A CONCEPTUAL GENEALOGY OF FRAGMENTATION RESEARCH:
FROM ISLAND BIOGEOGRAPHY TO LANDSCAPE ECOLOGY

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Abstract. The concept of habitat fragmentation has become an important theme in conservation research, and it is often used as if fragmentation were a unitary phenomenon. However, the concept is ambiguous, and empirical studies demonstrate a wide variety of direct and indirect effects, sometimes with mutually opposing implications. The effects of fragmentation vary across organisms, habitat types, and geographic regions. Such a contrast between a schematic concept and multifaceted empirical reality is counterproductive. I analyzed the stabilization of the schematic view of fragmentation by the early 1980s, using a genealogical narrative as a methodological approach. The main assumptions behind the schematic view were: (1) fragments are comparable to oceanic islands; (2) habitats surrounding fragments are hostile to a majority of the organisms; and (3) natural pre-fragmentation conditions were uniform. The stabilization loop of this view was supported by the reduction of empirical research to species–area curve fitting, which always produced expected results. I present a model of the dynamics of fragmentation research that shows the schematic, island-biogeographic view as an “intellectual attractor.” Since the 1980s, the theoretical presuppositions of the schematic view have been challenged, and empirical research has become multifaceted. Fragments of a particular habitat type are viewed as elements in a heterogeneous landscape rather than “islands” surrounded by a hostile “sea.” However, the island metaphor is still used in conservation contexts in the shape of species–area curves. It is backed by a presupposition that human-influenced environments are essentially different from so-called “natural” environments, but this is unfounded. My suggestion is that our perspective should be broadened still further so that habitat fragmentation is viewed as a particular form of human-induced environmental degradation; I discuss both theoretical and practical implications of this suggestion.

Key words: dynamics of research; ecological theory; ecology and environmentalism; environmental degradation; genealogy; habitat degradation; habitat fragmentation; island biogeography; landscape ecology.

Instead of an essentially continuous forest cover, with infrequent meadow-like openings along water-courses or small grasslands where fires had been unusually severe, the landscape now presents the aspect of a savana, with isolated trees, small clumps or clusters of trees, or small groves scattered in a matrix of artificial grassland of grains and pasture grasses, unstable and frequently devoid of plant cover as a result of regular plowing.

—Curtis (1956)

INTRODUCTION

“Habitat fragmentation” has become a major theme that conservation biologists consider when characterizing human-induced ecological deterioration of the environment, as is shown by any essay collection or textbook on conservation biology, from Soulé (1986) onwards, or declaration on the research needs in ecology defined by environmental issues (Lubchenko et al. 1991). This observation, however, presents us with a dilemma: the notion of “habitat fragmentation” is conceptually ambiguous, for three main reasons (Haila 1999a). (1) Habitat fragmentation always consists of both reduction in the area of the original habitat and change in the spatial configuration of what remains, but these give rise to different ecological processes and should, for the sake of clarity, be held separate (Haila and Hanski 1984, Haila 1986). (2) As all natural environments are fragmented to variable degrees, and are subjected to continuous change due to natural reasons, no straightforward standard is available for assessing human-caused fragmentation. (3) Different organisms and ecological systems “experience” the degree of fragmentation of a particular environment in variable, even contradictory, ways. Hence, a multiplicity of both spatial and temporal scales need to be considered, and the relevant scales probably vary across species, geographic regions, and types of environment. In conser-
vation thinking, however, fragmentation is often presented as a unitary phenomenon, always happening in the same way and having similar consequences. My aim in this paper is to explore the implications of this dilemma both for research and for practical conservation.

The accumulating empirical data on the ecological effects of habitat fragmentation hardly support a uniform conceptual framework, either. As an example, I analyze a recent fragmentation article (Stratford and Stouffer 1999). In the opening paragraph of the article, the authors present a list of “effects of habitat fragmentation on avian communities . . . well documented in various parts of the temperate zone.” This includes the following: reduction in abundance and richness of forest interior species; landscape-level effects such as reduced dispersal among fragments, weakened philopatry, and changes in demography; reduced genetic variation in isolated populations; fitness effects in populations in isolated fragments through increased nest predation and brood parasitism, and reduced pairing success; species exclusion by other species associated with disturbance; and direct effects on conditions in fragments, for instance, on the microclimate.

Stratford and Stouffer (1999) support their list with 12 references to specific, well-documented cases. The list invites two comments. First, several of the cases are connected indirectly with fragmentation; in other words, the actual causal relationships are ambiguous. Second, it is very unlikely that all of these effects could be demonstrated simultaneously in any single fragmented landscape. In fact, some of the cases are manifestly specific to particular regions. For example, increased brood parasitism in agricultural forest remnants by the Brown-headed Cowbird (Molothrus ater) is an issue in the United States, but there is no analogous species in similar landscapes in the Old World. Similarly, the Noisy Miner (Manorina melanocephala), an Australian honeyeater, is an aggressive colonial breeder that chases away other species from forest remnants in which the colonies are located, but this species has no analogy in Eurasia or North America. Effects like these are contingent upon natural history on the regional or continental scale.

Another type of contingency arises from historical variation in the ways humans have changed habitat configurations. The characterization by John T. Curtis (1956) of the mid-20th century landscape in Green County, Wisconsin, USA, cited in the epigram, fits some agricultural landscapes elsewhere quite well, but does not fit other landscapes at all. Does such variation matter? How certain can we be that harmful ecological effects observed in a particular human-modified landscape actually are due to changes in the spatial configuration of habitat instead of other types of ecological disturbance brought about by agriculture? The effects vary across regions, depending on ecological conditions and the history of human-induced environmental change.

These empirical problems really follow from the conceptual ambiguity of the term. The problem is simple: as fragmentation is expected to give rise to multiple, even contradictory, processes depending on the context, context-specific auxiliary factors are always needed to build up a connection between fragmentation and particular effects. Hence, the following dilemma concerning the concept of habitat fragmentation: Is a conceptually ambiguous and empirically multifaceted term fruitful as a generic description of human effects on landscapes?

I am not claiming that habitat fragmentation has no consequence in human-modified environments. Rather, I challenge the framing of the issue as always being of one and the same kind. Fragmentation gives rise to context-specific effects. The question is, how to integrate fragmentation effects into a general view of human-induced ecological change without lapsing into an overtly typological conceptual framework?

As a similar contradiction between general rules and local, context-specific peculiarities is potentially undermining all applications of conservation biology into practice, the story of habitat fragmentation has considerable general interest for conservation thinking. To set the stage for an analysis, I construct a genealogical narrative of the stabilization of a schematic view of fragmentation by the early 1980s, extracting the genealogy from a close reading of fragmentation literature, with a particular focus on critical background assumptions. I introduce the idea of genealogy in the next section. In the third section, I condense the narrative into five claims about how the schematic view became constituted. This is followed by a summarizing section in which I suggest a model of the dynamics of thinking that supported the schematic view. The schematic view has been challenged, and fragmentation research has greatly diversified: since the mid-1980s, habitat fragments are increasingly viewed as elements in dynamic landscapes. This shift opens space for understanding historical contingency and contextual specificity in the humanity–nature relationships, and directs research and management to specific problems and solutions. In conservation thinking, however, a schematic image of fragments as isolated islands in a hostile “sea” of human-modified environments is also still alive. I elaborate the tension between schematic theory and context-specific practical needs in the last sections.

**Research Problem and Methodology: Concepts, Genealogy, and Science**

The idea of habitat fragmentation was a conceptual innovation adopted in ecology in the 1970s. Why did this happen in the way that it did? My basic hypothesis is that the idea came about as a response to a new problem space that was opened by the “environmental
awakening” during the 1960s, that is, the amazingly sudden rise into public consciousness that human activity may seriously damage the global environment. New administrative bodies, in charge of environmental policy, were established in industrialized countries during the first years of the 1970s (Weale 1992). The “environment” became a common denominator of a large variety of specific problems, ultimately, a source of a moral protest (Haila 1999b), but I take it simply as an historical fact.

The new problem space opened by the rise of environmentalism posed a particular challenge to ecological research. An essential aspect of the new environmentalism was a fear that vital ecological processes would collapse on the global scale. Somebody was expected to specify what, precisely, such a collapse consists of. Ecologists originally took up the challenge with some enthusiasm, but this was soon muted by the sobering realization that basic ecology does not provide recipes for specifying environmental problems, let alone means of solving them. McIntosh (1985) describes the early responses; see Boucher (1998) for a personal narrative.

I specify the connection between fragmentation research and the rise of environmentalism in more detail in the next section. First, however, we have to ask how conceptual innovations arise in science.

For science to maintain conceptual coherence, novel ideas must be related to concepts and ways of thinking adopted previously. “Genealogy” is a systematic method for analyzing conceptual change that unfolds within a particular field of thinking. Genealogical analysis of a particular research field aims at more than merely documenting the historical development of the field. The aim is to analyze the dynamics of thinking within the field, positioned in a rich context of research practices and societal connections. New concepts bring about new perspectives on recognizing research problems, new ways of addressing the problems, and new criteria through which truth claims within the field are assessed. These ideas are applied to ecology in Haila (1998).

In a sense, an established concept turns into a “subject” that has the power to define research priorities, resolve disputes, and justify conclusions. Thus, as we shall see, the concept of habitat fragmentation was first presented as a hypothetical suggestion as to specified effects of human-induced change in natural landscapes. However, quite quickly the concept came to stand for a particular, island-biogeographic interpretation of species impoverishment in small habitat patches, and this interpretation began to lead its own life, offering justification for particular research projects and conservation recommendations. Through this process, fragmentation came to appear as a unitary phenomenon.

As data for the genealogical analysis, I used articles in the fragmentation literature that have been often cited; I introduce specific sources in context in the next sections. The analysis drew upon two specific theoretical ideas. The first one is Ian Hacking’s (1992) suggestion that “stabilization” of research is a precondition for the establishment of a successful research tradition. Such stabilization takes place through a self-vindicating structure, created by a circular process of trial-and-success within the field. This comprises all stages of research, from observations and experiments, through analysis of data, to drawing conclusions and matching them with existing theory, which may be modified as a result. Every particular success in this endeavor, at any stage, supports the credibility of the whole tradition and triggers further research that again supports the tradition, and so on. Generally accepted exemplars such as successful experiments play an essential role here: they form a resource on which further experimentation can draw.

Second, a precondition for the stabilization of research is explanatory closure. In the most elementary case, explanatory closure is achieved within a “contrast space” that defines alternative explanatory possibilities relative to the phenomenon to be explained (Garfinkel 1981, Dyke 1988). Within a fixed contrast space, credible alternatives are articulated and juxtaposed against each other: the exclusion of one supports the other(s). The credibility of any explanation, however, depends on how the corresponding contrast space is constructed.

**Stabilization of a Schematic View of Fragmentation**

The origin: theory of island biogeography

The origin of the idea of habitat fragmentation in ecological theory is easily identified: it was first articulated in MacArthur and Wilson’s (1967) monograph on island biogeography. However, the idea was mentioned only in one brief paragraph in the short introductory chapter of the monograph:

Insularity is moreover a universal feature of biogeography. Many of the principles graphically displayed in the Galapagos Islands and other remote archipelagos apply in lesser or greater degree to all natural habitats. Consider, for example, the insular nature of streams, caves, gallery forests, tide pools, taiga as it breaks up in tundra, and tundra as it breaks up in taiga. The same principles apply, and will apply to an accelerating extent in the future, to formerly continuous natural habitats now being broken up by the encroachment of civilization, a process graphically illustrated by Curtis’ maps of the changing woodland of Wisconsin . . . .

It is really remarkable, with hindsight, that this paragraph is all there is on fragmentation in MacArthur and Wilson, as the book was an essential reference in fragmentation literature in the early stages. In the par-
agraph, MacArthur and Wilson offered a metaphoric vision: increasing insularity is a dominant theme in environments under human influence, and the Galapagos is an appropriate model for insular environments. This may be the most beautiful example of a metaphoric meaning transfer that can be found in the ecological literature.

The irony is that, in fact, what is really ecologically peculiar about Galapagos and other oceanic archipelagoes has no relevance to habitat fragments created by human activity, such as the remnant forests in Wisconsin studied by Curtis (1956). The peculiarities of the fauna and flora of oceanic archipelagos result from their peculiar geological and evolutionary histories that, furthermore, are extremely variable from case to case. By contrast, forest remnants, as remnants, have no evolutionary history at all. Moreover, ecological processes in forest remnants are in various ways critically influenced by direct interactions with remnant surroundings, whereas such interactions are negligible on oceanic islands.

When fragmentation research started in the 1970s, it was firmly tied to the metaphoric analogy between fragments and islands (see also Wiens 1995a). As a specific example, I investigate the ornithological research conducted by Robert Whitcomb and his coworkers in the eastern deciduous forests of the United States in the 1970s (summarized in R. E. Whitcomb et al. 1981). The starting point for the research project was defined by Whitcomb (1977) as follows: “Since 1974 we have been examining oak-hickory woodlots in the Maryland Piedmont and Coastal Plains from the perspective of island biogeography.” The adoption of the island analogy was justified as follows: “(i)ntuitively, one would imagine that at least some of the principles regulating species richness on oceanic islands would operate on these mainland ‘habitat islands’ as well.”

The island-biogeographic framing of the research task fixed a contrast space within which questions were formulated: the focus was either on species number or on the presence or absence of individual species in fragments as a function of fragment area. This, however, is misleading because a small woodlot can sustain only a small number of individuals, and thus, of species, and a majority of these belong necessarily to the common species. Consequently, species assemblages in small fragments always appear “impoverished” compared with large fragments. This result is inevitable, given an appropriate size distribution of fragments censused. For instance, the study design in Whitcomb et al. (1977) included 25 fragments with an area range of 1–14 ha, and five fragments >70 ha used as a reference. A 10-ha woodlot cannot possibly host the same assemblage of species as a 70-ha one.

This inevitable species–area pattern came to dominate the imagination of the researchers: a small patch of whatever kind of environment implies impoverishment and extinctions. The conclusion is not amenable to empirical refutation because the pattern of apparently impoverishment is always observed in any particular fragmented landscape. Helliwell (1976) raised this point as a critique of a contemporaneous British study, but it has been all but neglected in the fragmentation literature (Haila 1988, 1999a).

Intermediary conclusion.—The metaphoric application of island biogeography to “all natural habitats” created a vision that species impoverishment in human-modified landscapes is directly comparable to the species impoverishment observed on distant oceanic islands; i.e., it is due to biogeographic processes. Recurring documentation of the expected pattern, reduced species number and absence of scarce species in small fragments, was accepted as evidence for such impoverishment, which helped in stabilizing the approach.

Pioneering works interpreted in new light: John T. Curtis and Wisconsin woodlands

As their example of habitat changes in human-modified environments, MacArthur and Wilson (1967) referred to John T. Curtis’ article entitled “The modification of mid-latitude grasslands and forests by man,” published in a famous symposium volume Man’s Role in Changing the Face of the Earth (Curtis 1956).

The context probably influenced the style of Curtis’ paper: it was a descriptive and somewhat speculative natural history commentary on human modification of mid-latitude habitats. He covered both the Old and the New World nominally in his chapter, but for specific examples, he drew mainly on his own data from Wisconsin. I summarize what Curtis wrote on fragmentation.

Curtis pointed out that, in agricultural landscapes, original forest cover is often extensively destroyed so that only small, remnant forests are left, surrounded by modified environmental types (see the epigram). He called this the “physiognomic result” of agricultural occupation of forested land. The matrix between the remnants was alien for practically all members of the forest biota. On the other hand, many members of the animal community greatly benefited from the increase in the total amount of “edge.” Second, Curtis took up biogeographic dynamics: as a consequence of changes in habitat proportions, some species of open country had extended their range “well into the original forest country of the eastern United States.” Next, he noted that species tend to vanish from small forest remnants, and he identified a possible mechanism: local populations that die out as a consequence of natural disturbances and catastrophes might not be able to recolonize from adjacent unaffected areas. Finally, Curtis suggested that the genetic composition of populations isolated in the remnants might change. He concluded by
predicting that such microevolution would provide a fertile ground for future study.

To sum up, Curtis’ short article drew the conclusion that human-induced modification of landscape structure helps species to spread to new regions, causes local extinctions, and creates new selection regimes for species populations isolated in small woodlots. This was a novel idea. Curtis did not have any theoretical framework to draw upon. Rather, he made specific suggestions on types of biotic change that the “physiognomic result” of agricultural land clearance might bring about. These were not restricted to impoverishment: edge effect opens living space for a set of species, and range shifts bring new species into new regions.

When Curtis’ work was incorporated into mainstream fragmentation research, his broad interest was truncated and cast into a biogeographic mold. The statistics and scheme compiled by Curtis on forest change in Cadiz Township, Green County, Wisconsin, USA, has become an emblem of forest fragmentation. This is ironic, because the most dramatic feature of the case is forest loss: according to Curtis, forest cover by 1950 had been reduced to 3.6% of the 1831 situation. In fact, the use of Curtis’ figure as an emblem of fragmentation has made it difficult to distinguish habitat loss and habitat fragmentation from each other.

Intermediary conclusion.—The use of Curtis’ work as an emblem of habitat fragmentation, interpreted in the light of the island-biogeographic theory, strengthened the inclination of ecologists to view human-modified environments as “archipelagoes” and to confuse habitat fragmentation and habitat loss.

Fragments vs. surroundings: a total contrast postulated

The island-biogeographic perspective on habitat fragmentation was first applied to reserve design; this created a series of influential articles from the mid-1970s onward, as well as criticisms somewhat later (see Simberloff 1997). The application was based on an analogy between reserves and islands, an analogy that was explicitly drawn by Frank Preston (1962), as was duly acknowledged later.

A critical background assumption of the “reserves equal islands” analogy is that areas surrounding insular preserves are completely hostile to species living in the preserves. I cite an example: “The fundamental assumption is that nature reserves act as habitat islands in an inhospitable sea of environment that has been modified by man, and thus that the empirical findings of island biogeography are pertinent” (Gilpin and Diamond 1980).

Evaluating this claim is, of course, an empirical matter, but it is untenable as a broad generalization. Even in agricultural areas, however intensive the cultivation methods, some species can forage outside forest remnants and thus include some of the surrounding area in their home range. Curtis realized this in Wisconsin. In forested environments, the situation is much more complex; I will return to this issue. Big predators have often been used as an example of species that supposedly require large, uniform, pristine habitats. For instance, Whitcomb et al. (1981:187) wrote: “A preserve large enough to maintain a viable population of timber wolves, for example, would be likely to preserve primary producers, herbivores, and insectivores as well.” It is more likely, however, that the big predators do not require large areas of pristine habitat. Big predators are excluded from human-modified environments by persecution. The recent recovery of the timber wolf (Canis lupus) in the western Great Lakes region in the United States is due to discontinuation of persecution, not to any particular features of forest structure (Mladenoff et al. 1995).

In fact, the provision of Gilpin and Diamond (1980) can be read the other way around: whenever the preserves or fragments are not surrounded by an “inhospitable sea,” the “empirical findings of island biogeographic theory” are not pertinent. This conclusion has seldom been drawn, however.

Intermediary conclusion.—Through the seductive analogy between fragments and oceanic islands, a strict contrast between fragments or preserves and the surrounding matrix was accepted as a fundamental assumption. Consequently, the mechanisms that supposedly make fragments “insular” were not scrutinized.

Assumed uniformity of unfragmented “reference” environment

Robert Whitcomb later characterized the background of his ornithological work conducted in Maryland in the 1970s as follows (R. F. Whitcomb 1987:165): “I believe that the eastern deciduous forest was essentially homogeneous from the point of view of forest interior bird species.”

This belief seems erroneous on two counts: (1) major climatic gradients cut through the area, and (2) there is ecologically significant variation in forest types on various spatial scales, from local to regional, according to topography, soil, disturbance history, and so on. Birds often respond to both types of environmental heterogeneity, as attested by their range variation and habitat distributions.

The uniformity assumption was tacitly accepted in early fragmentation studies: fragment area was regarded as an independent variable sufficient to explain statistically the variation in species numbers across a range of fragments of different size. Ambuel and Temple (1983) conducted the first ornithological study in which the effect of habitat variation was statistically controlled. The uniformity assumption is also implicit in how observations were extrapolated from small patches to the regional scale. Consider the following citation (Blake and Karr 1987:1724; references omit-
Many species do not occur in isolated woodlots even when area of the woodlot exceeds minimum territory requirements and large forest tracts are necessary for their survival.” The conclusion is logically invalid because the absence of a particular species from particular small woodlots can be due to the lack of suitable habitat in these particular woodlots. It can also be due to a “sampling” effect: a forest bird with an average density of, say, two pairs/km² and minimum territory requirements of 5 ha, not unreasonable figures at all, would be absent from four out of five 10-ha woodlots, on average, for statistical reasons alone.

As time and space are tied together in ecology (Preston 1960, Wiens 1981, Haila and Levins 1992), an assumption of spatial homogeneity implies temporal constancy. In the early fragmentation literature, the possibility that natural population fluctuations might influence the distribution of populations across fragmented landscapes was often neglected. B. L. Whitcomb et al. (1977) offer an example. They studied changes in bird species composition in one woodlot censused first in 1947 and a second time in 1975, i.e., with an interval of 28 yr. They noticed that, for instance, the Worm-eating Warbler (Helmitheros vermivorus) was present in 1947 with one pair, but absent in 1975, and considered this an interesting case of “turnover,” again raising the analogy with oceanic islands: “(t)urnovers of this type might be compared with those which occur on oceanic islands, which, for one reason or another, carry more species than appropriate.” This interpretation is not legitimate, however: in a period of 28 yr, pairs of breeding birds will shift their locations many times over, e.g., from one woodlot to the next. McCoy (1982) criticized too loose a notion of “turnover” on similar grounds. In fact, birds are known to shift their territory locations from year to year at the population level (Preston 1960, Haila 1983, Haila and Hanski 1987, Haila et al. 1993, 1996).

That spatial and temporal variability matters in ecology was, of course, common knowledge in the 1970s; hence, their neglect seems strange with hindsight. C. B. Williams (1943, 1964) and Frank Preston (1948, 1960, 1962), in particular, had demonstrated with database quantitative studies the influence of environmental heterogeneity on species richness and composition in local multispecies collections. Preston drew an explicit analogy between temporal and spatial variation in a sampling process, and presented small patches of land metaphorically as “drawing samples” from a surrounding universe. This extensive background knowledge was, however, pushed aside.

The uniformity assumption provides another example of the significance of the contrast space within which explanatory closure is reached. A contrast space focused on species number as a function of fragment area does not allow the articulation of spatial and temporal variability as significant factors. By contrast, Preston’s (1948, 1960) idea that local assemblages should be considered “samples” drawn from a surrounding “universe” offers another contrast space in which both spatial and temporal variability in the “universe” become focal questions (Connor and McCoy 1979, Haila 1983).

Intermediate conclusion.—Fragmented environments were projected against an idealized, spatially homogeneous and temporally constant natural background. As a consequence, well-established ecological knowledge on how environmental variation affects the composition of multispecies collections was ignored.

Fragmentation and the rise of environmentalism

I previously raised the hypothesis that the environmental awakening created a novel problem space for ecological research, which may explain the fascination of ecologists with habitat fragmentation in the 1970s. A number of ecological research traditions began to explore this problem space, and biogeographically inspired fragmentation research was one among them. The analogy of preserves and oceanic islands was thought to be fruitful.

I will not review the criticism raised against the analogy (see, e.g., Simberloff 1997), but will pay attention to a conceptual issue. Jared Diamond (1976) supported the island analogy with the following argument: “Recently several workers have recognized that a predictive understanding of extinction might be obtained from island biogeography, since refuges of natural habitat in a sea of human-altered environment behave as islands for species dependent on natural habitat.”

How should one understand the term “predictive understanding” in this argument? There are two alternatives. Successful predictions can be based either on a statistical regularity (reliable correlation) or on a correspondence with a causal relationship. The understanding offered by island biogeography is of the correlation type: area does not cause extinctions, although area does, by and large, correlate negatively with the risk of local population extinction. A critical question is whether this correlation is reliable enough to really allow predictions. Diamond’s argument is explicitly based on the “refuges equal islands” analogy. This is not allowable without empirical support, as I have already noted. Furthermore, there are both theoretical and empirical grounds to believe that critical ecological processes in isolated vs. non-isolated situations are different (Haila 1990); if this is the case, the analogy between islands and reserves fails (Saunders et al. 1991). The causes of local population extinctions vary across circumstances; hence, the ecology of the situation has to be known in each case.

Nevertheless, firm conclusions on conservation were drawn from research on small fragments from the very beginning. In fact, Robert Whitcomb and his colleagues presented conclusions from their ornithological work
for the first time in an exchange on the application of island biogeography to conservation in Science (R. F. Whitcomb et al. 1976); the exchange was started by Simberloff and Abele (1976). The central Maryland–Washington, D.C. database that Whitcomb et al. drew upon was not described in the article, but a footnote indicated that it was developed by many workers over three decades and included: “155 breeding bird censuses of 49 forest plots, 93 point surveys in deciduous forest fragments, three countywide bird atlas mapping projects, and 111 breeding bird surveys of 55 routes.” From this database, the authors drew the following conclusion:

Thus the available data for the Eastern forest, far from demonstrating that large faunal preserves are unnecessary, describe a troubled system in which local and regional extinctions of forest interior specialists are commonplace and in which large series of existing small, isolated forest areas have failed to preserve, even in contemporary time, many of the small avian species that once dominated the forest.

It is quite remarkable that this firm, purportedly data-backed position was printed in no less a forum than Science before any of the primary data had actually been analyzed and published. The data came out four years later in Whitcomb et al. (1981). I think that this incident provides an example of a “disciplinary promise” (Haila 1998), i.e., a promise that island-biogeographic conservation theory helps in addressing and solving conservation problems. Giving a disciplinary promise was a rhetorical strategy that helped to stabilize fragmentation research in the short run.

**Intermediary conclusion.**—The environmental awakening created a social demand for ecologically grounded theoretical perspectives on ecological problems. Fragmentation research was thought to provide insight on human-induced extinctions through the analogy between species impoverishment on islands and habitat fragments. This was supported with a rhetorical strategy of disciplinary promise.

**Schematic View of Fragmentation as an Intellectual Attractor**

A schematic view of habitat fragmentation was stabilized by the early 1980s. Its main elements were (1) the island analogy; (2) an assumed stark contrast between fragments and their surroundings; and (3) the assumed uniformity of natural background conditions. An essential part of the stabilizing loop was the reduction of empirical research to species–area curve fitting, which always produced expected results. The perceived need to provide scientific advice on conservation issues provided the ethos.

I next give a dynamic interpretation of the genealogical narrative. This is based on an analogy between the contrast space in which research questions are framed and a physical phase space. As Alan GarfinkeI (1981:40) wrote, defending such an analogy, a phase space is “a geometric representation of the possibilities of a system.” Accordingly, one can envisage ideas in a particular research field “moving” in a phase space that gives a representation of possible trajectories; my use of the analogy was originally inspired by Dyke (1993).

How is a phase space of ideas constituted? Intellectual trajectories are constrained by critical background assumptions; that background assumptions matter is a familiar idea by now, applied to ecology by Haila and Levins (1992). Hence, a phase space of ideas can be defined by identifying the issues on which critical background assumptions take a stand, and by defining main axes by these issues. Such axes, of course, are not linearly scaled; rather, possible positions along the axes are often separated into mutually opposing alternatives. In other words, each axis stands for a contrast space within which ideas are located.

I identified critical background assumptions of fragmentation research from the genealogical narrative. They are positioned as the axes of a two-dimensional phase space in Fig. 1. The first axis is constituted by assumptions on the relationship between human-influenced areas and natural areas. The contrast space behind this axis is between a dualistic opposition vs. context-specific interaction and interpenetration. The second axis is constituted by assumptions on the nature of spatiotemporal variability in ecological space. The contrast space is between a uniform, Cartesian equi-
librium space vs. a complex and heterogeneous non-equilibrium space.

The assumptions tacitly accepted about these two issues in the early fragmentation literature can be represented as follows. Along the first axis, fragmentation research was constrained by an assumed total contrast between human-influenced areas and natural areas. This was articulated by Gilpin and Diamond (1980) as cited previously. Along the second axis, fragmentation research was constrained by an assumption of uniform and unchanging natural background. This was articulated by Robert Whitcomb and his colleagues (B. L. Whitcomb et al. 1977, R. F. Whitcomb 1987) as cited previously.

These background assumptions meet in the upper right-hand corner of Fig. 1. This region constitutes an “intellectual attractor” in this phase space: the trajectory of thinking on fragmentation is directed toward this attractor, given the background assumptions. An intellectual attractor is effective because it seems difficult, even preposterous, to think in any other way, i.e., to challenge commonly accepted background assumptions.

Both of the issues that I used to delineate the phase space in Fig. 1 have been relevant in much of modern ecological thinking. The first, the contrast between human-influenced and natural areas, accords with a dualistic view of the relationship between culture and nature. Culture–nature dualism has ancient roots in the Western tradition and it still has considerable influence in environmentalism (Passmore 1980, Plumwood 1993, Haila 1999b, 2000). The second issue draws upon an equilibrium view of ecology (for analysis and criticism, see Wiens 1984, 1989a). The equilibrium view implies that every habitat comprises a uniform ecological space that is divided among competing species, and that different habitats are distinctly recognizable. In island biogeography, this view of habitat was implied through the concept of “the closed community” (MacArthur and Wilson 1967:94–104).

Environmental concerns make understandable the dynamics depicted in Fig. 1. The environmental crisis created a demand for ecologists to give scientific advice on conservation issues. The advice had to be backed by theories that conform to an ideal of modern ecology as an exact and predictive science, based on general principles. Kingsland (1985) traced the intellectual history of this ideal from the early 20th century through the influence of G. E. Hutchinson up to MacArthur and Wilson and Island Biogeography.

Daniel Simberloff (1997:275) characterized recently this urge as follows: “Until the mid-1970s, conservation biology was not a distinct science. Rather, it was part of ecology and wildlife biology and largely consisted of research on the autecology and habitats of species of particular concern. In 1974–1975, the application of the dynamic equilibrium theory of island biogeography to the design of nature preserves helped inaugurate a new conservation biology as well as a new kind of biogeography.” Simberloff’s characterization has paradoxical implications—a misleading metaphor inaugurating conservation biology as “a distinct science”—but it certainly supports my hypothesis on the importance of conservation issues.

The Schematic View Challenged

Fragmentation research has changed enormously since the early 1980s, and the questions asked have become much more variable than they were in the early stages. In this section, I first summarize results of a computer search from Biological Abstracts of 1998 using the key words “fragmentation and habitat” and “fragmentation and forest.” The aim of the search was to identify the range of study organisms and specified problems covered in recent fragmentation research. The search gave 93 and 75 relevant titles, respectively; 47 of the articles were on both lists, so the total was 121. The number of articles dealing with a single species vs. more than one species was almost equal, 62 and 57, respectively; in addition, two addressed landscape structures. The broad range of study objects is summarized as follows:

1) Taxonomically specified study organisms.—(A) Animals (total 71): mammals, 18; birds, 22; reptiles, 3; amphibians, 4; fishes, 4; insects, 14; crustaceans, 3; mollusks, 1; Monotremata (Platypus), 1. (B) Plants (total 24): flowering plants, 6; trees, 10; seaweeds, 1; algae, 1; unspecified, 6.

2) Taxonomically heterogeneous study organisms.—Various collections of species, 12; functionally defined groups of species, 4; species interactions, 2.

3) Models studied.—Eight models.

Research problems are more difficult to classify than study objects, but the following figures indicate approximate distributions of the types of problems addressed in the papers, as interpreted from their abstracts: population viability 47; species richness/poverty 24; ecosystem effects 23; specified processes such as dispersal, foraging, movements, etc. 11; descriptive studies 9. To summarize, a majority of the fragmentation studies conducted in the late 1990s addressed ecological processes influencing population viability, but descriptive research on ecosystem and community characteristics was almost equally popular. Taxonomically, the studies covered a broad range of organisms, but vertebrates were the dominant group. McGarigal and Cushman (2002) drew similar conclusions in their review of experimental approaches to fragmentation in the late 1990s: vertebrates, particularly songbirds, dominated as study organisms, and most studies were focused on patches instead of landscapes.

In what follows, I give a condensed interpretation of how the schematic view got to be challenged. This had
both theoretical and empirical sources. The theoretical criticism had several roots that essentially add up to challenging the assumption depicted on the y-axis in Fig. 1. An important root was the increasing criticism and, finally, almost unanimous rejection of equilibrium assumptions in ecology (see Wiens 1984, 1989a). This went together with a suspicion and rejection of the concept of a “closed community” maintained by interspecific competition (which, as we saw, was an explicit element in the theory of island biogeography). The autecology of individual species was emphasized instead. This emphasis found support from an older, individualistic view of ecological assemblages that has its roots extending to the early 20th century (McIntosh 1985). The rejection of equilibrium community ecology undermined the relevance of species number as a characteristic of species assemblages in islands and habitat fragments, i.e., the island-biogeographic explanatory closure was put into doubt.

Once the equilibrium assumptions were relaxed, new questions were opened for empirical investigation, e.g., whether the composition and diversity of local assemblages are regulated by local or regional processes (Ricklefs 1987). This also had implications for fragmentation studies: if regional processes are important, then what is observed locally may be an epiphenomenon of regional abundance variations. Issues of ecological scaling were brought to the foreground in ecological thinking (Wiens 1981, Delcourt et al. 1983). As Wiens (1989b) noted, “scaling” became almost a buzzword by the late 1980s. The problem of ecological scaling has two aspects: methodological, the design of sampling relative to the processes that are studied, and ontological, the organization of different ecological processes in space and time vis-à-vis each other. We can never be certain about particular ontological assumptions, but some assumptions are more plausible than others in the light of particular theoretical commitments and empirical results. Scaling problems have direct implications for the ecology of fragmented environments: different processes may be important depending on the scale of the fragments studied (Haila 1990, Lord and Norton 1990).

Landscape ecology originated as a new research program in the 1980s, in a way as an amalgamation of all these theoretical developments (Wiens 1995b): a uniform Cartesian space was replaced with environmental heterogeneity; equilibrium assumptions were replaced with spatial and temporal variability driven by non-equilibrium processes in various scales; and an unchallenged search for universal regularities was replaced with the acknowledgment of spatial and temporal specificity of ecological processes. New hypotheses were suggested about non-equilibrium processes determining landscape dynamics (Shugart 1998). Many of the basic ideas originated in previous decades, but these were put together in a novel way. For fragmentation research, particularly important emphasis was that relevant features of landscapes must be defined from an organismal perspective, in other words, the same physical landscape may be experienced very differently by different organisms (Haila 1991). Fragments were increasingly viewed not as analogues to “islands,” but rather as habitat patches embedded in a particular type of surroundings (Wiens 1995a).

Another challenge to the island-biogeographic view of fragmentation arose from experience accumulating in field research showing that the island-biogeographic approach did not allow the right questions to be asked about fragmentation effects. Effectively, the “area vs. species number” contrast space of framing questions faded into the background, and the focus shifted to population-level studies. This occurred in particular research programs as a time-bound transition: problematic species were identified by conducting quantitative surveys across a particular fragmented environment, and in the next stage these species were studied in detail (Haila and Hanski 1984). A good example of such a transition is Raimo Virkkala’s work on the avifauna in managed vs. old-growth forests in the Finnish Lapland, which started with surveys (Virkkala 1987) and then focused on a specialist of old growth, the Siberian Tit, *Parus cinctus* (Virkkala 1990).

Focused studies on ecological processes in fragmented landscapes have produced a great variety of results, as pointed out in the *Introduction* (see also Haila 1999a, Harrison and Bruna 1999). The perspective on landscape structure has inspired interesting modeling work (Andrén 1996, Fahrig 1998), but it is a difficult question to study empirically because of logistic problems. Research on the dynamics of single species on a landscape scale borders on metapopulation studies (Hanski and Gilpin 1997).

Similar theoretical developments inspired a “new paradigm” in conservation biology (Pickett et al. 1992). The determinants of population viability in heterogeneous and variable, non-equilibrium environments have become an important research focus. However, the island-biogeographic perspective is the dominant approach to evaluating extinction risks in conservation contexts; recent examples are several articles in Whitemore and Sayer (1992), Wilson (1992), and May et al. (1995). This is paradoxical because detailed reviews of the empirical relevance of the relationship tend to conclude that it is vacuous; the arguments to support this conclusion are summarized in Heywood and Stuart (1992) and Whitemore (1997). I believe that this paradox reflects a genuine contradiction in conservation thinking. On the one hand, the relevance of the species–area relationship depends on the validity of the “refuges equal islands” analogy, but this analogy is highly questionable. Hence, doubts arise whenever it is accurately assessed. On the other hand, conservation biologists feel an urge to use the relationship...
in a predictive fashion as a first approximation. This was indicated in my citation in this paper of Jared Diamond; another justification is provided by Wilson (1992:263): “Models of this kind are used routinely in science when direct measurements cannot be made. They yield first approximations that can be improved stepwise as better models are devised and more data added.”

The only possible solution to this paradox is to assess seriously and realistically whether the area surrounding particular habitat fragments is, indeed, an “ecological desert,” but this task has seldom been undertaken. A sharp distinction is certainly a good first guess in many agricultural regions (see Plate 1). By contrast, a detailed assessment is always needed in forested environments. In southern Finnish boreal forests, for instance, the percentage of species restricted to mature forests is \(~5\text{–}10\%\) in birds and ground arthropods (Haila et al. 1994). Whether a majority of the species in these taxa can persist in modified forests depends on fine-scaled details of forest structure (Haila et al. 1989, 1996, Niemelä et al. 1996). The percentage of obligatory old-growth species is certainly higher in other taxa, such as insects living in decaying wood (Väisänen et al. 1993), but this statement opens up a new problem: do these insects require old growth “per se,” or rather some microhabitat usually available in old growth? The second alternative may be true: several specialized beetles seem to persist in clearcuts if the right kind of dead wood is left behind (Kaila et al. 1997).

I think that the justification for the use of the species–area relationship given by E. O. Wilson in the previous citation is not valid. The logic of the model is misleading in a concrete way: it directs attention to a contrast space that does not allow one to ask the specific questions about extinction risks that need to be asked. “Area” is a poor indicator of the specific factors that cause extinction threats of particular species. In the southern Finnish taiga, for instance, it is not possible to define such criteria for “adequate habitat” that could be easily bounded on specific spots on the map and would be valid for any large collection of species. Specific criteria are valid for only a few species at a time, and “habitats” merge into one another in many more than two dimensions (Haila et al. 1996). “Valuable habitat” does not stand out as separate from a surrounding inhospitable “sea” of human-modified forests. On the other hand, this does not mean that we have to fall back to purely autecological, species-by-species consideration. Generalizations are possible as to what kind of species are vulnerable in a particular type of environment (Haila 1999a). Furthermore, such vulnerabilities can be identified through empirical surveys (for examples, see Margules and Austin 1995).

Broadening the Framework: Fragmentation as Habitat Degradation

To return to Fig. 1, the theoretical criticism voiced against the ideal of a uniform, Cartesian equilibrium world has pushed fragmentation research downward along the y-axis. However, my interpretation is that the region in the lower right-hand side of the figure does not have stable equilibria. If a total contrast between human-modified and natural environments is assumed, equilibrium thinking is smuggled in through the back door, as an idealization of a harmonious, pre-human, natural environment (Haila 1999b).

To get away from the basin of the dominant attractor, we need to move toward the left along the x-axis, i.e., to challenge the assumed universal contrast between human-modified and natural environments. This implies contextualization of environmental problems (Haila 1997, 1999b). To achieve this aim, I suggest that the perspective be broadened and fragmentation be regarded as a specific form of habitat degradation (for a similar suggestion, see Harrison and Bruna 1999). Then, habitat fragmentation merges together with other types of harmful changes induced by human activity.
This raises contextualized questions and also brings human actors into the picture in efforts to prevent or mitigate the harmful effects.

The urgency of this move depends on what kind of precision is thought to be necessary when conservation biologists characterize human-induced destruction of natural habitats. I believe that great precision is needed on the type of destruction in each particular case. Environmental problems can only be solved concretely, in specific places at specific times, and people have to be involved: managers, landowners, or local inhabitants, depending on the case. Hence, when conservationists address a particular problem, they should know the type of remedy that might work. When conservationists grope in the right direction, a process of social learning can start and strengthen the commitment of the people involved. If, instead, conservationists resort to an abstract model that says nothing specific about the situation at hand, such commitment may fade. Furthermore, too sweeping generalizations about human-caused destruction of nature support a metaphysical humanity–nature dualism that is counterproductive in the situation at hand, such a commitment may fade. Furthermore, too sweeping generalizations about human-caused destruction of nature support a metaphysical humanity–nature dualism that is counterproductive in environmental thinking (Haila 1999b, 2000). The issue also has an ethical dimension. Conservation recommendations are often intrusive upon ordinary people’s lives and subsistence; consequently, the recommendations must be well founded and specific in order to gain—or deserve—popular support.

The framing of questions should be sensitive to the historical context: the particular type of human-induced habitat degradation is variable from case to case (e.g., Landa et al. 1997, McIntyre and Hobbs 1999). Conservation biology seeks solutions to problems caused by human activity, and it simply cannot be assumed at the outset that different types of problems can be separated into well-defined “scientific kinds” (Hacking 1991) that would allow unambiguous explanatory closures. This is an empirical matter, not to be decided ex cathedra. To address the issue, ecologists should take human-modified environments seriously, as the rich complexes of human-induced and naturally occurring processes that they really are (Haila 1999b). This also means that assessing the variability of fragmentation effects in any particular situation is a research problem in its own right. Description of particular cases through long-term observational or experimental work is required; several examples are reviewed in the other articles in this Invited Feature. Other good examples include the long-term experiment in Wog Wog, New South Wales, by Chris Margules and coworkers (Margules 1992), and the detailed documentation of distribution patterns of a wide range of taxa in the western Australian Wheatbelt by Richard Hobbs, Denis Saunders, and others (Hobbs and Saunders 1993).

A good research strategy is to use specific, well-understood cases as “analog models” to identify important qualitative features that may have more general relevance. By the term, analog model, I refer to a material system that is known in detail and that thus constitutes a real-life model of an abstract idea. A particular analog model is a first test of whether a particular abstract notion is realistic at all. For instance, a real pendulum is an analog model of a harmonic oscillator. In ecological research, experimental model systems function as analog models in this sense, both in the laboratory (Griesemer and Wade 1988) and in the field (Ims et al. 1993). Analog models cannot be directly “fitted” from one situation to another; rather, they suggest qualitatively important aspects and processes that deserve particular attention in studying the other situation. The relationship between a pendulum and a mass-and-springs oscillator, for instance, is similar: they are both models of a harmonic oscillator, but knowing the mechanical principle of a pendulum does not help a bit if one has to construct a mass-and-springs oscillator.

Sound reason can and should be used whenever habitat fragmentation has to be addressed as a practical conservation issue. In the following, I list some obvious rules of thumb (a somewhat similar list is in Haila 1999a): (1) Avoid clearing native habitats, particularly in regions where this has already happened to a large degree. (2) Restore native vegetation by active measures such as planting, particularly in heavily cleared country such as western Australia. This helps the survival of the native biota and is also economically sound by rescuing some of the degraded lands back to agriculture (Saunders and Briggs 2002). (3) Cherish corridors and other connecting habitat routes in heavily cleared landscapes. Corridors are generally valuable in agricultural landscapes (Saunders et al. 1991), although statistically rigorous experimental testing of their significance may be logistically impossible. In forested environments, the role of corridors is more questionable. (4) Maintain environmental heterogeneity both on the landscape level and within landscape elements such as habitat patches. (5) Identify particularly important microhabitats (“key biotopes”) and preserve these both within and outside preserves. (6) Use umbrella species to assess the quality of the landscape: if they can persist, some other organisms can persist as well (Martikainen et al. 1998).

An important practical question is to get both managers in various practical fields and ordinary people involved. Conservation has to be integrated into human lived experience and daily practices. This is only possible if both the conservationists and the public understand what the specific issues are in each specific situation.

**AN AFTERTHOUGHT: LEGACY OF ISLAND-BIOGEOGRAPHIC FRAGMENTATION RESEARCH**

In hindsight, the island-biogeographic view of habitat fragmentation that took shape some two decades ago has contributed significantly to the understanding of many ecological processes. The island-biogeographic view of habitat fragmentation that took shape some two decades ago has contributed significantly to the understanding of many ecological processes.
ago can be criticized on several grounds. However, this does not entail a judgment that the view had no positive role in the development of conservation biology. I agree with Simberloff (1997; see the previous citation) that the framework paved the way for new approaches in conservation research. Haila and Järvinen (1982) made a similar assessment of the role of island biogeography in ecological theory. In particular, fragmentation research inspired by island biogeography represented an early articulation of the spatial dimension of human-induced, large-scale habitat degradation.

On the other hand, one should not be led to think that this episode in the development of ecological thinking was inevitable. Indeed, pre-island-biogeographic literature includes interesting studies of non-isolated real islands that are, after all, much more similar to habitat fragments that oceanic islands (Haila 1990). These present us with alternative trajectories that were available for research. For instance, in his inventory of the bird faunas of small British islands, David Lack (1942) specified very carefully both human-induced and natural factors, including habitat changes, that had affected the fluctuations in bird species composition and population numbers on different islands. Another example is the work of Edward Beals (1960) on the bird communities in the Apostle Islands of Lake Superior, Wisconsin, USA. Beals was primarily interested in the distribution of individual bird species across different types of forest found on different islands. His background assumption was that species are distributed across the total habitat space according to their habitat needs in an individualistic fashion. According to Beals, island area affected birds primarily indirectly, through the positive correlation between area and habitat diversity.

Conservation research based on natural history also reached important results in the era before island biogeography, but this is too large a topic to be covered here. Plant ecologists, in general, have been less susceptible than animal ecologists to grand and unifying explanatory schemes, as Mike Austin argues (e.g., Austin 1999). Such studies could have opened the way for a different style of research on ecological isolates and on conservation issues.

The history of research is readily “Whiggish”: alternatives that did not take off are buried and forgotten, and only the lineage of the mainstream remains. In the case of fragmentation research, however, pre-island-biogeographic alternative perspectives are still identifiable. They can be picked up and carried further.

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