more widely, so random chance or environmental catastrophes are less likely to wipe them out. Here, specialization is less risky. Bird species, for example, specialize to a narrower range of diets or habitats on larger land masses (Crowell, 1962; MacArthur & Wilson, 1967; Lack, 1976). Larger islands also allow new ways of life. As 9 g of predators exist per kilogram of their prey, on the average (Carbone & Gittleman, 2002), larger predators can live only on larger islands. Indeed, the largest carnivore, and the largest herbivore, are larger on larger land masses: their weights are roughly proportional to the square root of their land mass's area (Burness *et al.*, 2001). Large terrestrial carnivores are usually specialized to take large prey. Large herbivores are specialized to eat and digest abundant, low-quality plant matter: their adults are also too big to be eaten even by large predators.

Moreover, speciation *in situ* is more feasible on larger islands. Trees have speciated copiously on New Caledonia, an island of < 17 000 km² (Eibl *et al.*, 2001). In the West Indies, frogs, *Eleutherodactylus*, speciate on islands as small as 1800 km² (Heinicke *et al.*, 2007) whereas lizards, *Anolis*, speciate on islands over 8500 km² in area, but not on islands of less than 3000 km² (Losos & Schluter, 2000). Birds rarely speciate on islands of < 33 000 km² (Diamond, 1977; Mayr & Diamond, 2001). All these factors favour higher diversity on larger land masses.

Productivity

Several factors favour greater productivity per unit area on larger land masses. First, diversity enhances productivity by allowing more comprehensive use of environmental resources (Darwin, 1859). 'It has been experimentally proved, that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised' (Darwin, 1859: 113; see also Hector & Hooper, 2002).

On larger land masses, moreover, herbivore and predator pressure is more intense, increasing resource turnover, and therefore productivity. Small islands not only have smaller top predators, but their total predator pressure is lower. Consequently, animals mature later, reproduce less often, and live longer, than mainland counterparts, a phenomenon called the 'island syndrome' (Adler & Levins, 1994). Animals face a trade-off between long life and early reproduction (Rose & Charlesworth, 1981a,b; Calder, 1984; Sevenster & van Alphen, 1993). Well-known examples, not yet confirmed by comprehensive surveys, suggest that islands, with their few, small predators favour longer life, and lower turnover (Leigh *et al.*, 2007: 141–142). Small Hawaiian land snails, *Achatinella* and *Partulina*, start reproducing in their seventh year, and produce < 10 young per year

thereafter, whereas their introduced predator, the mainland snail *Euglandina rosea*, matures within a year, and lays more than 600 eggs per year (Hadfield, 1986; Simon, 1987: 178). New Zealand is noted for late-maturing, long-lived animals that produce relatively few young, such as giant carnivorous snails, *Powelliphanta superba*; tuataras, *Sphenodon*; geckoes, *Haplodactylus*; and kiwis, *Apteryx* (Daugherty *et al.*, 1993). Even in Madagascar, most lemurs and tenrecs live longer and reproduce more slowly than mainland ecological counterparts (Kappeler & Ganzhorn, 1993; Wright, 1999; Schmid & Stephenson, 2003), while predator pressure, especially on monkey-sized animals, is far higher in Africa (Leigh *et al.*, 2007: 143–144).

On an evolutionary time scale, more intense herbivory is essential to higher productivity (McNaughton, 1985). Herbivore pressure is lower on smaller islands, so their plants are less well defended (Carlquist, 1980; Bowen & Van Vuren, 1997) and turnover in vegetable matter, and plant productivity, are also lower. Not only are vertebrate herbivores smaller (Burness *et al.*, 2001), but effective invertebrate herbivores do not evolve on small islands (Vermeij, 2005). The largest prehistoric herbivore on the island of Hawaii was an 8.6 kg goose (Paxinos *et al.*, 2002). Thanks to low herbivore pressure, above-ground plant productivity in natural rainforests of Hawaii is much lower than in continental counterparts, even those on poor soils (Table 2).

Intensity of competition and pace of life

On larger land masses, successful populations spread more widely, and encounter more species of competitors and predators, which in turn have survived encounters with many other species (Darwin, 1859: 106), so competition should be more intense there. Because the diverse communities of larger land masses exploit

Table 2 Leaf litterfall, wood production, WP, and total above-ground net production, ANP, in metric tons dry weight per hectare per year at selected sites.

Site	Leaf fall	WP	ANPP
Hawaii, 700 m	5.4	1.0	6.4
Central Amazonia	6.2	3.9	11.5
Sabah, ultrabasic, 700 m	6.2	6.0	17.3
Borneo, heath forest	2.9	7.0	12.7

Total above-ground net production is measured as total fine litterfall plus wood production.

Data for Hawaii are from Austin (2002), data for forest on ultrabasic soil in Sabah, Malaysia, are from Kitayama & Aiba (2002), wood production for central Amazonia north of Manaus, Brazil is the average wood increment for BDFPP plots in Chambers *et al.* (2001), other central Amazonian data are from Table 6.17 of Leigh (1999), and data for heath forest in Borneo are from plot P4 in Miyamoto *et al.* (2007).

available resources more completely (Darwin, 1859: 112–114; MacArthur, 1972), their members must be more competitive to survive. Conversely, on the small, isolated Hawaiian Islands, competition for light is weak. These forests invest very little in making wood, a major aspect of competing for light (Leigh, 1999): they produce less than $2 \text{ t ha}^{-1} \text{ year}^{-1}$ (fig. 2b of Schuur & Matson, 2001; Austin, 2002). Hawaiian rainforests let nine times more light reach the forest floor than do continental counterparts, and Hawaiian plants of the forest floor need much more light to function than continental counterparts (Givnish *et al.*, 2004: 239). Is this true on other small, isolated islands? On large continents, superior competitors have eliminated 'living fossils' that still survive on smaller land masses, such as New Caledonia's *Amborella*, New Zealand's tuataras (*Sphenodon*) and leiopelmatid frogs, and Australia's monotremes (Leigh *et al.*, 2007).

Herbivory and predation represent competition between the victim and its would-be consumer for the resources in the victim's body. Therefore the circumstance, already discussed, that predation and herbivory are less intense on small islands, provides additional evidence that competition is less intense there. One example suggests that the 'struggle' between animals and their parasites is also less intense on small islands. In the Galapagos, small ground finches on larger islands are more likely to have avian pox, and they average more mites per bird. These finches' immune responses are adjusted to their island's density of pathogens and parasites. Birds on smaller islands, with fewer pests, keep their cheap-to-operate adaptive immune responses at higher alert, but their costly-to-use innate immune responses are slower and weaker than in birds on larger islands (Lindström *et al.*, 2004). Is this true on small islands elsewhere?

A land mass's size affects the intensity of competition in, and the very pace of life of, its ecosystem largely by restricting the activity levels and metabolic rates of its dominant predators. Flightless rails with low metabolism live on islands with no predators, or only marsupial predators, but they do not coexist with placental predators, which are more active, with higher metabolic rates (McNab & Ellis, 2006: 304–305). A flightless rail, the Tasmanian moorhen, lived in mainland Australia when Australia's terrestrial predators were all marsupials and reptiles: the spread of dingoes through Australia 5000 years ago confined these rails, along with the relatively slow-moving thylacines and Tasmanian devils, to Tasmania (Strahan, 1991: 27, 82; McNab & Ellis, 2006: 304). Although Madagascar is far smaller than Australia, it has active placental mammals, and its rails can fly (McNab & Ellis, 2006).

Indeed, several factors favour lower metabolism in animals of isolated islands. Lower metabolism reduces sensitivity to famine, making it easier to survive a long, foodless, water crossing to reach an island, and to survive food shortage on that island. Lower metabolism also

allows more individuals to live on the island's resources (McNab, 2000). In short, island life favours the capacity to endure shortages over being able to respond quickly and energetically to predators and competitors. Lower metabolism is another consequence of living longer, and reproducing later and less often (Calder, 1984; Van Voorhies & Ward, 1999; McNab, 2000), so typical a feature of island life (Adler & Levins, 1994). Basal metabolism of rails, pigeons and fruit bats on small South Sea islands is lower (Table 3) than those of similar-sized counterparts on the large island of New Guinea (McNab, 2000; McNab & Bonaccorso, 2001; McNab & Ellis, 2006). In sum, on isolated islands the pace of life and the intensity of competition are too low to permit the evolution of the rare, metabolically active, dominant predators, or the dangerous parasites, which maintain the intensity of competition in mainland settings.

Finally, the low level of competition characteristic of small oceanic islands reduces the need for relationships of interdependence. On such islands, insects are rare (Anderson *et al.*, 2001; Micheneau *et al.*, 2006), herbivory is low, and plants need not be rare to escape specialist pests. Accordingly, they do not need faithful pollinators that travel far to find a plant's conspecifics. Indeed, many of an island's insect pollinators are 'supergeneralists' serving many plant species (Oleson *et al.*, 2002). Many island plants seem not to compete vigorously for pollinators: island flowers are more likely to be small, inconspicuous and fragrance-free than mainland counterparts (Carlquist, 1974: 539–540; Anderson *et al.*, 2001). Thanks to the shortage of insect pollinators, many island plants depend largely on wind for pollination, whereas others depend on birds or even lizards, which may eat much else besides pollen and nectar (Anderson *et al.*, 2001; Oleson & Valido, 2003; Micheneau *et al.*, 2006). Finally, island plants tend to be far less dependent on outcrossing: they are more likely to be self-compatible (Anderson *et al.*, 2001). In short, the low level of competition on small oceanic islands has led many plants to abandon what over 100 million years of plant evolution achieved by domesticating faithful insect pollinators (cf. Regal, 1977).

Table 3 Per cent of normal basal metabolic rate (% BMR) for fruit bats, and pigeons and doves, on different-sized South Pacific islands, average \pm standard deviation (number of species measured).

Land mass area (km ²)	About 1000	About 10 000	> 100 000
% BMR, fruit bats	82 \pm 8 (3)	94 \pm 10 (3)	107 \pm 24 (7)
% BMR, pigeons and doves	67 \pm 9 (2)	91 \pm 4 (4)	102 \pm 8 (9)

The normal BMR is $2.14w^{0.806}$ for a w-gram fruit bat (McNab & Bonaccorso 2001: 210) and $695w^{0.606}$ for a w-gram pigeon or dove (McNab 2000: 323).

Data for fruit bats are from Fig. 6 and Table 1 of McNab & Bonaccorso (2001); data for pigeons and doves are from Fig. 6 and Table 7 of McNab (2000).

Invasibility

'Mature' island ecosystems are not readily invaded by species that disperse there without human help. Since Europeans settled the Hawaiian Islands, 21 species of ducks and geese, 23 species of sandpipers and waders, six species of hawks and eagles, 16 other species of non-marine nonpasserines and 10 species of passerines have been recorded as 'visiting stragglers' that reached these islands without human help (Pyle, 2002). None of these species established breeding populations on these islands. Ecosystems as isolated as the Hawaiian Islands appear adapted to resist the new species that disperse to them without human help: they offer few 'openings' for such species. Do the vast expanses of ocean screen out the metabolically active species that could invade successfully?

On the other hand, of 94 species of birds known to have been deliberately introduced to the Hawaiian Islands before 1940, 53 have become established, at least locally (Whittaker & Fernández-Palacios, 2007: 308). Indeed, long-isolated islands are notoriously vulnerable to invasion by species people transport from continents (Darwin, 1859: 306, 390). Their ecosystems tend to be more radically altered by these invaders (Darwin, 1859: 106, 390; Fritts & Rodda, 1998; O'Dowd *et al.*, 2003; Leigh *et al.*, 2007: 146–148; Whittaker & Fernández-Palacios, 2007: 320–321). For example, the proportion of indigenous bird species dying out after human beings colonize with rats and other commensal animals is much higher on smaller islands (Table 4).

Darwin (1859) argued that island ecosystems are more invulnerable because their level of competition is too weak to exclude introduced species. For example, an introduced fire-ant, *Wasmannia auropunctata*, is replacing all the native ants of a New Caledonia rainforest within its reach. The introduced ants find food far more quickly, and exploit food sources and nest sites far more thoroughly, so its populations soon become dense enough to exclude the natives. In its continental homeland, other dominant territorial ants severely limit *Wasmannia*'s abundance (Le Breton *et al.*, 2003, 2005). In the Hawai-

ian Islands, as in the smaller island of Réunion, introduced plants are invading native rainforest because they photosynthesize more effectively than, and outgrow, adjacent native counterparts; in Réunion, invaders also compete more effectively for nutrients (Pattison *et al.*, 1998; Tassin *et al.*, 2006: 41–42). On Mauritius, introduced species are not only invading but replacing native forest (Lorence & Sussman, 1988). On continents, by contrast, native vertebrate herbivores prefer invasive plants and depress their abundance relative to natives (Parker *et al.*, 2006), thus helping to defend natural ecosystems against invaders. Finally, the poor competitiveness of an island's parasites may also enhance invasibility. Pathogens and parasites native to small islands cannot afford to be very virulent. Small ground finches on smaller Galapagos islands with few pathogens and parasites have slow, weak, innate immune responses (Lindström *et al.*, 2004). If invaders bring in new pathogens or parasites that infect a small island's native vertebrates, will they respond with a strong innate immune response before the pathogens overpower their adaptive immune responses, weakening or killing them (Lee & Klasing, 2004; Ricklefs & Bermingham, 2007)?

The activity level of predators influences invasibility in several ways. Where predators are small and slow, as in the Hawaiian Islands and New Zealand, many animals produce few young, spaced over a long period. These slow reproducers are devastatingly vulnerable to introduced invaders with large appetites and rapid reproduction (Hadfield, 1986; Daugherty *et al.*, 1993: 439–440). Thus, when Pacific rats were introduced to New Zealand about AD 1250, they spread over its main islands within a century or two (Wilmshurst *et al.*, 2008). These rats eliminated slowly reproducing animals within their reach, such as the largest native frogs and skinks, tuatara and many large invertebrates (Worthy & Holdaway, 2002). Unlike New Zealand, Madagascar has native placental carnivores, which help create a more competitive ecosystem. There, introduced rats spread more slowly. Although these rats have now reached all of Madagascar's native forests, they apparently pose a serious threat only to the native rodents (Goodman, 1995; Goodman *et al.*, 2003). Continental rainforests, however, offer human-associated *Rattus* no openings. These *Rattus* are absent from natural forests in east Africa (Goodman, 1995). When an angry student trapped all the *Rattus* in the laboratory clearing of Barro Colorado Island, Panama, no rats recolonized the clearing from the surrounding forest (EGL, personal observation).

Introduced animals often speed the spread of introduced plants. Some introduced animals disperse seeds of invasive plants quickly and far. In the Hawaiian Islands, introduced birds and pigs disperse the seeds of the invasive plant, *Psidium cattleianum*, which has tasty fruits (Huenneke & Vitousek, 1990). In Mauritius, introduced pigs and deer created openings for invasives. In Réunion, these mammals are much rarer, and intact forest resists

Table 4 Number of indigenous land bird species *S* surviving, and number *E* known to have died out since human colonization, on isolated islands of different sizes.

Island	Area (km ²)	<i>S</i>	<i>E</i>
Easter Island	166	0	6
Hawaiian Islands	16 700	35	62
New Zealand (main islands)	268 000	40	48
Madagascar	587 000	193	20

Data for Easter Island and the Hawaiian Islands are from Whittaker & Fernández-Palacios (2007: 307–310), data for New Zealand are from Appendix 1 of Worthy & Holdaway (2002), and data for Madagascar are from Table 12.1 and p. 1026 of Hawkins & Goodman (2003).

invasive plants far more successfully (Strasberg, 1995: 177). In Réunion, however, introduced plants are colonizing new lava flows. Most of their seeds were carried in by introduced birds (Strasberg, 1995: 178; Tassin *et al.*, 2006: 43). The attractiveness to active introduced dispersers of introduced fruits, designed to attract dispersers in a more competitive world, is a major force for change in ecosystems of recently settled islands (Tassin *et al.*, 2006: 44). Indeed, an alliance often forms between active, gap-creating, soil-disturbing mammalian herbivores and introduced, weedy, fast-growing, abundantly reproductive plants whose fruit and seeds attract introduced dispersers. The potential for interdependence among introduced invaders may not be the least of the threats to island ecosystems.

Many of the ways an island's size affects its ecosystem's characteristics have yet to be fully established, such as effects on plant productivity, insect abundance, plant-insect interactions and the spectrum of ecosystem services. Yet two things are clear. First, the effects of island size are many, varied and profound. Second, the impact of island size involves effects on herbivores, predators, parasites and mutualists. Thinking based on a single trophic level is far too narrow to provide the understanding we need.

Fragmentation and limits on ecosystem 'development'

What can fragmentation tell us about how an island's size affects its ecosystem's characteristics? Fragmentation by new reservoirs isolates islands, thereby disrupting relationships of interdependence, causing local extinctions and reducing species diversity (Terborgh *et al.*, 1997, 2006). Reservoirs merely isolate islands: unlike fields or pastures, water spawns few disruptions analogous to cows, fires or weed trees (Leigh *et al.*, 2002). A new reservoir creates islands of different size, with similar climate and initial biota, allowing us to pose detailed questions about the effects of isolation on islands. What animals disappear from different-sized islands? What services cease when these animals disappear, what populations are released by these disappearances, and how do these changes affect island communities? By revealing answers to these questions, forest-fragmenting reservoirs can show what roles different species play in organizing intact ecosystems, and how fragmentation into islands affects formerly intact ecosystems.

Diversity

Many less mobile animal species disappear immediately from newly isolated islets too small to support their specialties (Terborgh *et al.*, 1997; Cosson *et al.*, 1999; Dalecky *et al.*, 2002). Diversity in plants and animals declines further as chance events eliminate rare popula-

tions, and other plant species die out for lack of pollinators, seed-dispersers or seed-buriers. Seventy-year-old islets < 1 ha in Gatun Lake lack resident mammals (Adler & Seamon, 1991), although howler monkeys still remain on some 20-year-old islets < 1 ha in Venezuela's Guri Reservoir (Feeley & Terborgh, 2005).

In Gatun Lake, tree diversity on 70-year-old < 1-ha islets exposed to trade winds is far lower than in similar-sized plots of mainland second-growth forests (Table 5), even though these islets were never deforested (Leigh *et al.*, 1993). On the four most wind-exposed of these islets, which presumably had the highest tree mortality, the increase relative to similar-sized mainland plots in the probability that two trees sampled from the same plot are the same species, was over twice what neutral theory predicted for 70 years of isolation. On the two largest plots this increase was over 25 times the neutral theory prediction (Table 5). What drove this decline? Four tree species, all with rather large seeds, were far more common on these islets than on the mainland. Seeds of three of these species, and late-falling seeds of the fourth, escaped insect attack without being buried by agoutis (Leigh *et al.*, 1993). Insects eat unburied seeds of other large-seeded species: absence of agoutis apparently contributed to these islets' decline in tree diversity.

Productivity

Does primary productivity also decline on small islets? No one has yet tried to measure this decline. The Guri islands, however, provide a relevant natural experiment. Different islets have different numbers of howler monkeys, *Alouatta seniculus*. Is productivity higher on islets with more howlers? Feeley & Terborgh (2005) found that annual basal area increment ΔBA , ($m^2 ha^{-1} year^{-1}$), of

Table 5 Tree diversity on 70-year-old islands in Gatun Lake, and on nearby mainland plots of comparable size.

Site	<i>N</i>	<i>S</i>	<i>F</i> (obs.)	<i>F</i> (pre.)
Mainland	62	23	0.0938	
Vulture island	59	10	0.2427	0.1627
Mainland	125	35	0.0788	
Camper Island	125	19	0.2456	0.1126
Aojeta Island	128	26	0.1514	0.1188
Mainland	250	46	0.0701	
NWJG Island	340	25	0.4148	0.0828
Annie Island	399	37	0.4197	0.0809

N is the number of trees ≥ 10 cm trunk diameter on the island or mainland plot. *S* is the number of species observed among these *N* trees. *F* (obs.) is the observed probability that two trees sampled with replacement from these *N* trees are the same species. *F* (pre.) is neutral theory prediction of the probability that two trees sampled from these *N* would be the same species if, 70 years earlier, the island's *F* were similar to that of a modern mainland plot with similar *N*, and if no trees immigrated after the island was cut off from the mainland. Data are from Leigh *et al.* (1993).

trees ≥ 10 cm dbh is higher on islets with a higher density N of monkeys/ha: $\Delta BA = 0.04975 + 0.03782N$ ($r^2 = 0.82$). Factoring out the impact of islet area, islets with greater basal area increment supported more species of bird (Feeley & Terborgh, 2006). Apparently, food as well as wood production was higher on islets with more monkeys (Feeley & Terborgh, 2005). If small islets usually have lower herbivory, is their productivity/ha also lower?

Intensity of competition and pace of life

Fragmentation had other effects. Spiny rats, *Proechimys semispinosus*, resident on 2-ha islands in Gatun Lake had higher body weight and shorter breeding seasons, and lived longer, than mainland counterparts, thanks to low predation pressure (Adler, 1996). In this same lake, insectivorous birds, and bats that glean insects from foliage, were less common, and insectivorous lizards with much lower metabolism more common, on isolated islands ≤ 20 ha than on the mainland (Wright, 1979; Meyer & Kalko, 2008).

One fragmentation study suggests that herbivore pressure is *higher* on smaller islands. Herbivore populations exploded on < 1 -ha islets newly created by Venezuela's Guri reservoir, greatly increasing herbivory on these islets (Terborgh *et al.*, 1997, 2001, 2006). Leaf-cutter ants multiplied, probably thanks to absence of predators (Rao, 2000). Howler monkeys, *Alouatta seniculus*, were stranded on some islets in unnaturally high densities (Feeley & Terborgh, 2005). They were unable to disperse; they survived thanks to lack of competition from other howler groups. Will stringent selection for less edible plants and chance extinction of herbivore populations make such intense herbivory unsustainable (Feeley & Terborgh, 2005: 122)? Evidence from older islets in Gatun Lake suggests that herbivory rates will fall below mainland levels. Damming the Chagres River in 1910 to form Gatun Lake in central Panama created islets of many sizes. Comparing leaf damage in trees of four species on 90-year-old islands of different size in Gatun Lake, including the islets' most common tree species, *Protium panamense*, Arnold & Asquith (2002) found that 18% of the leaves on < 1 -ha islets were damaged by caterpillars, compared to 32% on 10-ha islands and 42% on the 1500-ha Barro Colorado Island. In general, the damage on damaged leaves was greater on larger islands.

Islets in reservoirs: concluding remarks

Ecological studies of how fragmentation by reservoirs affects forest ecosystems are restricted to two sites. Even so, these studies have shown how disrupting relationships of interdependence by local extinctions of animals reduces tree diversity, and how smaller islands favour longer life, lower reproduction and lower metabolism among their animals. They suggest how herbivores

enhance an islet's primary production. Studies of other sites, including St Eugène in French Guiana where studies began before fragmentation (Cosson *et al.*, 1999), are needed to confirm and expand these lessons.

Larsen *et al.* (2005) found that in the Guri Islands, large dung-beetles that bury more dung, more effectively, are most liable to local extinction. Many more studies are needed to learn how extinctions from newly isolated islets affect ecosystem services. In Gatun Lake, fast-growing fig species are common on small islands because certain fruit-eating bats cross the water to eat their fruit, bringing fig seeds from the mainland, and their pollinating wasps bring pollen over the water from conspecifics several kilometres away (Nason *et al.*, 1998). On these islets, will tree species maintaining wide-ranging relationships of interdependence prevail over more 'self-sufficient' species? Or does their fast growth depend on other relationships, now disrupted, such as fertilization by the faeces of herbivores? Islands in reservoirs are laboratories where we can learn what relationships of interdependence enable ecosystems to maintain high productivity and diversity.

Implications for future ecosystems

One of the most dramatic consequences of human activity is the progressive transformation of continuous expanses of natural ecosystem into island-like fragments separated by transformed habitat inhospitable to most of the natural ecosystem's inhabitants (Schelhas & Greenberg, 1996; Laurance & Bierregaard, 1997; Laurance *et al.*, 2001). Biotas of such fragments will eventually assume many characteristics of biotas of heavily colonized oceanic islands. Thanks to their sparse populations, metabolically active, competitive dominants dependent on natural habitats, or hunted when they leave them, will die out. Relationships of interdependence will be disrupted. As their biotas become more island-like, these fragments will be more readily invaded by species that thrive in the intervening human-dominated habitats, especially where these habitats harbour many potential invasives such as rats, cats, cows, weeds and pioneer trees (Laurance, 2008). Indeed, just as companies based in larger nations subsidize exports to small countries without the means or governmental will to resist, creating monopolies for their products by driving local competitors out of business, so populations 'subsidized' by the reproductive overplus in human-dominated habitats invade 'natural' fragments, replacing many native species. These natural fragments will be too small, and will offer too little opportunity for, the origin and diversification of species; competitive dominants that can restore their ecosystem's competitiveness cannot evolve there. As an ill-policed globalization could cause extensive, counterproductive homogenization among cultures and economies, so indefinite fragmentation could cause extensive homogenization in terrestrial ecosystems.

As every conservation biologist knows, fragmentation disrupts many relationships of interdependence (Laurance *et al.*, 2006) and eventually reduces diversity (Wilcove *et al.*, 1986). Especially where human-dominated habitats are intensely exploited, the largest predators, herbivores and seed-dispersers will disappear from natural fragments (Laurance, 2008): pressure from large predators will decrease, herbivore pressure will be altered. Even in the Malay Peninsula, where some effects of fragmentation are slow to appear (Thomas, 2004), the long-isolated fragments of primary forest in Singapore have lost half their recorded species of forest bird, including all the large seed-dispersers, the largest mammalian predators and herbivores and many plant species (Corlett & Turner, 1997; Lum *et al.*, 2004; LaFrankie *et al.*, 2005: 17–19). Exotic lianas are smothering natural regrowth in one 4-ha fragment of primary forest in Singapore (Corlett & Turner, 1997: 340) and exotic birds in nearby secondary forest eat eggs and nestlings of some primary forest birds (Lum *et al.*, 2004: 471–472). How will such developments affect the productivity, resistance to invaders and resilience to disturbance of forest fragments? In conclusion, the worldwide fragmentation by human activity of terrestrial (and many marine) ecosystems will have consequences far beyond the acknowledged decline in local and regional diversity.

What is to be done?

To predict the consequences of fragmentation by pasture, farmland or urbanization reliably enough for planners to use, the ideas presented here need close scrutiny from ecologists and evolutionary biologists. Species diversity is only one of the ecosystem characteristics affected by fragment size (Laurance, 2008). Future work must focus on other ecosystem characteristics that reflect the impact of fragment size on evolutionary potential and response to exotic invaders. First among these is primary production, and the factors that enhance it, such as light capture, tree lifetime, nitrogen fixation, mycorrhizal activity and other ecosystem services that facilitate nutrient cycling. Second is the factors shaping the intensity of competition, rates of herbivory, predation and parasitism, and the characteristics of the fragment's surviving competitive dominants.

The nearest we can come to comparative experimental analysis is the natural experiments provided where reservoirs fragment intact forest (Diamond, 2001; Leigh *et al.*, 2002). Microbial systems have been used to test a few of these ideas (Venail *et al.*, 2008), but these experiments 'simulate' only a single trophic level. As we have seen, single-trophic-level thinking is too narrow to comprehend phenomena where herbivores, predators, parasites and mutualists play so great a role. We must continue comprehensive observational comparisons among continents, long-isolated islands, and fragments of different size and similar climate. On

islands and other fragments, the contribution of native species to their habitat's productivity, invasibility and intensity of competition must be distinguished from those of exotics that evolved in competitive continental ecosystems.

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