

Taxon Cycles

INSIGHTS FROM INVASIVE SPECIES

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The taxon cycle consists of phases of expansion and contraction in the geographic and ecological ranges of populations, easily visualized in island archipelagoes but also a feature of continental regions. Taxon cycles and human-aided introductions of invasive species share phases of colonization, establishment, range expansion, and eventual contraction. The primary difference between the expansion phase of a natural taxon cycle and the invasive phase of an introduced species is that human-assisted introductions do not require adaptations for long-distance dispersal. Thus, trade-offs between dispersal ability and competitiveness may be circumvented by introduced species. Because the eventual decline of naturally expanded populations probably requires evolutionary time spans, the commonalities between species invasions and taxon cycles speak to the qualities that lead to population expansion. Most of the variance in range size and ecological distribution of native species resides at a low taxonomic level, suggesting that the traits that influence the “success” of a population are evolutionarily labile and probably do not include conservative adaptations for tolerance of physical conditions or use of particular habitats. Recent analyses have failed to identify attributes of receiving communities, such as native diversity, that make them more or less resistant to invasion. More likely, invasion success hinges on coevolutionary relation-

ships with predators and pathogens, which might depend on a small number of gene mutations in native populations. Phylogenetic analysis of character evolution among closely related species with varied geographic and ecological distributions might help to identify traits associated with invasiveness and to understand the forces that drive taxon cycles.

Introduction

The term “taxon cycle” was coined 45 years ago by E. O. Wilson (1959, 1961), but its basic premise has been a common theme among evolutionary biologists for over a century (Willis 1922; Darlington 1943; Brown 1957; Brown and Lomolino 1998; Ricklefs and Bermingham 2002). Wilson’s insight, based on detailed studies of the evolution and distribution of ants in Melanesia, was that taxa at all levels, but most noticeably and accessibly at the species or population level, go through phases of geographic expansion and contraction associated with similar changes in ecological distribution. These cycles tend to degrade toward eventual extinction, moving from larger to smaller landmasses and islands. However, populations at any point are capable of initiating a new cycle. During expansion phases, populations can be considered invasive species—that is, species that become established and spread in non-native regions.

Expansion presumably follows release from factors that control populations, or at least the relaxation of these constraints. Limiting factors potentially include extrinsic properties of the environment, such as climate and other physical conditions, and intrinsic features of biological systems, as in the case of control by predators or pathogens.

Examining species that have become invasive in association with human activities—for example, species transported between regions or gaining footholds in altered landscapes—can provide insights into taxon cycles in natural systems, and vice versa. It is reasonable to ask whether human-assisted invaders share attributes with natural invaders in the early, expanding stages of the taxon cycle. Of particular interest are features of invasive species that enhance their competitive success and extrinsic factors that influence colonization and the spread of populations in new areas.

Four stages of invasion can be recognized: colonization, establishment, spread, and decline. When comparing the establishment and invasion of non-native species with natural invasions, the most obvious differences are seen in the first two stages. Invasive species often gain transport from their native area to other regions with the intentional or unintentional help of humans, and they often become established in habitats that have been modified by humans. In contrast, natural invaders must traverse barriers under their own steam. This requirement sets constraints beyond the ability shared by all invasive species to spread through biological communities in their new homelands.

Natural invasions are often considered primarily in the context of island colonization, whereas human-aided invasions include introductions to islands

and continents alike. The key point is that one can identify the invasive spread of a population most readily when it colonizes an area away from its native range. Nevertheless, an equally important aspect of natural range expansion is the spread of populations into new habitats and areas within their native regions. This phase of spreading by a native population may parallel the expansion of established non-native species, and this is where the most useful parallels between native and non-native invasive species might be developed.

This chapter considers the qualities of invasive species and factors contributing to invasion success in the context of the taxon cycle concept. Special attention is paid to the idea that invasive species, non-native and native alike, are released from herbivores or predators and pathogens, which contributes to their productivity and competitive ability (Keene and Crawley 2002; Torchin et al. 2003). Even in the absence of change in the physical environment, a shift in the balance between consumer and resource populations can shift a species from an endemic to an invasive (expanding) phase.

Although non-native invasive species often bypass long-distance dispersal, natural colonists of islands and both native and non-native invasive species may share attributes if the demographic basis for habitat expansion and long-distance dispersal have common roots in increased population productivity. This possibility can be explored by comparing the distributions within continental regions of populations that have or have not been sources of colonists to islands. Particular consideration will be given to the land birds of the Lesser Antilles, whose evolutionary and geographic history I have investigated for several years with my colleague Eldredge Bermingham of the Smithsonian Tropical Research Institute (Ricklefs and Bermingham 1999, 2001, 2002). The methods of molecular phylogenetics allow one to distinguish species in early stages of the taxon cycle from older colonists in the declining phase of the taxon cycle. If young colonists were to occupy particular habitats or could otherwise be linked by common ecological associations, one might identify extrinsic drivers of expansion and invasion. In contrast, idiosyncratic emergence of natural colonists from a potential source biota would strengthen the case for coevolutionary dynamics having a role, perhaps based on the unpredictable generation of genetic variation.

One may ask whether it is useful to seek insights from invasive species if one is uncertain about the application of such insights to natural populations. Two answers come to mind. First, insight is often complementary, and we may be able to learn something of invasive species from natural colonizers, as well as vice versa, by considering the two together. Second, invasions depending on human assistance by means of transportation or habitat alteration are much more frequent and better characterized than natural range expansions. We know so much more about non-native invasive species than native invasive species that those of us interested in natural processes cannot afford to ignore them.

To provide a proper context for comparing native and non-native invasive species, it will be useful to briefly describe the taxon cycle and related ideas about natural invasions, and to address the more general issue of equilibrium

and change in biological systems as it relates to expansion and contraction of the ranges of individual species. This discussion is followed by a consideration of key issues in the taxon cycle and invasion biology literature and an explicit comparison of the taxon cycle with species invasion. The chapter ends with some concluding thoughts and suggestions for future work.

What Is the Taxon Cycle?

The idea that the distributions of species go through phases of expansion and contraction has been a persistent theme in evolutionary biology and biogeography (Ricklefs and Cox 1972; Ricklefs and Bermingham 2002). The idea has taken many forms, from comparison with the life cycles of individuals through growth, maturity, and senescence (Cain 1944; Simpson 1949) to extrinsically driven cycles paralleling change in the physical environment (Pregill and Olson 1981; Dynesius and Jansson 2000) and cycles expressing the changing balance of host-pathogen coevolution (Ricklefs and Cox 1972). Interest in such cyclic dynamics extends far beyond individual populations, even to the rise and fall of states (Turchin 2003).

The evidence for historical expansion and contraction of populations is most apparent in archipelagoes because island systems have a discrete geography that clearly reveals variation in distribution and where telltale signs of extinction appear as gaps in distributions. Thus, it is no accident that the concept of the taxon cycle was formalized by E. O. Wilson based on his studies of the systematics, geographic distribution, and ecology of ants on Melanesian islands (Wilson 1959, 1961). Wilson distinguished expanding and contracting species by a combination of geographic and habitat distributions. Expanding species had identifiable continental sources and occupied marginal habitats, through which they spread to other islands by rafting. Colony sizes were generally large, and expanding species were considered good competitors. After invading a new island, colonists extended their distributions into the larger area of less densely occupied forested habitat in the island interior, eventually evolving smaller colonies in more cryptic microhabitats (Wilson 1959). Competition from new invaders at the margins of islands helped to push this process along. Once a species had become restricted to interior habitats, it lost much of its potential colonizing ability, and contraction and fragmentation of the range began to follow upon loss of individual island populations. The eventual fate of ant species in the archipelago was extinction. Wilson's concept of the taxon cycle included evolution, competition, and habitat shifts, and therefore invoked the interplay of many processes.

Wilson presumed that ant species in marginal habitats in continental source areas initiated taxon cycles, but he did not discuss the origins of further population expansions, except that these involved a reinvasion of marginal habitats. Ricklefs and Cox (1972), in applying Wilson's taxon cycle concept to the birds of the West Indies, proposed that the expanding and contracting phases

of the cycle reflected the balance between the adaptations of populations and those of their antagonists, whether predators, pathogens, competitors, or food resources. They referred to this process as “counteradaptation” and, following upon the experimental work of David Pimentel and his colleagues on flies (Pimentel 1961; Pimentel and Al-Hafidh 1963; Pimentel et al. 1965), they suggested that the relative success of antagonist populations might shift owing to frequency dependence coupled with evolutionary lag times.

Several studies of the distributions of birds and insects within archipelagoes uncovered patterns similar to those described by Wilson (Greenslade 1968; Greenslade 1969; Ricklefs 1970; Ricklefs and Cox 1972). Since 1961, several modifications of the taxon cycle have been published, notably Erwin’s (1981) taxon pulse and Roughgarden and Pacala’s (1989) variant of the taxon cycle for Lesser Antillean *Anolis*, and the concept has been subjected to further analysis and criticism (see Ricklefs and Bermingham 2002). Nonetheless, recent molecular phylogeographic studies have confirmed the existence of expansion and contraction phases previously inferred from distribution and taxonomic differentiation (Ricklefs and Bermingham 2001). To fully understand both the potential and the difficulties of the taxon cycle concept, it is useful to consider perceptions of ecological systems more generally.

Static versus Dynamic Views of Ecological and Geographic Distributions

Ecology has for the most part been an equilibrium science. Population and community processes have been perceived as leading toward equilibrium states. Populations grow toward a carrying capacity, and species coexist stably within a community having a particular matrix of interaction coefficients (Vandermeer 1972; May 1975). This perspective led to the idea of community saturation, whereby ecological space became filled with species and further invasion of a community was prevented (MacArthur and Levins 1967; Terborgh and Faaborg 1980; Alroy 1998; McKinney 1998; Kelt and Brown 1999). Accordingly, differences between communities in numbers of species reflected the influence of the physical environment on either the ecological space available in a community or the average ecological space occupied by each species (MacArthur 1965; Cody 1975; Cody and Diamond 1975). MacArthur and Wilson’s (1963, 1967) equilibrium theory of island biogeography envisioned a balance between the rate of colonization of an island by new species and the rate of extinction of island populations. Although their model of island diversity was dynamic, they did not discuss in detail the origin of new colonists or the factors resulting in extinction of established populations, topics that have remained relatively unexplored in the ensuing decades (Whittaker 1998). In particular, whether new colonists hasten the extinction of established island populations is obscure. David Lack (1976) retreated further from a dynamic concept of island biogeography when he asserted that few island populations

went extinct; he believed that colonization stopped when islands became saturated with species. For Lack, diversity on islands was correlated with the ecological variety of habitats and the structure of those habitats—that is, the total ecological space available to be occupied (Ricklefs and Lovette 1999; Ricklefs and Bermingham 2004). Several new analyses suggest that establishment of exotic plants on islands has not caused extinction in the native floras (Sax et al. 2002; Davis 2003; Sax and Gaines 2003).

According to this equilibrium view of ecology, changes in communities are driven by external factors, primarily changes in the environment, including its physical conditions and biological resources. For example, warm-cold and wet-dry cycles associated with the advance and retreat of continental glaciers are seen as external forces that shifted ecological conditions and the distributions of species, changing the composition of communities locally because of the different responses of their component species to changes in different aspects of the environment. In many cases, this process must have led to disruption of communities as well as their shifting in space, although even this point is contentious (Davis 1986; Jacobson et al. 1987; Webb 1987; Jackson et al. 2000). A view of ecology in which species are conservative entities whose distributions are pushed about by the physical environment is essentially static or, at least, passive (Janzen 1985). Colonization is perceived as haphazard, caused by storms or currents that transport animals or seeds from one place to another (Lack 1976; Pielou 1979), or serendipitously resulting from the dispersal of occasional individuals into the void. The tropical ecologist Daniel Janzen (1985) has said that if a population arrives at a place and it “fits” ecologically, it will persist. Sometimes the fit is aided by individual phenotypic flexibility (Callaway et al. 2003) or by the absence of coevolved antagonistic species (Callaway and Aschehoug 2000; Callaway et al. 2004).

Many ecologists believe that ecological systems are intrinsically more dynamic than this view allows because of the evolutionary responses of species to one another and to changing environments. The question for ecologists has been whether evolution occurs rapidly enough compared with the approach of systems to ecological equilibrium to influence the composition of communities (Ricklefs 1989). In the present context, are invasive species afforded enough time to evolve an improved fit to available ecological space? More generally, is evolution relevant to ecology?

Ehrlich and Raven (1964) made ecologists aware of the importance of coevolution, but the outcome they envisioned was a conservative association between particular groups of herbivores and particular groups of plants, punctuated at times by shifts onto new host plants (Farrell et al. 1992; Farrell and Mitter 1994). Robert H. Whittaker (1972, 1977) and Leigh Van Valen (1973) adopted a more dynamic view focused on populations of predators and prey, herbivores and plants, pathogens and hosts, and so on, each engaged in a continuing coevolutionary struggle to improve its position with respect to mutually antagonistic interactions and changing environments. Presumably, coevolution maintains the relationships between species in a community in a

dynamic state. However, in developing the idea of coevolution, ecologists did not explicitly address community relationships or changes in the composition of communities. Indeed, most believed that coevolution leads to a dynamic equilibrium, at least over ecological time spans (Rosenzweig 1973; Ricklefs 1990). That is, although particular adaptations for attack and defense come and go, the outcome of the interaction between antagonists remains more or less a stalemate. Indeed, coevolved relationships between antagonists can become entrenched and static, as in the case of many insects specialized to feed on plants with particularly toxic compounds (Berenbaum 1983).

In this context, several ecologists have emphasized the long evolutionary history of herbivore-plant and predator-prey relationships, which fossils suggest have persisted more or less unchanged for millions of years (e.g., Opler 1973). The literature on the evolution of virulence in pathogens emphasizes conditions that can shift the equilibrium level of virulence achieved (Ewald 1983; Bull 1994; Day 2001). Thus, in spite of the evolutionary changes occurring within communities, these changes are not seen as challenging the outcomes of species interactions or the stability of community composition. A static, equilibrium view does not readily allow for the reshuffling of ecological relationships, which would otherwise boost some populations into phases of expansion or provide openings for the invasion of new species from outside. This view is consistent with the prevalent ideas that intact communities are resistant to invasion, and that invasive species do best where human activities have badly torn the fabric of the community (Elton 1958; Williamson 1996; Hector et al. 2001).

The most important sources of transformation in dynamic models of ecological systems are lag times in the responses of biological systems to change. Delays in the population responses of predators to changes in the numbers of their prey, and vice versa, destabilize population interactions and are responsible for the dramatic cycling of some predator-prey systems (Nisbet and Gurney 1982; Ricklefs 1990). The time required in consumer and host populations for shifts in the frequencies of virulence and resistance genes can establish population limit cycles with dynamics on the order of tens to hundreds of generations (Lenski and May 1994; Frank 1996; Roy and Kirchner 2000). When coupled to other populations in a system, these cycles could lead to changes in community composition and provide openings for new "invasive" species (e.g., Shea and Chesson 2002). Longer-term dynamics in ecological systems might reflect the origin of new variation in species interactions that depends on functionally important mutations arising by chance and becoming established at long intervals.

An Empirical Look at Natural Range Expansions

Natural invasions involving colonization

Islands have provided important settings for examining natural invasions and the development of ecological communities (Carlquist 1974; Wagner and Funk 1995; Losos 1996; Williamson 1996; Whittaker 1998; Ricklefs and Bermingham

2001). Islands are discrete geographic entities with well-defined biotas. Multiple islands in archipelagoes provide an opportunity to examine generalized (i.e., consistent across islands) aspects of invasion and community development (Losos et al. 1998). Individual large islands and groups of small islands also illustrate the buildup of communities internally through evolutionary radiations of endemic lineages (Givnish and Sytsma 1997; Schluter 2000). Where these radiations involve allopatric formation of new species, they can lead to repeated reinvasion of areas (secondary sympatry), which increases diversity locally (Lack 1947; Grant 1986). Thus, the dynamics of this community-building process might provide insight into the likelihood of a species becoming established in an intact natural community, especially one that includes a sister species that, because of common ancestry, is ecologically similar.

Adaptive radiation within isolated islands and island groups can build diversity more rapidly than repeated colonization of an island from outside sources (Losos and Schluter 2000). For example, the contemporary passerine (songbird) avifauna of the Hawaiian Islands represents the establishment of only six non-native lineages. Yet, one of these, the Drepanidinae (honeycreepers), derived from a cardueline finch colonist, has diversified into 30 or so named species and others known only from the bones of extinct forms (James and Olson 1991). At least 15 species co-occur on the largest (and youngest) of the islands, Hawaii, all of them having colonized the island from elsewhere. The morphological and ecological diversity of the drepanid clade, which has diversified over perhaps 5 million years (Fleischer et al. 1998; Fleischer and McIntosh 2001), exceeds that of all other passerine birds in several respects, particularly the morphology of the beak (Lovette et al. 2002). Similarly, a single lineage of *Drosophila* fruit flies that reached the Hawaiian Islands has diversified into hundreds of species that collectively exceed both the non-Hawaiian species richness and the morphological diversity of the genus worldwide (Carson and Kaneshiro 1976). Although one can argue that these radiations build diversity within relatively empty ecological space, there is no evidence that the accumulation of diversity is slowing or that it will reach a saturation level (compare Terborgh and Faaborg 1980; Ricklefs 1987; Ricklefs 2000; Ricklefs 2004a).

Ricklefs and Bermingham (2001, 2004) used a molecular phylogenetic approach to examine in more detail the dynamics of bird species in the Lesser Antilles. These islands are relatively close to sources of colonists in northern South America and the Greater Antilles. The contemporary small land bird fauna of the archipelago includes 57 lineages, the oldest of which may be approximately 10 million years old. Based on the distribution of colonization times, there appears to be little or no background extinction of lineages within the archipelago as a whole, but gaps in the distributions of some old taxa indicate that individual island populations have disappeared. Established populations on the larger core islands of the Lesser Antilles (Guadeloupe, Dominica, Martinique, St. Lucia) appear to have life spans averaging about 2 million years. The molecular phylogenetic data also indicate that endemic lineages occasionally undergo phases of reexpansion within the Lesser Antilles, which

undoubtedly minimizes archipelago-wide extinction. Phases of contraction and expansion apparent in the molecular phylogenetic record occur at intervals of hundreds of thousands to millions of years, making their connection with currently invasive species tenuous and reinforcing the appearance of stability in natural systems. Three “natural” invasions of islands by land birds within the Lesser Antilles have occurred during the past century: the shiny cowbird (*Molothrus bonairiensis*), Carib grackle (*Quiscalus lugubris*), and bare-eyed thrush (*Turdus nudigenis*) (Raffaele et al. 1998). All these species are closely associated with landscapes altered by human activities, particularly agricultural and residential areas.

Only two small evolutionary radiations have occurred within the archipelago, one producing two species of *Eulampis* hummingbirds (E. Bermingham and R. E. Ricklefs, unpublished data) and the other producing four species of endemic thrashers (Mimidae) in three or four genera, depending on the taxonomy adopted (Hunt et al. 2001). The absence of marked adaptive radiation of land birds in the Lesser Antilles as compared with Hawaii supports the idea that invasion and secondary sympatry are hindered when ecological space is densely packed. Indeed, the endemic thrashers were one of the earliest of the currently extant lineages to invade the islands, and they might initially have diversified within relatively open ecological space. Examination of island biotas thus presents conflicting views. On one hand, existing species and packed ecological space appear to constrain evolutionary radiation within island groups, while on the other hand, colonization from outside appears to face little resistance.

Natural range expansion within continental regions

Invasion dynamics are more difficult to perceive within large continental areas than on islands. The biota of a region can be considered as a single large community within which the distribution of species among areas and habitats reflects the evolutionary history of their ecological relationships (Ricklefs 2004b). These relationships are established partly through adaptations for tolerance of physical conditions of the environment and ability to utilize ecological substrates unique to particular habitats. Thus, the ecological (and geographic) distributions of species within a region expand and contract because of changes in the physical environment (e.g., climate), but also in response to the relative balance of adaptations for defense against consumers and exploitation of resources (Ricklefs 2004b). In the first case, species with similar tolerances would exhibit parallel changes; in the second case, phases of expansion and contraction would probably be more idiosyncratic.

The relative importance of general and particular factors is apparent in the distribution of variation among levels of the taxonomic hierarchy. If variance in range size or breadth of ecological distribution, for example, is concentrated at a high taxonomic level, then differences between taxa most likely reflect conserved adaptations to stable attributes of the environment, including physical

conditions and general habitat preferences. If most of the variance resides at a lower taxonomic level, then differences are more likely reflect special relationships between organisms and their environments, including specialized herbivores, predators, parasites, and pathogens, as well as physiological adaptations to particular physical conditions. Ricklefs and Cox (1972) argued that the lack of association between expansion or contraction phases of West Indian birds and taxonomic affiliation reflected special relationships of this kind with predators or pathogens, although no data were (or are) available to assess this directly.

More recently, Gaston (1998, 2003) conducted nested analyses of variance on range size in a variety of organisms, finding that most of the variance resided on the taxonomic level of species within genera. In a similar analysis, Webb and Gaston (2003) found no correlation of range size in 103 pairs of avian sister species; if range size were conservative, the correlation should have been strong and positive. Thus, most of the variation in range size occurs between species in the same genus. The implication of these findings is that the factors that determine range size are unrelated to the general adaptations of organisms to climate or the relative availability of different habitat types, which one would expect to be more conservative.

Scheuerlein and Ricklefs (2004) conducted a similar partitioning of variance in a large sample of European passerine birds. They found that variation in most measures of distribution, including overall population size and the north-south location of the midpoint of a species range, resided at the level of species within genera (85% and 87% respectively). In contrast, 80% of the variance in distribution along a habitat gradient from open habitats, including wetlands, to forests was at the level of genera within families, reflecting more conserved adaptations for using different vegetation strata and habitat types. Variation in several life history traits, such as body mass, clutch size, and the duration of incubation, resided primarily at the level of genera within families or families within passerine birds. The implication of this finding for invasion biology is that habitat structure is probably more critical to establishment success than climate. As Janzen (1985) pointed out, the ranges of many organisms extend from temperate regions right through the tropics.

Stotz et al. (1996) compiled several measures of abundance and breadth of ecological and geographic distributions for all Neotropical birds. As found by Gaston and by Scheuerlein and Ricklefs, between 74% and 87% of the variance in relative abundance, number of habitats occupied, and number of zoogeographic regions occupied in species of non-raptorial land birds resided at the level of species within genera (Table 7.1). Only the stratum of vegetation (i.e., terrestrial, understory, mid-canopy, canopy, and aerial) varied substantially among genera within families (45%) and families within orders (43%), again reflecting more conserved morphological adaptations for performing well in different parts of the habitat (R. E. Ricklefs, unpublished data). At a more local scale, 71% of the variance in abundance of trees on the 50-ha Forest Dynamics Plot on Barro Colorado Island, Panama, resides at the level of species within genera, with an additional 22% among genera within families

TABLE 7.1 *Distribution of variance in measures of ecological and geographic distribution of Neotropical nonraptorial land birds within a nested taxonomic hierarchy*

	df	Stratum ^a	Relative abundance ^b	Sqrt (min) ^c	Sqrt (max) ^c	Nhab ^d	Logzoo ^e
Order	8	1.3	1.3	3.8	0.0	0.0	0.7
Family	48	42.7	1.8	1.5	5.7	8.8	6.3
Genus	684	45.4	20.8	40.5	24.1	17.3	6.5
Species	2292	10.5	76.2	54.3	70.1	73.9	86.5

Source: Based on data in Stotz et al. 1996.

^aStratum: terrestrial (1), understory (2), midstory (3), canopy (4), aerial (5).

^bRelative abundance: rare (1), uncommon (2), fairly common (3), common (4).

^cSqrt, square root of the minimum (min) elevation and maximum (max) elevations (meters).

^dNhab, number of habitats (out of 15 forest and 14 open scrub/grassland habitat types).

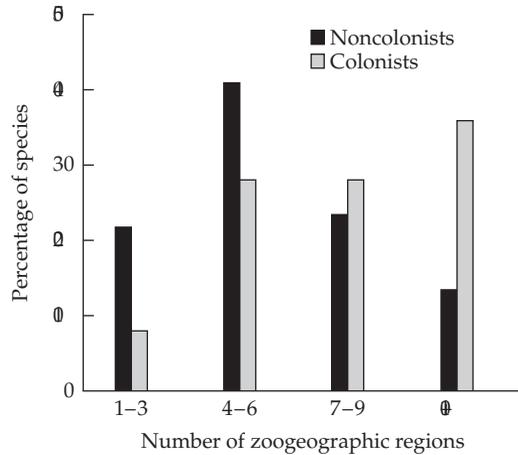
^eLogzoo, logarithm of the number of zoogeographic regions (out of 22).

(Ricklefs 2005). These analyses imply that local communities must be dynamic on time scales that correspond to the formation of new species within genera, and conceivably on shorter time scales. Thus, species continually establish themselves in and disappear from habitats and zoogeographic regions, creating continental-scale expansions and contractions of ecological extent and geographic range. Relative abundance, number of habitats, and number of zoogeographic regions are also significantly correlated with one another at the level of species within genera, suggesting that geographic extent and habitat breadth share a common, local, demographic basis (Ricklefs and Cox 1978). This pattern could reflect the relative balance of adaptations governing relationships with other, relatively specialized organisms.

The connection between natural colonization and ecological spread

If a population's distribution reflected specific attributes or interactions, natural colonization might be relatively deterministic; for example, following release from consumer pressure resulting in high population density and an increase in dispersal. Although it has been difficult to predict which species should make good colonists at any particular time (e.g., Ricklefs and Cox 1972; Terborgh et al. 1978), one can test whether colonists to one destination have independently colonized other destinations accessible from the source area. If so, this would indicate that some species have attributes that generally enhance their capacities as colonists (Simberloff and Boecklen 1991; Duncan 1997). It is probably more than a coincidence that many resident birds of the Galápagos Islands are derived from taxa that have colonized other islands off the west coast of the Americas or in the West Indies [for example, mockingbirds (*Mimus*), yellow warblers (*Dendroica petechia*), *Myiarchus* flycatchers, *Tiaris*-like emberizid finches, *Zenaida* doves].

Figure 7.1 Number of zoogeographic regions throughout the Neotropics occupied by birds that occur on the island of Trinidad and which have, or have not, colonized the Lesser Antilles. (Zoogeographic data from Stotz et al. 1996: $G = 8.7$, $df = 3$, $P = 0.034$; analysis from R. E. Ricklefs and E. Bermingham, unpublished data).



Of the small, non-raptorial land birds present on Trinidad, 25 species have invaded the Lesser Antilles, separated from that island by a 150-km water gap to the north, whereas 169 have no extant descendants in that archipelago. The colonists have a wider distribution among zoogeographic regions in the Neotropics than the noncolonists (Figure 7.1; see also Blackburn and Duncan 2001).

The determinism of colonization among species that have invaded the Lesser Antilles, as well as its transient nature, can also be seen by examining the occurrence of the source populations on small islands close to their distributions in northern South America (islands off the northern coast of Venezuela) or the Greater Antilles (small islands close to Puerto Rico). Colonizing species are distinguished as being young colonists (less than 2% mtDNA sequence divergence [ca. 1 million years] and taxonomically undifferentiated) or old colonists. Twenty-four of 33 young colonists to the Lesser Antilles, but only 7 of 24 colonists that have given rise to older, generally endemic species, occur on these peripheral islands ($G = 10.6$, $df = 1$, $P = 0.001$) (R. E. Ricklefs and E. Bermingham, unpublished data). Evidently, the colonizing ability of the source populations of the older Antillean taxa has waned, and extinction has claimed former peripheral island populations.

The picture of natural invasiveness that emerges from such analyses of birds is one of substantial dynamism of ecological and geographic distributions of species within regions and of turnover of species within local communities following disappearance of established species and establishment of new species from outside. The time scale of these processes appears to be less than the durations of species, but how much so remains unclear. Our work on Lesser Antillean birds suggests that 10^5 to more than 10^6 years separate phases of expansion (including initial colonization). The lability of geographic and ecological distributions indicates that the dynamics of natural invasions are largely independent of evolutionary change in relation to the physical environment, which has gone through dramatic glacial cycles over this period. Rather, this lability

appears to reflect changing demography influenced by the balance of evolutionary relationships of populations with various types of consumers. These processes are difficult to observe on the time scales of natural expansions and contractions of ranges and ecological extents. Thus, an examination of invasions assisted by human interventions might provide insight into natural processes.

Key Issues in the Taxon Cycle and Invasion Biology Literature

Recent invasions and the properties of invasive species

The study of invasive species has led to a number of generalizations about the qualities of good invaders and the susceptibility of environments to invasion (Mack et al. 2000). Conventional wisdom states, first, that species invasions are limited to the range of conditions to which the colonists are adapted in their native areas (Peterson 2003), and second, that intact natural habitats resist invasion because ecological space is saturated and invading species cannot get a foothold (Williamson 1996). This is equivalent to saying that non-native species are not good competitors because they are not adapted to local environments. The first statement surely must apply to invasive species over the short term, which does not provide time for tolerance ranges to evolve. Each species occurs within what is called an environmental envelope circumscribing the range of environmental conditions over which the population extends in its native area (Cumming 2002). This range of conditions, when overlaid on an area of introduction, frequently determines the range within which a species can become established (Peterson 2003). In this context, Blackburn and Duncan (2001) determined that the invasion success of birds depended on how well the abiotic environment at the introduction site corresponded to conditions within the native range. In their analysis, the relative paucity of successful avian introductions in tropical regions was statistically unrelated to the resistance of these regions to invasions because of their high species richness, but rather resulted from poor matches, or "ecological fits" (Janzen 1985), with the native ranges of most introduced species.

The generalization that intact, diverse communities resist establishment of non-native species derives from the susceptibility of islands to introductions and the common occurrence of invasive species as weeds in disturbed habitats. It seems possible to me that this pattern is seen because both intentionally and unintentionally introduced species most often originate from human-influenced environments in their native ranges. Few truly forest-inhabiting species of birds have been introduced to Hawaii, for example, and the failure of introduced species to penetrate native forests in the Hawaiian Islands (Scott 1986) could be attributed in part to this selectivity. Where suitable intact environments are available, introduced species sometimes do quite well. For example, in an extensive survey of alien species in mixed-grass prairie in North Dakota, Larson et al. (2001) determined that despite the influence of anthropogenic dis-

turbance, habitat type, and alien plant invasion, five of the six most abundant alien species had distributions unrelated to disturbance.

WHAT MAKES A SPECIES A GOOD INVADER? There have been many attempts to link introduction success and invasiveness to intrinsic properties of species (e.g., Rejmánek and Richardson 1996). Characteristics proposed to enhance the invasion success of plants have included various life history traits associated with weediness, particularly those contributing to a high reproductive rate and the ability to become established on disturbed or degraded areas (Daehler 2003). Among birds, invasion success has been linked to body size (Cassey 2001), behavioral flexibility (Sol et al. 2002), habitat generalism, lack of migratory tendency, and sexual monochromatism (Cassey 2002).

If invasive species have particular attributes that make them good invaders, then independent introductions to different areas should produce a strong correlation in invasion success, as is evident in natural colonizations. Such a pattern was found in an analysis of the introduced birds of Hawaii by Simberloff and Boeklin (1991). With respect to birds introduced to New Zealand, Duncan (1997) reported a high correlation in success or failure between attempts when species were introduced to more than one area. Duncan also showed that this correlation was probably an artifact of propagule pressure (introduction effort), which was highly correlated between different introduction locations for the same species. In another analysis that considered a broader geographic region, Duncan found no correlation in the invasion success of the same bird species in different places. However, the eventual sizes of the ranges of introduced species in New Zealand were correlated with their native ranges in Great Britain (Duncan et al. 1999).

Ricklefs and Cox (1972) determined that recent immigrants to the Lesser Antilles from South America tend to inhabit open country, including grasslands, agricultural habitats, and gardens, and are relatively abundant in those habitats within their source areas. P. Cassey et al. (unpublished data) recently examined avian introductions on a global scale, analyzing the influence of introduction effort and several attributes of species (body mass, native geographic range size, annual fecundity, dietary generalism, habitat generalism, sexual dichromatism, and migratory tendency) on invasion success. In this analysis, introduction effort was the most important factor, and among the species attributes, only habitat generalism (the number of seven major habitat types included in a species' range: mixed lowland forest, alpine scrub and forest, grassland, mixed scrub, marsh and wetland, cultivated and farmlands, urban environs) had a significant effect. Diamond (1975) emphasized that not all successful colonists are good competitors. Indeed, many species of birds that are widely distributed throughout Melanesia and Micronesia, called "supertramps," are restricted to small islands with few other species. Diamond inferred that while these species readily colonize larger islands with well-developed avifaunas, they do not become established there.

PROPAGULE PRESSURE The importance of propagule pressure suggests that the best intrinsic predictor of invasion success is the desirability of a species to humans—its sporting, aesthetic, biological control, and other values—which determines introduction effort. Of course, naturally invasive species colonize new areas under their own steam, and determinants of propagule pressure in such cases are more likely to include the intrinsic properties of species that make them capable of crossing barriers to dispersal or the demographic pressures of high population density that cause individuals to seek living space away from their natal areas. Psychological and physiological factors might also be important in the sense that few inner forest species—for example, antbirds, ovenbirds, woodcreepers, and manakins from South America—colonize islands across water (Ricklefs and Cox 1972), or even venture across narrow roadways through Amazonian forests (Laurance et al. 2004).

Colonization, which is aided by human intercession in the case of most present-day range expansions, is only the first step to becoming invasive. It must be followed by establishment and then spread throughout the new area. In the case of natural invasions, we have little evidence of failed colonization events, which, because they are transient, leave little or no trace. The stochastic element of invasiveness owing to small propagule size must cause many colonists to fail to become established (Williamson 1996).

In the Lesser Antilles, two major colonizations of land birds in the last century, the glossy cowbird and the bare-eyed thrush, have moved northward from island to island in a remarkably deterministic manner (Bond 1956). Thus, whatever qualities have made these species effective colonizers from northern South America to Grenada, the first island in the chain, have led to repeated success in crossing further gaps between islands. The intervals between colonizations were about 20 years, which would allow time for populations to fill available habitat on one island before moving on to the next. It is clear that these species have generated their own propagule pressure, which has depended on the intrinsic qualities of the colonizing species and the availability of favorable agricultural and garden habitats.

The distributions of older colonists of the Lesser Antilles suggest a difference between those with northern and southern origins (Ricklefs and Bermingham 2004). Many invasions from the south stop somewhere short of the northern Lesser Antilles, whereas most from the north extend all the way to Grenada (but rarely invade South America) (Figure 7.2). The cause of the truncated invasions of the southern species, of which approximately 20% with established populations have not colonized the next island, could be either a stochastic failure to become established and spread or a reduction of propagule pressure, caused by changes in the ecological relationships of a species on an island, as the invasion proceeds. As far as I can surmise, successive island-hopping along this linear chain depends on the establishment and growth of populations on each island independently. The more consistent penetration of the archipelago by species colonizing from the north may be related to the fact that these pop-

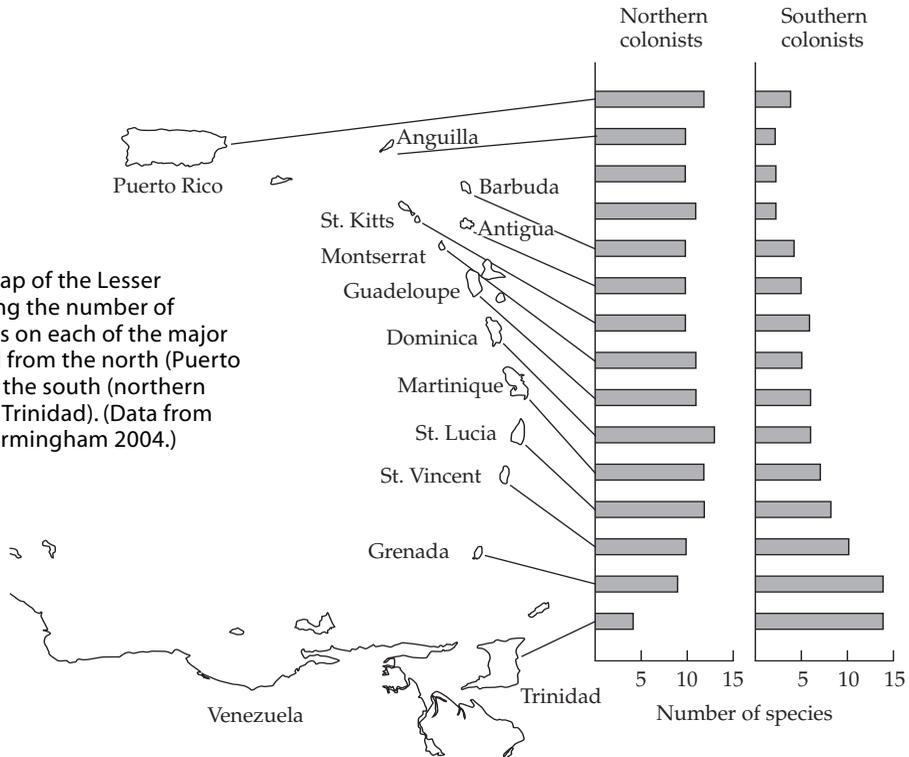


Figure 7.2 Map of the Lesser Antilles, showing the number of young colonists on each of the major islands derived from the north (Puerto Rico) and from the south (northern Venezuela and Trinidad). (Data from Ricklefs and Bermingham 2004.)

ulations started from island sources in the Greater Antilles (presumably Puerto Rico). They had to cross a larger water gap against prevailing winds to colonize smaller islands with less favorable habitats before arriving at the larger core islands of the Lesser Antilles.

Lessons from biotic interchanges

Occasionally, changes in climate or the bridging of land or water gaps by sea level change and tectonic movements lead to major exchanges of species between regions, commonly referred to as biotic interchanges. One of the best documented of these cases resulted from completion of the land bridge between North and South America during the Pliocene, creating what Simpson (1980) and Webb (1991) have called “the Great American Interchange.” Many lineages of mammals crossed the Isthmus of Panama in both directions. In South America, several of these lineages underwent rapid adaptive radiations, apparently at the expense of the native mammalian fauna. Other exchanges have been equally spectacular, including the invasion and eventual dominance of the Holarctic by passerine birds with evolutionary roots in Australasia (Ericson et al. 2002) at the expense of many diverse non-passerine clades

(Mayr and Manegold 2004); broad exchanges between the Nearctic and Palearctic across Greenland and the Bering Strait at various times during the Tertiary (Tiffney 1985; Donoghue et al. 2001; Sanmartin et al. 2001); and exchanges across a Miocene mesic land connection between Africa and Eurasia (Cooke 1972; Kappelman et al. 2003). Vermeij (1991), who reviewed cases of marine biotal exchange during the Neogene, pointed out that invaders usually constitute a small percentage—typically less than 10%—of the available species pool, and that invaders constitute a variable percentage of the recipient species pool depending on the relative diversity of the regions and the asymmetry of movement during the interchange (also see Vermeij, this volume). Nonetheless, these exchanges can have dramatic and long-lasting effects on species pools and local communities.

Biotic interchanges could teach us useful lessons about biotic invasions if we had information about the attributes of the species taking part in the interchanges and the fates of those species and the of regional species pools following their establishment in a non-native area. Specifically, one would like to know whether exchanges of species between regions increased their species pools. One explanation for the greater plant species diversity in temperate eastern Asia compared with similar environments in eastern North America is the broad boundary over which species can colonize temperate Asia from more diverse tropical areas to the south (Latham and Ricklefs 1993a,b; Qian and Ricklefs 2000). As in the case of species diversity on islands (MacArthur and Wilson 1967), colonization pressure from outside tends to increase native species pools. When that pressure is released, do native species pools return to pre-exchange levels? In the case of North American mammals, pulses of immigration of taxa from Asia in the Miocene and Pliocene did not boost species richness regionally or locally (Van Valkenburgh and Janis 1993). Indeed, Webb (1989) argued that immigration from Asia was possible only after extrinsic climatic factors had reduced local species richness and opened ecological space for new colonists. Webb has not, however, applied this argument to the Great American interchange.

Range expansion

DIVERSITY AND RESISTANCE TO INVASION In a given environment, increasing numbers of species should pack ecological space more tightly and offer increasing resistance to the establishment of new invaders. This reasoning has led to the idea that diverse communities resist invasion by non-native species (Tilman 1997; Wisser et al. 1998; Knops et al. 1999; Levine and D'Antonio 1999; Levine 2000; Naeem et al. 2000; Sax and Brown 2000; Hector et al. 2001; Shea and Chesson 2002), although not all empirical studies support that idea (Hawkins and Marino 1997; Wisser et al. 1998). A corollary is that colonists should become established in island environments more readily than in similar continental environments. In apparent confirmation, few cases of island forms invading continents are known. This observation should be tempered, however, by the

possibility that colonizers from islands might be difficult to identify as such. A second caveat is that the odds of invasion from continent to island overwhelm the odds of events in the reverse direction because of the difference in relative diversities and population sizes between islands and continents. This difference makes cases of avian invasion of South America from the Lesser Antilles—for example, the bananaquit (*Coereba flaveola*: Seutin et al. 1994), *Icterus* orioles (Omland et al. 1999), and possibly *Tiaris* finches (Burns et al. 2002)—all the more remarkable.

With respect to human-assisted introductions of birds, Blackburn and Duncan (2001) determined that the diversity of species in the non-native area was not an important consideration in invasion success. However, this test is meaningful only when diversity is scaled with respect to the capacity of an environment to support coexisting species. When natural biotas have achieved ecological equilibrium diversity, resistance to invasion should be uniformly high and not strongly dependent on local species richness. Sol (2000) came to the related conclusion for birds that invasion success on islands was no greater than within continental areas.

Evidence that competition or other interactions restrict the establishment of species comes from studies relating the composition of communities on islands to that of communities drawn at random from potential colonists. Such tests have been conducted for a number of island systems, including the native avifauna of the West Indies, based on species-area relationships for members of different feeding guilds on islands (Terborgh 1973; Faaborg 1982), saturation curves relating local diversity within selected habitats to total island (regional) diversity (Terborgh and Faaborg 1980; but see Ricklefs 2000 for conflicting data on this point), size distributions within feeding guilds on islands compared with null distributions (Faaborg 1982; Case et al. 1983), and distributions of species among feeding guilds on oceanic and land-bridge islands (Faaborg 1985). These studies provide evidence for ecological sorting and species interactions on islands, but they do not directly address whether colonization is depressed by high species diversity on islands.

Working with the introduced Hawaiian avifauna, Moulton and Pimm (1983) showed that failures of introduced island populations increased dramatically with increasing diversity of introduced species, implying that the intensity of competition set upper limits to the size of the avian community. Alternatively, because introductions to Hawaii came to a halt by 1940, the pattern observed by Moulton and Pimm might have resulted simply from stochastic extinctions with time lags of a few years to a few decades combined with reduced introduction pressure. Furthermore, extinctions were strongly concentrated among doves and pigeons on some islands, suggesting that these results might not be generalizable.

In another analysis of the introduced Hawaiian avifauna, Moulton and Pimm (1987) demonstrated that average morphological minimum spanning tree segments constructed from successfully introduced species that have invaded native forest were significantly greater than those calculated by ran-

dom draws from all introduced species, successful or not. The implication of this result is that extinctions were more frequent among groups of similar species (see also Moulton 1985). However, the morphological positions of the native Hawaiian avifauna were not included in this analysis, and it is unclear how the introduced species fit into native communities. Moulton and Lockwood (1992) obtained a similar result showing overdispersion of surviving introduced populations of finches on Oahu. These finches inhabit primarily open, disturbed habitats that harbor few species of native Hawaiian birds, so these results pertain more to the *de novo* construction of avian communities than to the establishment of new species in endemic communities. Viewed as a whole, the evidence concerning the role of competition in organizing the species that constitute a community is more convincing than that for the role of competition in preventing invasion.

Although species interactions structure relationships in established ecological communities, they do not necessarily limit membership in those communities. Nor does the establishment of new colonists necessarily lead to extinction of natives (Sax et al. 2002; Davis 2003). One strong lesson from MacArthur and Wilson's equilibrium theory is that island biotas are shaped by extrinsic factors and that the pressure of colonization influences diversity, both for entire islands and within local habitats. Terborgh and Faaborg (1980) found evidence for saturating species richness in island habitats, but only on the largest islands in the Greater Antilles. Cox and Ricklefs (1977) and Ricklefs (2000) found, instead, that diversity within individual habitats increased continuously as approximately the square root of island diversity, indicating graded resistance to establishment in new habitats by colonists, but not saturation of local communities. Based on a morphological analysis of land bird communities in the Caribbean basin, Travis and Ricklefs (1983) concluded that assemblies of species within individual habitats on small islands in the Lesser Antilles (St. Lucia and St. Kitts) were less densely packed than on the mainland (Panama and Trinidad) and Greater Antillean islands (Jamaica). The latter had nearest-neighbor distances in morphological space typical of continental assemblages. Ricklefs and Bermingham's (2001) analysis of the distribution of colonization times of Lesser Antillean birds suggested that the avifauna was not close to saturation.

RELEASE OF INVASIVE SPECIES FROM PATHOGENS An important point that has been made with respect to introduced species is that invasion success is associated with a release from herbivores, parasites, and pathogens (Maron and Vila 2001; Keene and Crawley 2002; Wolfe 2002; Mitchell and Power 2003; Torchin et al. 2003; see also Lafferty et al., this volume), although factors such as range sizes of native and non-native species might confound this relationship (Clay 1995). Small propagules probably sample only a small part of the total pathogen community in the native range, and additional pathogens can be lost after introduction owing to stochastic effects in initially small populations and absence of suitable vectors or environmental conditions for free-living stages of pathogens (Dobson and May 1986). Provided that introduced species do not pick up new

pathogens, they may experience rapid population growth and superior competitive ability in the absence of suppression by parasites, herbivores, and disease. This is the rationale behind biological control programs that seek to reverse this situation by restoring consumers of invasive pest species from their native areas wherever possible (Charudattan 2001).

Ricklefs and Cox (1972) also suggested that release from predators and pathogens could lead to the initiation of an expansion phase of the taxon cycle, although there may be essential differences between natural and human-aided invaders. While species that naturally colonize new areas might escape pathogens in a manner analogous to anthropogenic introductions, this release cannot explain increases in propagule pressure that might lead to colonization success in the first place. In the framework of coevolution, loss of pathogens depends on the acquisition of genetic factors through mutation and selection that effectively defend the individual against infection or predation or control their harmful effects at a low level. Simple models of the cycling of virulence and resistance genes in pathogen and host populations have dynamics that are too fast to explain the long intervals between expansion phases in natural populations (Lenski and May 1994; Frank 1996; Roy and Kirchner 2000). If host resistance depended on the fixation of rare mutations that could not be readily countered by pathogen evolution, then phases of expansion might arise abruptly, but at long intervals determined by the appearance of suitable genetic variability.

If coevolution were important, colonizing and noncolonizing species would not necessarily differ ecologically, and the composition of invaded communities would be relatively unimportant. Rather, invasion success would be determined by demographic rather than habitat factors, the dispersal of individuals from crowded populations would be the major driver of range and habitat expansion, and invasiveness would decline over time owing to pathogen coevolution independently of change in the physical environment. Presumably, any advantage that a host population enjoys owing to escape from pathogens would be transient because the diverse array of pathogens in the new environment would be selected to utilize the newly abundant resource. Thus, one might expect the colonization phase of the taxon cycle to be relatively short-lived. Rapid coevolution of pathogens and hosts is well known from studies of human diseases, including syphilis (Knell 2003) and falciparum malaria (Hartl et al. 2002), and one would not expect a host species to maintain an advantage over a pathogen population for long.

Torchin et al. (2003) and others have demonstrated that introduced individuals of non-native species typically harbor fewer parasites than individuals in their native range. Relatively few data are available to address this point in the case of natural introductions. Most examples come from islands, which typically lack diverse communities of parasites and pathogens. A classic case concerns birds in the Hawaiian Islands (Van Riper et al. 1986). Prior to colonization by Europeans, the islands lacked suitable mosquito vectors of such avian diseases as poxvirus and malaria (*Plasmodium/Haemoproteus*). As a result, the introduced species (that is, the now native honeycreepers and other line-

ages that colonized the islands on their own) had lost most of their genetic defenses against these pathogens. When *Culex* mosquitoes, and then both poxvirus and *Plasmodium relictum*, were introduced to the Hawaiian Islands during the nineteenth and twentieth centuries, these diseases decimated many of the native populations. Bird species introduced more recently from continental areas are infected by the malaria pathogen, but host individuals control infections at low levels (Van Riper et al. 1986; Jarvi et al. 2001).

Loss of parasite diversity is evident in bird communities on small islands in the West Indies, but the patterns of parasite distribution are also idiosyncratic. For example, populations of bananaquits and of Lesser Antillean bullfinches (*Loxigilla noctis*) on Barbados harbor only the commonest one of the variety of malaria parasite lineages found in these species on St. Lucia and St. Vincent (Fallon et al. 2005), which were the source areas for the Barbados populations (Lovette et al. 1999). Yet, on Barbados, that single parasite is now found in other species of avian hosts that are not infected by the lineage elsewhere. Clearly, the colonization of Barbados acted as a filter for avian malaria parasites, but the one parasite lineage that became established there was also able to switch to new hosts.

Variation in the relative prevalence of particular lineages of malaria parasites in different island populations of the same host species suggests independent host-parasite coevolution in each of the island populations (Fallon et al. 2003). The further observation that the total prevalence of all parasite lineages in a particular host is relatively constant suggests that these pathogens interact with one another, potentially indirectly through the host immune system.

Another aspect of invasion is that colonizing species might bring endemic pathogen populations with them, which might spread to the detriment of native species in the colonized areas, increasing the competitive ability of the invaders. This has certainly been the case with the European colonization of the New World (Diamond 1997). This model has many interesting implications for natural invasions and the structuring of natural communities. For example, invasion might be easier in remote islands because the few pathogens there cannot prevent the establishment of invading populations. Beyond this, the absence of pathogens might remove a block to the establishment of secondary sympatry within archipelagoes, facilitating evolutionary radiation of species (R. E. Ricklefs and E. Bermingham, unpublished data). Pathogens might also control the direction of invasion between continental regions and islands where islands are fairly close to the mainland. Invaders from more diverse communities might harbor more varied pathogens and present a formidable defense against new pathogens.

Range contraction: Decline and extinction of populations

The eventual fate of a species is to decline in numbers and distribution and eventually to disappear. Although extinction is accepted as a fact of life, just as mortality is the accepted fate of individuals, its causes are not well understood and may be quite diverse. In the case of non-native species, notable

declines have been brought about by the importation of natural enemies. Examples include myxoma virus in the case of the European rabbit introduced to Australia (Fenner and Ratcliffe 1965; Kerr and Best 1998), the cactus moth for the prickly pear cactus introduced to Australia (Dodd 1959), and chrysomelid beetles for Klamath weed introduced to western North America (Huffaker and Kennett 1959; Harris et al. 1969). In most cases, control agents have been effective in controlling populations at endemic levels, but rarely in causing extinction. Indeed, most invasive populations coexist with these control agents in their native ranges.

In recent times, humans have been the most effective agents of extinction in many regions. Relatively few cases of introduced species causing extinction of native island populations through competitive interactions have been reported (Sax et al. 2002; Davis 2003; Sax and Gaines 2003). However, many introduced species have greatly expanded their distributions at the expense of native populations, particularly in continental regions. Examples include the shrub *Miconia calvescens* on Pacific islands (Meyer and Florence 1996), the American crayfish in Europe (Lodge 2001), zebra mussels in North America (Martel et al. 2001; Nalepa et al. 2001), various fishes in North America (Miller et al. 1989), and gray squirrels in Great Britain (Usher et al. 1992). Most extinctions on islands are caused by human activity, either directly by hunting or indirectly by introduction of predators and pathogens. The lack of strong evidence for competition in such cases further undermines the idea that higher diversity or greater community “intactness” helps communities resist invasion. If this were so, then one would expect cases in which excess diversity and community saturation drive extinction to be more apparent.

In a detailed examination of extinction in the New Zealand avifauna, Duncan and Blackburn (2004) distinguished a “prehistoric” period of Maori colonization of the islands and a “historic” period of European colonization. During the first period, hunting of large species by native islanders and egg predation of small species by introduced Polynesian rats appear to have been the major factors in the disappearance of bird species. Later, after Europeans had introduced Norway rats, cats, and other highly effective mammalian predators, direct predation on adult birds, particularly flightless species, wiped out a different set of the native avifauna. Introduced birds were not a factor in prehistoric extinctions, and there is little evidence that they played a direct role in later extinctions through competition. Few introduced birds have penetrated native habitats. Extinction was also well under way in the Hawaiian avifauna before Europeans reached the islands (James and Olson 1991) and before the introduction of potentially competing species of birds. Historic population declines and extinctions in Hawaii can be related to the combined effects of hunting, introduced predators, introduced diseases, and habitat destruction, rather than competition from non-native species.

What characteristics make a species vulnerable or, alternatively, resistant to extinction? Are the same factors relevant in both natural and human-caused extinctions? All species present today are the living representatives of lineages

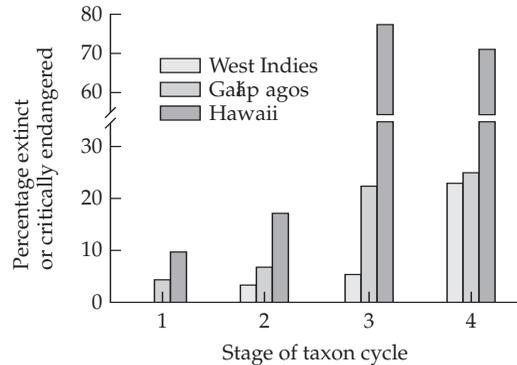
that have not gone extinct. And because these species represent the totality of contemporary diversity, it follows that all have features that resist extinction. Any morphological or physiological attribute that is shared among close relatives cannot be the cause of extinction of any species independently of the particular environment of that species. Thus, natural extinctions in the contemporary biota of the earth must be independent of most characteristics that we associate with their life histories and general ecological relationships.

Human-caused extinctions, and other mass extinction events, appear to be selective (e.g., Jablonski 1989, 1991; McKinney 1997; von Euler 2001), resulting from specific mortality agents whose effects are generally beyond the capacity of evolutionary response. Bolide impacts causing mass extinctions are the extreme example. Unless the normal fate of all species is not to become extinct, and extinction results primarily from catastrophic agents, human-caused extinctions can provide little insight into the natural decline of species. Clearly, however, the distributions and abundances of species vary tremendously, notably among closely related species, and this variation suggests a more dynamic aspect to the normal condition of life on earth. Many observers have commented on the vulnerability of large ground-dwelling animals to hunting by humans. Other attributes make certain island populations particularly vulnerable to introduced predators. Small population size is also seen as an important factor, although this might be like saying that old age is a factor in human mortality; that is, small populations may simply be the penultimate stage of a long decline.

The concept of the taxon cycle encompasses both expansion and decline toward extinction. Before species disappear, they are likely to exist as small populations with limited distributions. How they become so is the important issue. Ricklefs and Cox (1972) recognized stages of the taxon cycle in West Indian birds and devised a logical analysis for inferring both the relative ages of species in different stages, taking into account the fact that expansion phases could be initiated by declining taxa. The temporal sequence of the stages was confirmed by molecular phylogenetic analyses (Ricklefs and Bermingham 1999; Ricklefs and Bermingham 2002). Ricklefs and Cox (1978) had already shown that late-stage species, regardless of their taxonomic relationships or general ecological position, exhibited restricted habitat distributions centered on forested and montane habitats and were less abundant within occupied habitats than were early-stage species. Furthermore, individual island populations of species in later stages of the taxon cycle were more likely to have gone extinct during historic times or to be in a precarious position owing to hunting, introduced predators, habitat destruction, and other human-related causes (Figure 7.3).

This picture, which has been developed for a very limited sample of the earth's biota, suggests that the normal progression for invasive species is to decline and, in the extreme, to disappear. About the causes of this decline, and its reversal when new phases of expansion occur, I can do little more than speculate. I am reasonably certain that phases of expansion are short-lived and reflect transient periods of release from factors that limit populations under

Figure 7.3 Proportion of individual island populations that either became extinct since their scientific discovery or are in critical danger of extinction at present, as a function of their stage of the taxon cycle, in three archipelagoes. Taxon cycle stages, which represent increasing age in the West Indies (Ricklefs and Bermingham 1999), as defined by Ricklefs and Cox (1972), are (1) widespread and undifferentiated taxonomically; (2) widespread and differentiated; (3) differentiated with distributional gaps; (4) single-island endemics. (Data for the West Indies are from Ricklefs and Cox 1972; others are unpublished data from R. E. Ricklefs.)



normal circumstances. I am even more confident that subsequent decline takes place over evolutionary time spans—in the case of birds on islands, perhaps hundreds of thousands of generations. The lack of coincidence in taxon cycle stages among closely related species suggests that expansion and decline depend on the special relationship of each species to factors in its environment. These factors are most likely to be other specialized resources, consumers, or pathogens. The fact that small island populations persisted through major cycles of climate change in the Pleistocene suggests that such changes are not important and that populations adjust easily. Following a decline, extinction may depend on the colonization of an area by new predators, diseases, or competitors. Thus, species in late stages of the taxon cycle might persist for very long periods on isolated islands. The implication of this pattern for non-native species is that, once invasive species have become firmly established, it is unlikely that they will decline and disappear rapidly through restorative community processes. The responsibility for controlling invasive species would appear to lie with their initial benefactors—namely, us (Simberloff 2003).

Explicit Comparisons of the Taxon Cycle and Species Invasions: Reciprocal Insights and Predictions

The general attributes of human-assisted and natural invasions are compared in Table 7.2. All invasions are destined to pass through four distinct phases: (1) introduction or colonization, (2) establishment or naturalization, (3) geographic range expansion within the non-native area, and (4) eventual decline. Observations on natural range expansions and their eventual decline—a complete taxon cycle—suggest that phases 1 through 3 are relatively brief, at least in geologic and molecular-clock time, and that, once established, the decline stage may last for time spans recognizable only in the fossil record or through inference of evolutionary diversification within the expanded range. The complete revolution of the taxon cycle is most readily recognizable in island archipela-

TABLE 7.2 *General attributes of invasions aided by human activities compared to natural invasions*

Invasion stage	Human-assisted invasion	Natural invasions	
		Colonization-based	Expansion-based
Introduction or colonization	Intentional or accidental human-assisted introductions; highly dependent on introduction effort	Depends on ability to disperse across barriers and on population pressures that promote dispersal; haphazard introductions	Dispersal ability generally not a factor, as this type of invasion involves expansion into adjacent habitats
Establishment or naturalization	Requires a suitable environment; environment often anthropogenic, generally within the range of conditions in the native area	Less of a consideration because these invasions usually involve nearby areas having similar conditions	Not a factor, as the initial stage is an established population
Geographic range expansion	Must be able to fit into the competitive and pathogenic environment; evolutionary adjustment may play a role	Presumably the same criteria of ecological compatibility apply to both colonization-based and expansion-based natural invasions; evolutionary adjustment to new environments may be important in both cases (see Cox 2004)	
Eventual decline	Rarely a consideration; generally not observed without substantial human intervention	Over evolutionary time, taxa eventually decline ecologically and withdraw from invaded habitats or become extinct in colonized areas; this phase most apparent in island systems	

goes, in which distribution is partitioned into discrete island units, history reveals itself through genetic divergence between island populations, and decline is apparent as gaps in the distribution of a species across islands.

Typically, studies of human-assisted species invasions address the first three stages of this process, particularly establishment and geographic range expansion. Nevertheless, relatively little is known about colonization—the rain of propagules that arrive in areas and soon disappear without becoming established. The transience of this stage of the taxon cycle makes it difficult to observe, except in the case of intentional human introductions (e.g., Duncan 1997). At the other end of the cycle, except in the case of obvious habitat change or human control programs, declining phases are rarely observed in human-assisted invasions. Once established, populations are difficult to get rid of, and left on their own they tend to persist for evolutionary time spans.

Early stages of colonization and establishment often include periods of rapid evolutionary adaptation to local conditions and in response to interactions with local species (Cox 2004). This adaptation process may account for a lag time between the first establishment of a population and its subsequent expansion to occupy a substantial part of its adopted region. Why some species expand in their non-native ranges and others do not is an open question. Ecologists

have not reached a consensus concerning the general attributes that make a species a good invader. Those species that eventually do expand their ranges following establishment are thought to benefit from leaving behind in their native ranges consumers and pathogens that could otherwise keep their populations in check. This demographic release is thought to be a factor in natural invasions as well. Indeed, it is my belief that the acquisition of natural genetic resistance to one or more significant predators, parasites, or pathogens provides the initiation for new phases of expansion.

The decline phase of the taxon cycle under natural conditions may require substantial time for evolutionary adjustment of native populations to the new invader or for the arrival of new competitors as colonists from elsewhere (Wilson 1961; Ricklefs and Cox 1972). Thus, it is unlikely that recently established non-native species will provide insights into the historical decline of natural populations, or that inferences about these declines from the fossil record or molecular phylogeographic analysis will enlighten us about the fates of recently established non-natives or the control of those non-native populations that we would like to be rid of. Nevertheless, natural and human-assisted invasions can inform each other in a number of ways.

Perhaps the most important insights to be gained will come from continuing studies of the attributes of species that determine naturalization success and expansion within non-native areas. Considering that closely related species vary tremendously in this regard, as well as in range size and ecological distribution within their native areas, success may depend on subtle genetic factors, possibly associated with herbivore or disease resistance or with direct competitive abilities (e.g., Callaway and Aschehoug 2000; Callaway et al. 2001, 2004).

In many cases of human-assisted invasions, particularly intentional introductions, dispersal ability is not a critical factor for initial establishment, and colonization can occur over global distances to regions greatly isolated in evolutionary time. With intentional introductions, population bottlenecks are less frequent, and genetic diversity is maintained in the colonizing population (see Wares et al., this volume). Indeed, multiple introductions from different parts of a species' natural range might lead to increased genetic variation in local non-native populations, as in the case of the brown anole (*Anolis sagrei*), introduced to Florida from several locations in Cuba and the Bahamas (Kolbe et al. 2004; see also Novak and Mack, this volume). In bypassing adaptations required for long-distance dispersal, such colonists might be in a position to take advantage of traits that enhance their competitive ability in diverse communities. Cody and Overton (1996) demonstrated rapid loss of dispersal ability in several weedy plants that colonized islands in Barkley Sound, British Columbia, suggesting that light, wind-dispersed seeds, which are essential for dispersing to disturbed habitats, are impediments to persistence on small offshore islands.

Whether a general trade-off between dispersal and competitive ability is a general feature of invasion biology, as it seems to be for "supertramp" species of birds in Melanesia (Diamond 1975), may depend on the remoteness of the destination. However, for the rare colonists to Hawaii and other similarly iso-

lated spots, competitive ability might not be a critical attribute early in the development of the island fauna. In general, however, one expects a decline in long-distance dispersal ability, including the loss of flight in insects and birds, following colonization of remote sites (Darlington 1943; Carlquist 1974). To the extent that humans introduce species that otherwise lack the capacity for long-distance dispersal, they short-circuit this natural phase of the taxon cycle and potentially increase the probability of establishment and expansion.

The contributions of human-assisted introductions to our understanding of the initial phases of the taxon cycle lie in the large sample sizes available for comparative analyses, the experimental manipulations of introduction effort and the conditions in receiving environments that can be performed, and the detailed historical records of the establishment and spread of introduced populations. Studying the fates of naturally expanding and contracting populations emphasizes the importance of evolved interactions of species with other populations, including competitors, predators, and pathogens, in determining distribution and abundance. The long persistence times of established natural populations suggest that individuals can tolerate broad ranges of physical (climatic) conditions and that coevolutionary relationships tend to strike long-term balances. The implication for the control of invasive species is that their populations will not tend to dwindle of their own accord; rather, their control will often require substantial human intervention.

Conclusions and Suggestions for Future Work

Easily measured attributes of species are unlikely to predict relative invasion success beyond broad generalizations. Success or failure is more likely to depend on finer adjustments to environmental conditions or with respect to relations with predators, pathogens, and perhaps mutualists and competitors. These relationships reveal themselves in the ecological and geographic distributions of species within their native areas, and possibly also in their relative abundances within their natural ranges. The two are often correlated (Bock and Ricklefs 1983; Brown 1984; Brown 1995; Blackburn and Gaston 2001). Most introductions involve species that are common and widespread in their native ranges, and thus the correlation of invasion success with native distribution might not be adequately quantified. However, although many naturally rare and localized species have been successful in horticulture or captive propagation (for example, *Metasequoia*, *Ginkgo*, *Franklinia*), such species do not often become invasive. Nonetheless, a more systematic examination of the relationship between invasion success and distribution within the native range would provide useful indications of the types of factors that are likely to influence invasion success (e.g., Duncan et al. 1999). Factors responsible for variation in native ranges are also an important open question for ecological research.

Certainly, physiological tolerance ranges must have some bearing on the location of a population's center of abundance and in some cases the condi-

tions within which a population can maintain itself. However, because common and rare species within the same lineages often live side by side in some environments, physiological tolerance is not likely to provide the entire answer to distribution.

To the extent that variations in range size and ecological distribution reflect coevolved relationships with predators, pathogens, and perhaps resource populations, ecologists will have to undertake detailed experimental studies on, for example, host-pathogen and host-parasite relationships to evaluate the effects of these factors. In addition, these studies will have to be carried out within the context of community ecology, rather than the more typical perspective of population interactions in narrowly circumscribed systems. One can imagine broadly comparative studies of experimental infection or parasitism involving both common and rare (hence logistically challenging) host species. Considering the nature of this work, invertebrates will perhaps be more felicitous subjects than vertebrates, and plants more than animals. The simple prediction is that common and widespread species not only should exhibit lower intensities of infections and infestations, but also should resist infection better than narrowly distributed host species. Common species might also be expected to harbor fewer specialized parasites and pathogens that can circumvent the main host defenses. Understanding the mechanisms by which resistance is achieved would indicate the kinds of evolutionary adjustments that are responsible for variation in distribution and abundance.

The history of these evolutionary adjustments, or at least their effects on abundance and distribution, might be appreciated in some cases by tracing character change over phylogenetic trees. Of course, extremely labile characters responsible for variation in distribution would not exhibit a recognizable history of change on the scale of phylogenetic relationships of species or higher taxa, because such characters would change within terminal branches. Nonetheless, to the extent that the distributions of smaller, population-level units could be characterized within species, phylogenetic analysis might provide a picture of infraspecific evolution. Within the Lesser Antilles, for example, populations of some species on different islands vary widely in both habitat distribution and abundance.

At a larger scale, ecologists could use historical-phylogenetic analyses of the development of island and continental biotas to gain insights into community assembly (Ricklefs 2002, 2004c; Webb et al. 2002; Ackerly 2003; Cavender-Bares and Wilczek 2003). Such longer-term processes, which must involve evolutionary adjustments of ecological distributions that govern competition and other relationships, would not be closely related to expansion and contraction phases in the context of taxon cycles. They might, however, indicate prerequisites for species to fit into established ecological assemblages. Discrete islands or habitat continua would provide suitable contexts for investigating these processes. Contemporary assemblages of species on an island or at a point along a continuum have a history of assembly (Ricklefs and Bermingham 2001; Ricklefs 2004b) that might involve the nonrandom accumulation of species over time

or the nonrandom selection of colonists from a potential pool (Terborgh et al. 1978; Weiher et al. 1998; Weiher and Keddy 1999). The autochthonous buildup of diversity within a region through adaptive radiation might also require predictable adjustments of morphology and behavior before reproductively isolated sister populations can tolerate secondary sympatry. Aspects of genetic incompatibility have been discussed (e.g., Coyne and Orr 1997), but ecological compatibility has received less attention (see, however, Schluter 2000).

Taxon cycles represent one point along a continuum of phenomena that involve evolutionary adjustment of ecological relationships, and they reflect the balance of these relationships in the demography of populations. The success or failure of non-native species introduced to new areas presumably also depends on the kinds of attributes that control distribution and abundance in native species. Thus, it is likely that studies of each kind of phenomenon will benefit from keeping the other in mind.

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