

The ecology of extinction

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Studies of species-area curves and of the spatial correlation of biogeographic ranges with climatic variables may allow some crude prediction of amount of extinction over large regions in the face of major environmental change. However, these approaches tell little about the proximate causes of species loss. The contention that failure of metapopulation dynamics is at the root of many species extinctions is so far not borne out by observed rates of inter-population movement. Rather, most species that have a metapopulation structure seem to have central source populations and peripheral sink populations. Much of the extinction recorded in the ecological literature is probably of such peripheral populations and their loss has little to do with species extinctions. The disappearance of central, source populations is more important but its causes are not well documented. Habitat loss is the single greatest ultimate cause of current extinction. However, disappearance of the very last individuals of the last population of a species may not be obviously related to habitat loss. Rather, it may seem mysterious, because the last individuals will look healthy, or it may seem attributable to one of the stochastic forces widely assumed to set minimum viable population sizes.

Key words: biogeographic range, body size, extinction, metapopulation, minimum viable population size, species-area curve

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Are there ecological reasons for extinction?

Raup (1991) argues that virtually all geological mass extinctions, not only the one at the end of the Cretaceous, were caused by meteorite impacts. From the images that spring up in the mind's eye of a huge meteorite striking the earth, one could easily conclude that there really is no ecology that separates survivors of such impacts from species that are extinguished. It is just a matter of luck – who happens to be in the wrong place at the wrong time.

Or are there biological reasons why most of the survivors are winners and most of the extinct species are losers? Raup (1991) finds evidence for this possibility to be very weak. He admits that some large taxonomic groups seem to have survived mass extinction events better than others, and that this tendency probably has to do with biological characteristics of species in those groups, but that is as far as he goes. Most people who have delved further have focussed on either body size or geographic range.

For body size, it has been claimed for both the Cretaceous mass extinction (e.g. LaBarbera 1986) and some individual extinctions occurring recently (e.g. Pimm *et al.* 1988) that large body size is correlated with high extinction probability. It is not that body size *per se* is thought to place a species at risk, but that it might be correlated with various life history features, like relatively low reproductive rate or low density, that predispose a species to be extinction-prone. For geographic range, the idea is that large geographic range helps a species avoid extinction, simply by making it more likely that part of its range is far away from whatever events cause the extinction (e.g. Hoffman & Szubdzia-Studencka 1982; Martinell & Hoffman 1983; Jablonski 1986), or that *a* species' range might just happen to constitute a refuge, even if the range is small, because it happens to be far away from the events that cause extinction (Vermeij 1986). Both of these claimed correlates of resistance to extinction have been criticized (e.g. Tracy & George 1993), and, in any event, neither would tell us very much about the causes of population extinctions occurring today or suggest ways to prevent them.

The species-area curve and other large-scale biogeographic approaches

The tremendous attention focussed on extinction nowadays, motivated by the prospect of an imminent or already begun mass extinction generated by habitat destruction like the clearing of tropical moist forest, seems to approach the problem from two very different directions. On the one hand, one can look at the situation globally and try to think about global rates of species-extinction that one might expect given global rates of environmental habitat change. For example, I have considered what species-area relationships tell us about current and future extinctions (Simberloff 1986a). Given current rates of destruction of moist neotropical forest, and the fact that only about 1.5% of the habitat is set aside as reserves, I suggested that, if current rates of destruction continue and if typical species-area relationships hold, at some time in the next century, the stage will be set for a loss of about 2/3 of all plant and bird species. There is no theory or even good empirical basis for saying how long the extinctions will take, but if species richness of birds and plants in these remaining islands of habitat conforms to typical species-area relationships (e.g. $S = cA^z$, where S = number of species, c is a constant, and z is approximately 0.26),

this would be the rough magnitude of the loss we could expect over at most a few centuries.

As another example of global or large-scale regional predictions of species extinction, numerous authors have recently attempted to map species biogeographic ranges, relate them to isopleths of temperature, then predict what will happen to the ranges as global warming proceeds (e.g. Schwartz 1993, and references therein).

But there are limits to how far one can take such approaches. For species-area curves, some researchers have argued that the forces that determine species-area relationships of very large areas like continents or even 1/100 of a continent differ from those that determine species-area curves for small or medium-sized areas like islands and quadrats. The latter comprise most of the empirical basis for the use of species-area curves for prediction (Kangas 1987). In other words, just the fact that islands conform to $S = cA^z$ needn't mean that one can extrapolate the relationship to continents. For the global warming example, it has been argued that range limits are not usually set simply by temperature (e.g. Hengeveld 1990).

A very common complaint is that it matters a lot exactly which sites would be left, since all areas of the same size do not have the same richness. For example, Jablonski & Flessa (1986; cf. Jablonski 1986) have effectively argued that a species-area relationship is an insufficient explanation for the Permo-Triassic mass extinction because, if one looks at the distribution of marine families, a disproportionate fraction of them are found in the shallow water around oceanic islands. Thus, even if one eliminated all continental shelves, it still would not eliminate the habitat of all species in most families (but see Paulay 1990). Many people have argued similarly that one can forestall many of the extinctions predicted from species-area relationships in moist tropical forest by saving particular 'hot-spots' of very high species richness (e.g. Myers 1990).

Probably the biggest problem with using our knowledge of species-area relationships to predict extinction is that if, in spite of our arguments and efforts, habitat continues to be destroyed, we not only cannot predict very precisely how many extinctions there will be and when they will occur, but the species-area relationship tells us nothing about how to prevent some of these extinctions. That is because the species-area relationship is agnostic about the cause of extinctions. It is a rough empirical guide, not a deductive law. Several forces singly or together might cause species to be extinguished with loss of area, and the species-area relationship does not show us which ones are acting to what extent. So of course it cannot tell us what to do to counteract these forces. Nor does the relation of species' ranges to temperature isopleths suggest how one might stem extinction in the face of global warming. An approximate correlation of a range limit with an isopleth does not, by itself, reveal exactly what physiological responses prevent a species from persisting beyond this isopleth (Piggott 1970; Jablonski *et al.* 1985; Carter & Prince 1988).

Local population extinction and its relationship to species extinction

Because of these shortcomings in the use of the species-area relationship and other large-scale approaches, many ecologists have lately focussed their attention much more narrowly, on the extinction of particular populations rather than of entire species, to try to gain insight into the extinction of entire species. This approach is far afield from the normal ambit of paleobiologists and has led to a separation of the paleobiological and neobiological literatures on extinction. It has also led to confusion about the meaning of the word 'extinction'.

A lot of population extinction must go on continually at the margins of species ranges (Williamson 1989). Biogeographers and paleobiologists have not usually referred to such range changes as 'extinction', but lately some do (e.g. Hengeveld 1990). People who considered the phenomenon of range changes at all, and it was until quite recently a rather arcane branch of biogeography, seemed not to conceive of them as population extinction or establishment, but rather as simply contraction or expansion within a population. Of course, without detailed information on which individuals move where and who mates with whom, it is impossible to determine whether these peripheral isolates are parts of a big population, independent populations themselves, or parts of a 'metapopulation', a concept I will discuss in the next section.

Almost certainly many of these peripheral isolates qualify as 'populations' by any traditional definition of 'population'. In a classic study of the distribution of *Clematis fremontii* var. *riehlii* (Erickson 1945), at a high resolution of the mapping, 'colonies' occupying 'glades', some glades are so isolated from other glades that gene flow by either immigration or pollen transfer must be very rare. The same is true of the highest level of resolution, 'aggregation'. Now, Erickson did not map any part of this biogeographic range periodically for an extended time, but, if he had, I am certain he would have found it changing from generation to generation. Anyone who works with species in the field knows that published range maps, including those that are dots in map squares, are a caricature of a dynamic entity with the dynamism and most of the detail omitted.

For example, for years I have sporadically sought red mangrove, *Rhizophora mangle*, on the Gulf Coast of Florida. I knew at the outset the range is dynamic not only from having seen entire mangrove forests killed by hurricanes, but because I found recent large herbarium specimens from sites many kilometers from any known *Rhizophora* I was excited in 1970 to find what I assumed to be the northernmost Florida population of red mangrove at Cedar Key (29° 10' N), consisting of three individuals, two of which were producing seedlings. After many hours searching, I was convinced there were no other *Rhizophora* within many kilometers. Of course, only 100 km south, there are several small, dense mangrove swamps. Further north I searched many coastal areas and found no

Rhizophom. This situation persisted until at least 1980. In 1986 I found two *Rhizophora*, one of which was producing seedlings, in a remote site about 60 km north of Cedar Key. I am certain there were no others within 2 km. And in 1988, these two individuals were gone. In other words, the boundary of the range of this species was changing by virtue of population extinction and initiation.

This dynamism must typify many species, but this process is rarely studied. Rapid range expansions, including disjunctions, are sometimes published, but contractions are less frequently published, and the details of the disappearance of peripheral populations almost never. There is not even much research on the exact reasons why ranges terminate where they do, which would have to be understood in order to understand why the boundaries shift. Good studies are very rare, and usually entail both laboratory tests and experimental transplant outside the existing range. For example, Neilson & Wullstein (1983) asked exactly why the range of Gambel's oak (*Quercus gambelii*) stops where it does in the American West. The northern limit is set by seedling mortality caused by spring freezing and summer drought, with a patchwork of suitable microsites getting sparser and sparser as one moves north, until they are so sparse that they are rarely or never colonized. Given the vicissitudes of summer drought and spring freezing, it is obvious that these peripheral populations go extinct every so often.

Carter & Prince (1985), Prince & Carter (1985), and Prince *et al.* (1985) studied the range limit in Britain of prickly lettuce (*Lactuca scariola*) with some surprising results – the species does not get progressively rarer towards the range limit, nor does plant vigor decrease. Instead there is a rather sharp boundary, with plants appearing healthy right up to it and completely absent beyond it. There is no obvious single climatic correlate of this boundary. They depict a situation much like that with *Clematis*. Though there are no data on gene flow or other interactions, they view British *Lactuca* as a metapopulation of more or less distinct populations. They interpret the sudden range limit in terms of an epidemiological model for fugitive species in which a very small decline in suitability of the environment, probably caused by many factors acting in concert, can produce a distributional boundary that is much sharper than the environmental gradients that cause it (Carter & Prince 1981, 1988). They conceive of this phenomenon as one of populations going extinct or starting, and data from one area show a big range expansion consisting of new populations in 1977, followed for several years by range contraction consisting of disappearance of populations.

Whether this situation would obtain or this model apply to other species is not known. But red mangrove is not a fugitive species and I have just described some rather similar observations for this species. Both of these situations seem to me to approximate the metapopulation model of Boorman & Levitt (1973), with a large central population that never goes extinct surrounded by a bunch of small ephemeral populations. Pulliam (1988;

cf. Pulliam & Danielson 1991) describe a very similar model in which a 'source' part of the population provides most or all recruitment to other parts of the population, denoted 'sinks'. He conceives of these dynamics as within-population and the habitat as key to whether an area and its associated individuals constitute a source or a sink. As will be discussed in the following section, the designation of these dynamics as within-population or metapopulation is quite arbitrary. In any event, the only real difference between the red mangrove and prickly lettuce situations and the Boorman-Levitt model is that the large central population might itself comprise many more or less distinct populations. But the important point would still be that these central populations do not go extinct, or do so at a much, much lower rate than the peripheral ones. One might even ask if the processes that cause occasional extinction of a peripheral population are the same ones that would threaten central populations. It is still an unanswered question, in spite of dogmatic statements to the contrary in some conservation biology literature (e.g. Noss 1993), whether substantial immigration into central populations is important for their persistence.

Whatever the significance of this extinction of peripheral populations, quotes of extinction rates citing this phenomenon can be very misleading in terms of the threat of species extinction. There is a related way in which ecologists sometimes inflate extinction rates. With increasing interest in introduced species and the colonization process in general, there is a growing tendency not to distinguish between propagules that never 'take' and populations that did increase initially, but then disappeared. Many times, the former are tallied into extinction rates; I have probably done this myself at times when talking about disappearance of species from small mangrove islands. It would be very difficult to prove, but almost certainly the great majority of propagules that land either within or outside the range of any species die without reproducing. This is almost certainly the fate of most propagules deliberately or inadvertently introduced far from their normal ranges. The disappearance of propagules can be called 'local extinction', but its causes may not be closely related to those causing the disappearance of existing, reproducing peripheral populations, and are certainly not closely related to the disappearance of species.

Williamson (1989) suggests that many classic published examples of 'extinction' of populations on mountaintop islands as ranges retracted with Pleistocene climate change might not have been extinctions at all, because the species might not have been maintaining populations there in the first place. Another possibility is that these populations were sinks, maintained not by recruitment from within the site but by frequent dispersal from elsewhere, and these populations thus did not contribute to the regional persistence of the species.

Metapopulations as a hedge against extinction

There is intense interest in metapopulation structure as a hedge against extinction nowadays; several models are reviewed by Hanski & Gilpin (1991). The result of all these models is very straightforward. Single populations that would not persist, or pairs of populations that could not coexist, in one large population might do so, given the right parameters, in a metapopulation of populations. Levins (1969) modeled this situation and coined the term 'metapopulation', though other work like that of Andrewartha & Birch (1954) suggested the same phenomenon even earlier. In the conservation literature, metapopulations are usually presented as an alternative to equilibrium island biogeographic models and have largely replaced the latter (Merriam 1991). Some authors go so far as to say simply that most species are distributed as metapopulations (e.g. Carter & Prince 1988; Wilson 1992; Noss 1993). But is this true?

Hanski & Gilpin (1991) formally define a metapopulation as an ensemble of interacting populations, each with a finite lifetime, and a population as an ensemble of interacting individuals. The key is obviously the definition of 'interacting' – how much, and what kind of interaction? They suggest that individuals that interact with one another in the course of routine feeding and breeding constitute the local population, whereas the metapopulation comprises populations united by infrequent movement of individuals from one population to another, typically across unsuitable habitat. So the key now becomes the definition of 'infrequent'. The problem is that this last definition of a metapopulation is very close to a popular definition of species, namely an interbreeding or potentially interbreeding group of populations. Are there many species that are not, by definition, metapopulations? Some ecologists apparently think not – they view any set of individuals that shows aggregation at any spatial scale as a metapopulation. But **all** species show aggregation at some scale.

Harrison (1991) recently clarified this matter greatly. She pointed out that the essence of the metapopulation concept, from the standpoint of persistence and extinction, is whether regional persistence of the species is maintained in the face of occasional local extinction of each discrete population by recolonization from existing populations. She then scanned the literature on local extinction and found very few examples that accord with this model. Two situations were most common. One was the situation I described in the preceding section – small peripheral populations that do occasionally go extinct and are re-established by colonization from larger populations that are effectively immortal. So the prevention of species extinction in this case has nothing to do with the ongoing redressing of local population extinction. Bahamian orb-weaving spiders fall into this category [Schoener & Spiller 1987]. So apparently do many butterflies (Harrison 1991).

The second common situation she found was species with aggregated distributions, but with dispersal among the aggregates so frequent that

the entire system is effectively one extinction-resistant population. Of course there is no sharp distinction between metapopulations with true local extinction and aggregated populations in which the aggregations shift. But, as Harrison indicated, if individuals typically inhabit more than one patch in their lifetimes, one would have to strain to call the system a metapopulation. Very many of the classic cases pointed to in the conservation literature as validating the metapopulation model may fall in this category.

The misappropriation of the term 'metapopulation', and the dynamics that it implies, has already led to questionable management recommendations. For example, consider the study of risk of extinction by Pimm *et al.* (1988) based on annual censuses of breeding birds on small islands off the coast of Britain. This research has already been used as part of the basis for the recovery plan of the northern spotted owl in the United States and suggested as a guide to the mechanics of introduction or reintroduction plans for endangered birds on the small islands of New Zealand. This study has been criticized on many grounds (Tracy & George 1993), but I think the key problem was raised by Haila & Hanski (1993) – the data are not about extinction at all, but about spatial shifts in aggregation within large populations. Actually, Smith (1975) anticipated this criticism in his presidential address to the Ecological Society of America. He pointed out that he could census an apple tree in his backyard, each time tabulating the bird species present. The list would change, and one could call these changes 'extinction' and 'immigration', but this terminology would not elucidate either the occupation of his tree by birds or the processes of extinction and immigration.

A third sort of situation that Harrison found in the literature, although again not conforming to the metapopulation model, is perhaps more germane to extinction as an ecological process and as a conservation concern. This was regional decline of a species, usually in the context of long-term habitat change entailing fragmentation. The most famous example she cited is Brown's depiction of a series of extinctions of mountain populations of mammals caused by reduction and isolation of mountaintop habitats during post-Pleistocene warming (Brown 1971). The key is that the decline of the species does entail the apparent 'winking out' of isolated populations, but these local extinctions are not usually redressed by recolonization; it is a non-equilibrium situation leading to the regional extinction of the entire species. As noted in the preceding section, Williamson (1989) suggests that many of these abandoned sites never supported ongoing populations to begin with, but even if they had [and some fossil evidence (e.g. Grayson 1987; Harris 1990) argues in favor of the hypothesis], the fact that some of the loss is of isolated, distinct populations is irrelevant to understanding why the loss is happening or what had maintained the species before the loss.

In fact, it is likely that the aggregated nature of all species, whether caused by habitat heterogeneity or any other forces, would lead any

gradual species extinction to appear, at some point during the process, as a metapopulation process. If we discount the sudden elimination of all individuals by a catastrophe like a meteorite or a hurricane, the typical extinction probably entails the disappearance of some aggregates rather than others.

A good example is the scops owl, *Otus scops*, a small bird that used to be ubiquitous in south and central Europe, extending all the way to Asia. Since the 1950s, everywhere throughout its range, it is declining, and in some places it has disappeared. Arlettaz (1990; cf. Arlettaz et al. 1991) seems to be the only one studying this decline in great detail, and he is studying it in only part of its range, Switzerland. Until the 1950s, this owl was quite common in many parts of Switzerland, with five major more or less discrete aggregations; how much movement there was among them is unknown. Now they remain only in the southwest, in the upper part of the Rhone valley in the canton of Valais. The nearest remaining populations in France and Italy are far away and rapidly declining themselves.

No one knows exactly how many owls there were in 1950, but it must have been at least a few hundred, spread throughout the valley. By 1986 there were only 22 pairs, by 1988 only 16–19 pairs. Two things happened. First, until recently there was simply increasing loss of peripheral individuals, some of which probably constituted populations. But for most of this time, there was not a decrease in density in the center of the range. In 1982 there were six occupied areas that probably constituted populations, spread out over about 26 km; the largest population was in the middle. By 1985, the two westernmost and one easternmost populations had disappeared, leaving three. By 1988, only the central one of these was left. And, beginning about five years ago, this central one began to decline.

The first part of the decline, beginning in the 1950s, is not very mysterious. There was a major intensification of agriculture, primarily a doubling of the amount of vineyards, at the expense of the farms, open woodland, and oak groves inhabited by the scops owl. As the vineyards ascended the sides of the mountains, the scops owl retreated, until it is no longer found below about 840 m, which happens to be the upper limit of the vineyards. It cannot survive in the pine forests above 1200 m, so it is now in a narrow band. Worse, it does not favor steep slopes. The last, declining population is in the single site that one would have said has the best habitat, from previous studies of habitat requirements.

But the decline in this last site, and the disappearance from the five sites near it, is not wholly explained by agricultural change, because in this one region the habitat has not been changed as much. It could well be that the five extinction sites were simply sinks in a Boorman-Levitt type metapopulation, whose local populations were continually replenished by the central population which no longer produces individuals. If this were so, the failure of metapopulation dynamics with the loss of individuals from the five nearby sites would be irrelevant to the decline of the last, central population. The decline in the central population is the most

puzzling. Arlettaz (personal communication 1993) thinks it is simply a case of recruitment falling to a point where it does not redress mortality, but exactly why recruitment has fallen, if it has, is not known. This certainly looks like a paradigmatic example of a minimum viable population size (Shaffer 1981; Simberloff 1988), but it will probably be impossible to determine why populations below this minimum cannot persist before the population goes extinct.

There is one fly in the ointment. Probably the fact that the scops owl has declined everywhere is due to intensified and changed agriculture everywhere, but one cannot discount the possibility that increased desertification of the Sahel, its overwintering area, plays a role. However, at least for the Swiss population, no matter what happened in the Sahel, this owl was doomed by habitat destruction.

So what is causing extinction of species nowadays?

Several tabulations recently of the known causes of contemporary extinction for various taxa are unanimous in agreeing that virtually all of it is caused by humans, and that, of the human agencies causing extinction, habitat modification is by far the most common, though hunting and the effects of introduced species are both important contributors (Ziswiler 1967; Fitter 1968; Ehrlich & Ehrlich 1981; Atkinson 1989; Johnson & Stattersfield 1990). One extinction may produce others by removing a key resource. The loss of American chestnut (*Castanea dentata*) to introduced chestnut blight (*Cryphonectria parasitica*) extinguished or endangered several host-specific insects (Opler 1979). Such cascades of extinction are probably common but are rarely studied intensively.

The recent focus of paleobiologists on both mass extinction and impacts as their likely cause (e.g. Raup 1991) has tended to cause ecologists not to pay much attention to the paleobiological literature on extinction. Similarly, paleobiologists view lists of causes of current extinction as not too relevant to their concerns. Most of the current examples are of birds and plants, rather than of marine invertebrates, and many are of populations or subspecies, so would not easily have been detected if one had been forced to depend on the fossil record. However, it seems possible that greater attention by paleobiologists and marine ecologists to local disappearance might inform the ecological literature and effect a rapprochement.

I think it is important to recognize that, except when all individuals of a species are simultaneously eliminated, as by a meteor or a hurricane, extinction is a multi-stage process (Simberloff 1986b). For example, lists of causes of extinction have the eastern subspecies of the heath hen (*Tympanuchus cupido cupido*) as having been eliminated in 1932 from the United States because of habitat alteration by humans plus hunting, but the story is more complicated (Bent 1932; Simberloff 1986b). Hunting and

habitat alteration in the heath hen's range stopped years before 1932. Originally heath hens were found from Maine south to Virginia and were common on sandy scrub-oak plains. They were hunted out of Connecticut and mainland Massachusetts by 1850. A few persisted in Long Island, New Jersey, and the foothills of the Pocono Mountains of Pennsylvania, but by 1870 the last heath hens were restricted to Martha's Vineyard, an island off southeastern Massachusetts. By 1890 there were 200 birds left; by 1896, fewer than 100 survived.

Extinction would have followed quickly except for the establishment in 1908 of a refuge of 700 ha for the last 50 birds. The refuge habitat was improved and by 1915 the population was estimated at 2,000. Then came a series of disasters that ended in extinction. In spite of precautions, a fire during a gale in 1916 swept through the breeding area. A hard winter followed, punctuated by an unprecedented flight of goshawks, and the population was reduced to fewer than 150, mostly males. A slight rally occurred during the next few years, but extensive inbreeding appeared to be accompanied by a decline in sexual vigor and a persistent great excess of males. Worst of all, in 1920 a disease of domestic poultry killed many heath hens. By 1927 there were only 13 birds, of which 11 were males. In 1928 only two birds were left, and the last one was last sighted on March 11, 1932. Many bird-watchers travelled to Martha's Vineyard to see the last heath hen.

In other words, even with habitat deterioration redressed and hunting virtually stopped, several forces conspired to extinguish the heath hen. One can say that the ultimate cause of death was human activity, but eventually extinction was assured even if direct human activity stopped. It is exactly like assigning death in some human diseases. The cause of many cancer deaths is listed on death certificates as 'congestive heart failure', but the patient was doomed by the cancer.

Soulé (1983) has argued that the proximate causes of extinction are not very important: 'The extinction problem has little to do with the death rattle of the final actor. The curtain in the last act is but a punctuation mark – it is not interesting in itself. What biologists want to know about is the process of decline in range and numbers'. In a sense, he is correct. The literature on minimum viable population sizes (e.g. Shaffer 1981; Simberloff 1988) suggests that several forces – environmental events, demographic stochasticity, various behavioral problems, and genetic stochasticity – **all** conspire to place very small populations at disproportionately great risks. For the heath hen, there are at least hints that all of these forces came into play (Simberloff 1986b). So there is no doubt that, if we are going to be left with entire species consisting of single, rather small populations in single refuges, we are going to lose many of them.

Unfortunately, I think we have to accept that this is going to happen even if we argue as forcefully as we can against it, and we should study the proximate causes as we fight the ultimate causes. There are two reasons. First, we are losing the war to save many large reserves, even

though we are winning some good battles. In many regions, like most of Europe, the war is already lost. We should keep fighting, but we are derelict if we ignore the likelihood that, at least for now, we cannot make conservation a high enough priority to stop the habitat destruction. Second, even though it is much harder to save small populations, it is not always impossible. The clearest evidence of this is that many species and subspecies, even of vertebrates, are endemic to tiny islands and probably never had more than a few hundreds or even a few tens of individuals in their entire history, yet have persisted long enough to have evolved into distinct taxa and would probably not be considered tremendously threatened were it not for human activity (e.g. Walter 1990). Most of these, of course, are threatened now, but that is always because their populations have been even further reduced by human activity (Johnson & Stattersfield 1990).

Above I argued that the local extinctions of populations at the edge of a species range were not usually likely to tell us much about the reasons for the extinction of entire species, except perhaps in the case of range contraction generated by global warming. But I believe that, nevertheless, from a conservation standpoint, it behooves us to study these small populations carefully to see exactly why they are declining, if they are declining, if we are to have any hope at all of saving them, at least temporarily, until humankind comes to its senses and we can have broadscale habitat restoration.

One good example is the Puerto Rican parrot (*Amazona vittata*). Until Hurricane Hugo struck in 1989, there were about 50 individuals in the wild, all restricted to one forest that happened to be hit by the hurricane, and another 50 in captivity. The hurricane killed about half the wild birds. Plans had been afoot to re-establish a second population. But intensive study of the last population had already led to a big advance that had, until the hurricane, stabilized the situation and led to an increase from the low of 13 individuals in 1975. This was the discovery that nest predation and nest competition by the pearly-eyed thrasher (*Margarops fuscatus*) were crucial, and the development of nest modifications and nest boxes that the parrot would tolerate and the thrasher would not, plus nest boxes that the thrasher would use (Snyder *et al.* 1987). Each thrasher pair established near a parrot nest excludes other thrashers from the vicinity because these birds are highly territorial. This research, though seemingly mundane, single-species natural history in an age that prizes overarching theory, could be very consequential because other endangered West Indian parrots are also affected by the thrasher.

Of course, any species restricted to a single population at one small site is greatly endangered by major catastrophes like cyclones. The only known recent extinction of a bird by hurricanes is that of a bullfinch subspecies (*Loxigilla portoricensis grandis*) restricted to the small island of St. Kitts (Raffaele 1977), but other species have come close (cf. Simberloff 1986b, 1988), and tiny single populations of species endemic to sites in cyclone

belts, such as several birds of the Mascarenes (Simberloff 1992), must be at great risk. In one sense, one could attribute extinctions by this route to a failure of metapopulation dynamics – there is no second population to provide new colonists. However, the original maintenance of the species need not have entailed occasional recolonization following occasional local extinction.

Finally, it is well to bear in mind, with respect to any declining species, that the fact that some individuals at a site seem healthy and reproduce does not mean the population can persist even in the absence of idiosyncratic catastrophes like cyclones. For a species to dwindle to extinction, or to fail to colonize an area even where propagules continually land, it suffices that the average rate of reproduction be only slightly less than the average rate of mortality, the average taken over generations. Thus, many populations, including the last populations of some species, might be superficially healthy but among the living dead. It could be that range contractions generated by global warming will seem mysterious for this reason. If we are to know why remnant populations are declining, and possibly how to alter their environment to change this situation, we have to have very detailed study.

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Streszczenie

Powiązanie wiedzy o arealach zajmowanych przez poszczególne gatunki ze zmiennością klimatu może pozwolić na przybliżone przewidywanie intensywności wymierania na dużych obszarach w wyniku wielkich przemian środowiska. Podejście takie niewiele jednak pomaga w ustaleniu ostatecznej przyczyny wymierania.

Większość gatunków ma swoje centralne populacje źródłowe i peryferyczne populacje zanikowe. Większość zapisanych w materiale paleontologicznym przykładów wymierania odnosi się do populacji peryferycznych. Ich koniec niewiele ma wspólnego z rzeczywistym wymieraniem gatunku. O wiele istotniejszy jest zanik populacji centralnych, ale przyczyny tego zjawiska nie są dostatecznie udokumentowane.

W czasach nam współczesnych zanik środowiska właściwego dla gatunku jest najpoważniejszym czynnikiem wymierania. Śmierć ostatnich osobników ostatniej populacji nie musi być jednak w oczywisty sposób związana ze zmianami w środowisku. Najczęściej jest skutkiem działania nieidentyfikowalnych, zapewne przypadkowych czynników.