perhaps thousands, of species are endangered by river degradation and conversion. One analysis of North American crayfishes and unionid mussels estimated that 63% of the crayfish species (198 of 313) and 67% of the unionid mussels (201 of 300) were either extinct or at some level of risk (Master 1990). Another analysis of the freshwater fauna of North America demonstrated that the recent (since 1900) extinction rate of these animals was about five times greater than that of terrestrial vertebrates and that this difference was likely to persist in the future (Ricciardi and Rasmussen 1999). A similarly dramatic story could be told for Asian rivers – home to over half of the world's large dams (over 15 meters tall) and a large portion of the world's freshwater crabs, snails, turtles, crocodilians, river dolphins, and fishes (Dudgeon 2000, 2002). For example, there are 105 families of freshwater fishes in Asia compared with 74 in Africa and 60 in South America. For many taxa we do not even have enough information to evaluate rarity or endangerment. For example, 388 algal species were recorded in one stream in southern Ontario (Moore 1972), but few streams have been inventoried this thoroughly, and thus virtually all of their algal species could be eradicated without documentation of their disappearance.

Fragmentation

When early explorers of wild regions found a high vantage point from which to scan the terrain, they often wrote of a "sea of green" to convey the unbroken vastness of the forests and grasslands they traversed. A modern traveler, looking down from a plane, is likely to describe a typical landscape as a "patchwork quilt" – a mosaic of pastures and croplands, woodlots and house lots and parking lots. The process by which a natural landscape is broken up into small parcels of natural ecosystems, isolated from one another in a matrix of lands dominated by human activities, is called *fragmentation*. Because fragmentation almost always involves both loss and isolation of ecosystems, researchers would like to distinguish between the effects of these two processes but it is not often practical to do so (Guerry and Hunter 2002; Fahrig 2003).

Fragmentation is a major focal point for conservation biologists, both because it has degraded many landscapes and because many nature reserves have become isolated fragments or are in danger of becoming so (Saunders et al. 1991). In addition, it captured the interest of many conservation biologists because it was recognized as an issue at about the same time that conservation biology was emerging as a new discipline; in other words, it was new ground for conservation biology to plow. Furthermore, it appeared to have a theoretical foundation in an intriguing body of ideas and observations known as island biogeography (Box 8.1). It seemed reasonable to assume that the effects of isolation on the biota of oceanic islands might provide a model for understanding the effects of isolation on populations inhabiting patches of natural ecosystems that were isolated in a sea of human-altered land.

Most conservation biologists have come to recognize that the applicability of island biogeography theory to fragmentation issues is quite limited, primarily because fragmentation "islands" are not nearly as isolated for most species as true oceanic islands (Zimmerman and Bierregaard 1986; Debinski and Holt 2000; Haila 2002). Nevertheless, island biogeography does provide a conceptual foundation for understanding fragmentation and is the origin for two important ideas. Small fragments (or islands) have fewer species than large fragments, and more isolated fragments

BOX 8.1

Island biogeography theory

The fundamental idea of MacArthur and Wilson's (1967) equilibrium theory of island biogeography is that the number of species on an island represents a balance between immigration and extinction. The rate of immigration is determined largely by how isolated an island is; the more isolated, the lower its immigration rate. This is represented in Fig. 8.12, with the curve for remote islands (far) being lower than the curve for islands that are near the mainland (near). Extinction rates are a function of island size; populations on large islands tend to be larger and thus less vulnerable to extinction. In Fig. 8.12 the extinction curve for large islands is lower than the curve for small islands.

For any given island there is an extinction rate and an immigration rate that will balance one another and keep the number of species relatively constant. In this example, the numbers of species for four equilibria are represented as follows: *SFS*, number of species on a far, small island; *SFL*, far, large island; *SNS*, near, small island; *SNL*, near, large island. *P* is the total number of species that could potentially immigrate to the island from a nearby landmass.

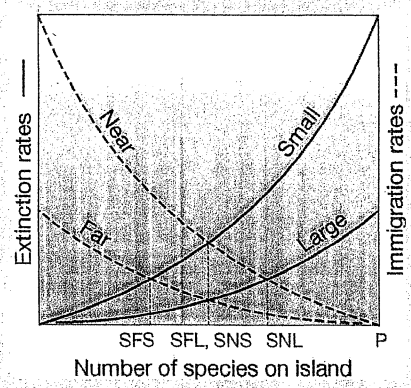

Figure 8.12 A graphical representation of island biogeography theory. (From Hunter 1990, reprinted by permission of Prentice-Hall, Englewood Cliffs, New Jersey.)

have fewer species than less isolated fragments. We will begin by considering these two ideas further.

Fragment Size and Isolation

There are three main reasons why large fragments have more species than small fragments (Fig. 8.13). First, a large fragment will almost always have a greater variety of environments than a small fragment (e.g. different types of soil, a stream, a rock outcrop, an area recently disturbed by fire), and each of these will provide niches for some additional species.

Second, a large fragment is likely to have both common species and uncommon species (i.e. species that occur at low densities), but a small fragment is likely to have only common species. This idea is easy to grasp when we consider species that have large home ranges; for example, it means that we are unlikely to find a bear in a tiny fragment. However, it also applies to species that have rather limited home ranges but still actively avoid small fragments. For example, certain small birds such as Sprague's pipits and grasshopper sparrows have home ranges of only a few hectares, but are usually not found in habitat fragments less than 100 ha in size (Davis 2004). Species that do not occur in small patches of habitat are called *area-sensitive species* and are often of concern to conservationists. Furthermore, uncommon species that are not area-sensitive (i.e. that can find habitat in a small fragment) are also unlikely to occur in a small patch by chance alone. This last point is a subtle one that is often overlooked (Haila 1999), but it is easily explained with an example. Imagine there was an uncommon tree species that had an average density of one individual per 1000 ha; all other things being equal, a 100 ha sample plot would have a 1:10 chance of

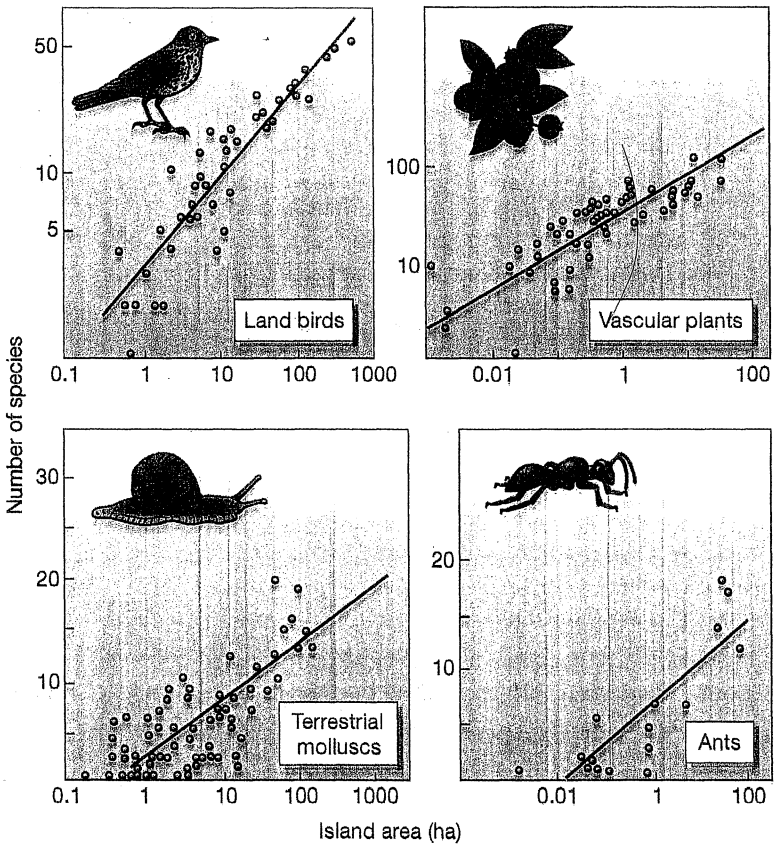

Figure 8.13 The number of species in a sample plot or on an island increases as area increases, but the steepness or slope of the curve varies considerably among taxa. Note that in these graphs for taxa on islands in the Baltic Sea some of the *y* axes are linear and some are logarithmic. All of the *x* axes are logarithmic. Recall from Chapter 6 that these lines are described by the formula $S = CA^z$, where *S* is number of species, *A* is area, and *C* and *z* are constants. (Redrawn from Järvinen and Ranta 1987.)

containing this species, but a 10 ha plot would have only a 1:100 chance. This sampling effect, added across many species, would mean that a small fragment would have fewer species than a large fragment simply because it is a smaller sample. To adjust for this phenomenon, fragmentation studies should focus on number of species per unit area (e.g. Rudnicky and Hunter 1993), but most only report the number of species in each fragment.

Third, small fragments will, on average, have smaller populations of any given species than large islands, and a small population is more susceptible to becoming extinct than a large population (Henle et al. 2004). This idea was a key point in the preceding chapter.

Fragments that are isolated from other, similar patches by great distances or by terrain that is especially inhospitable are likely to have fewer species than less isolated fragments for two reasons. First, relatively few individuals of a given species will immigrate into an isolated fragment. Immigrating individuals are important both because they can "rescue" a small population from extinction and because they can replace a population that has already disappeared (Brown and Kodric-Brown 1977). Second, species that are mobile enough to use an "archipelago" of small habitat patches to collectively comprise a home range are less likely to use an isolated fragment simply because it is inefficient to visit it. For example, the copperbelly water snake travels among ephemeral wetlands foraging for frogs and it seems to fare badly when wetlands are lost and the average distance among the remaining wetlands increases (Roe et al. 2004).

Causes of Fragmentation

The fundamental cause of fragmentation is expanding human populations converting natural ecosystems into human-dominated ecosystems. Fragmentation typically

begins when people dissect a natural landscape with roads and then perforate it by converting some natural ecosystems into human-dominated ones (Fig. 8.14). It culminates with natural ecosystems reduced to tiny, isolated parcels. Thus fragmentation almost always involves both reducing the area of natural ecosystems and increasing their isolation, although some authors have advocated reserving the term for isolation (Fahrig 2003). As the single largest user of land, agriculture is the proximate cause of most fragmentation. Certainly, for many terrestrial species, a large expanse of cropland is a barrier nearly as effective as a stretch of water. Urban and suburban sprawl may be a more effective barrier to movement, but their total area is much more limited than that of agriculture. Some writers use "fragmentation" to describe any process that breaks up extensive ecosystems, including natural events such as fires, whereas other writers restrict the term to human-induced changes. In any case, human activities are the major cause of fragmentation in most landscapes.

Sometimes, it is unclear whether human land uses cause fragmentation. Consider clearcutting forests; if this leads to the forest's being converted to farmland, then clearcutting obviously contributes to fragmentation. However, if the clearcut site is allowed to undergo succession and return to forest, this may or may not constitute fragmentation, depending on whether the clearcut is extensive enough to constitute a significant barrier to the movement of plants and animals (Haila 1999, 2002). Of course, this will vary from species to species. A slow-moving, moisture-loving slug is far more likely to be deterred by a clearcut than most birds that can fly across a clearcut in a few seconds. Similarly, at what point on the continuum of desertification does fragmentation occur? A plant whose seeds are dispersed long distances by wind may cross a desertified barrier easily, whereas a short-dispersal plant may be incapable of crossing the barrier in one trip and unable to establish a population halfway across in the degraded habitat.

Consequences of Fragmentation

Ecosystem destruction is the driving force behind fragmentation, and thus it is inevitable that fragmentation is associated with negative effects on biodiversity. The reason why fragmentation elicits so much special concern from conservationists is that its consequences are greater than we would anticipate based solely on the area of ecosystems destroyed. Notably, remnant ecosystems that seem to have escaped destruction may no longer be available for area-sensitive species that cannot use small patches of habitat. Most prominent among these are large predators that need extensive home ranges to find enough prey (Crooks 2002). Some small species with limited home ranges also avoid small habitat patches: for example, birds (Davis 2004) and beetles (Laurance et al. 2002). This may occur because they require the microclimate characteristic of the interior of large habitat patches, or because they select habitat patches large enough to support other members of their species (a type of loose coloniality) (Stamps 1991), or because of their interactions with other biota as predators, prey, or competitors (Gibbs and Stanton 2001).

In highly fragmented landscapes, it is difficult for individuals (usually juvenile animals, seeds, or spores) to disperse to another suitable patch of habitat. If immigration and emigration are very limited, then the individuals occupying a fragment may effectively constitute a small independent population and, as we saw in Chapter 7, small

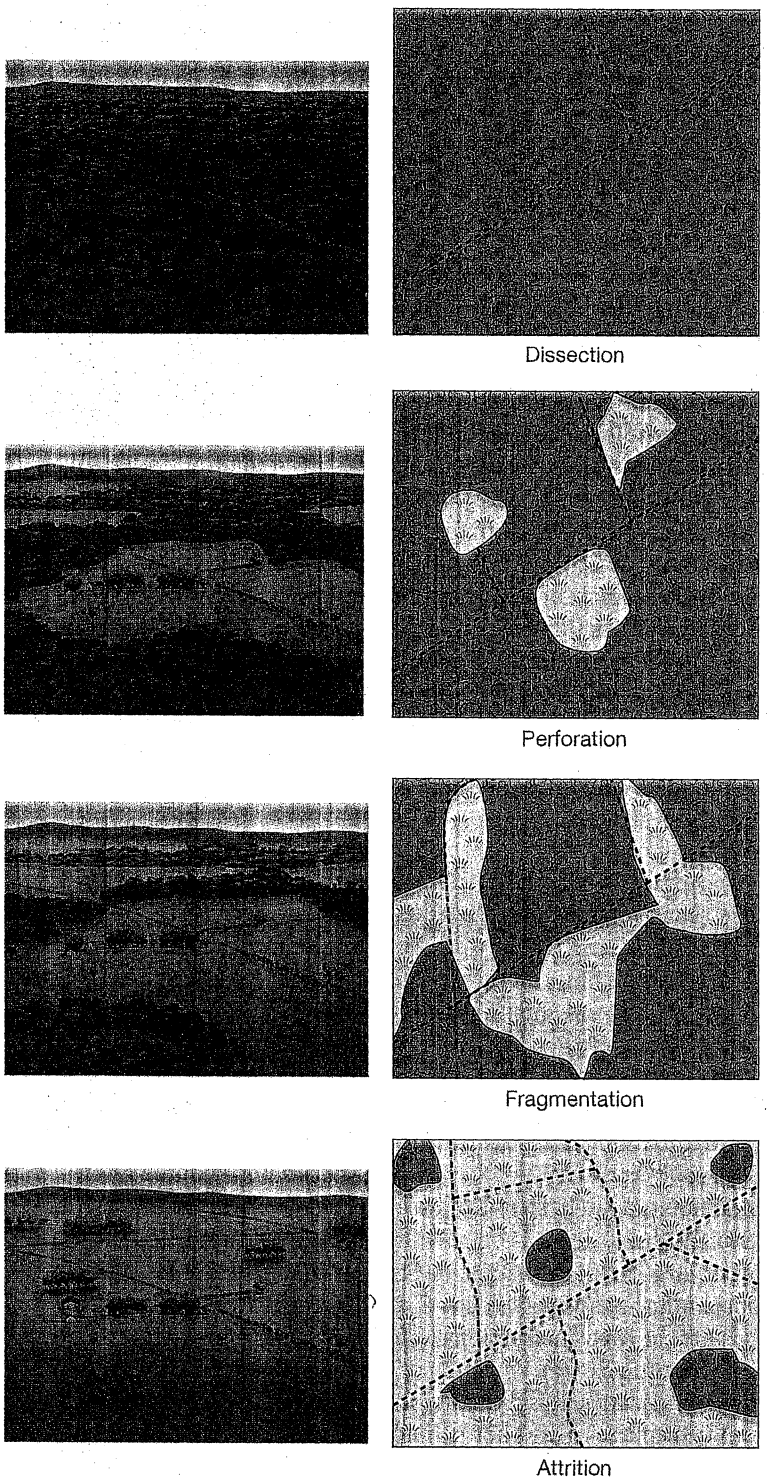

Figure 8.14
People usually initiate fragmentation by building a road into a natural landscape, thereby *dissecting* it. Next, they *perforate* the landscape by converting some natural ecosystems into agricultural lands. As more and more lands are converted to agriculture, these patches coalesce and the natural ecosystems are isolated from one another; at this stage *fragmentation* has occurred. Finally, as more of the natural patches are converted, becoming smaller and farther apart, *attrition* is occurring. (Terminology from R. Forman, personal communication, and 1995; also see Collinge and Forman 1998.)

populations are more likely to disappear. Furthermore, if a population does disappear, a low immigration rate will mean it takes much longer to establish a new population. Even if fragmentation only leads to partial isolation, this may change one large population into a metapopulation, which may also affect population viability and persistence. The dispersal of fire is also an issue; fragmentation has greatly disrupted natural fire regimes in regions where fires once swept across the landscape (Van Lear et al. 2005).

The migration of animal species that travel between habitats seasonally could be impeded by fragmentation (Hunter 1997). In practice, this is likely to be a problem mainly for species that walk, such as large mammals that travel up and down mountains in spring and autumn, or amphibians that migrate to and from spring breeding pools. Similarly, the climate changes described in Chapter 6 require species to shift their entire geographic ranges over long periods. In a fragmented landscape this may be difficult for species with limited dispersal abilities, such as many plants (Pearson and Dawson 2005).

Finally, one consequence of fragmentation is based on a simple rule of geometry: the perimeter length of a patch changes as a linear function, whereas its area changes as a square function. To take a simple example, a 4×4 km patch has a perimeter of 16 km and an area of 16 km^2, and if we decrease it to 2×2 km, its perimeter halves to 8 km, but its area decreases fourfold to 4 km^2. This means that as fragmentation makes patches smaller and smaller, their ratio of edge to interior increases disproportionately (Fig. 8.15). Similarly, if we define a zone in the patch that is within a certain distance of the patch's edge, the relative area of this edge zone will also increase disproportionately as the patch gets smaller. Finally, although fragmentation does not necessarily affect the shape of a patch, it should be noted that another rule of geometry (a circle is the shape with the shortest perimeter) means that the further a patch's shape departs from circular, the longer its edge will be.

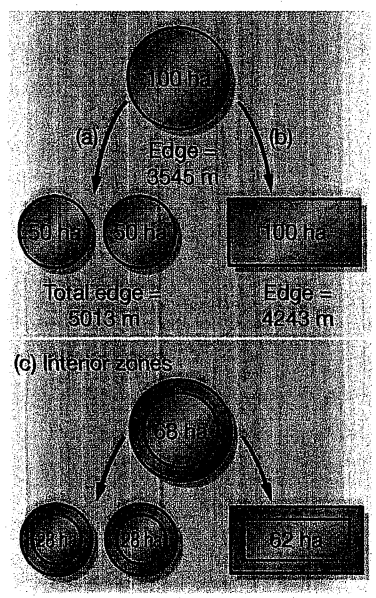

Figure 8.15 Three principles of geometry that affect the edge-to-area ratios of patches. (a) Small patches have relatively longer edges than large patches. (b) Patches that are less circular in shape have longer edges than circular patches. (c) The interior zone of a small or noncircular patch is relatively small compared with that of a large, circular patch. (In these patches the shaded edge zone is 100 meters wide.)

Why is it important that small patches have relatively more edge or ecotone habitat and less interior habitat? This is a complex topic (Ries et al. 2004), but one basic issue is that the physical environment near an edge is different. For example, in a forest fragment bounded by fields, the edge zone will often be windier, drier, and warmer than the forest interior, and this may increase tree mortality and prevent some species, especially certain plants, from inhabiting this zone (Laurance et al. 2002; Harper et al. 2005). Edge zones are also different because early-successional species associated with the surrounding disturbed environment often penetrate the edge. These are likely to include exotic species (e.g. competitors such as weeds, and predators such as cats, rats, and people) that we will discuss in Chapter 10, "Invasive Exotics." One of the most extensively studied aspects of edges concerns the reproductive success of birds nesting near forest–farmland edges. Many studies have reported unusually high levels of nest predation near the edges of forest fragments, although it is difficult to distinguish the specific effects of edges from the overall effects of fragmented landscapes (Stephens et al. 2003). In general,

it seems clear that whenever we have a natural ecosystem surrounded by a disturbed ecosystem, the natural ecosystem is going to experience some disturbing effects, what Dan Janzen (1986) has called "the eternal external threat." The width of these "impact zones" will vary greatly, from tens of meters in the case of microclimate issues to kilometers in the case of poachers invading a protected reserve (Laurance et al. 2002) (Fig. 8.16).

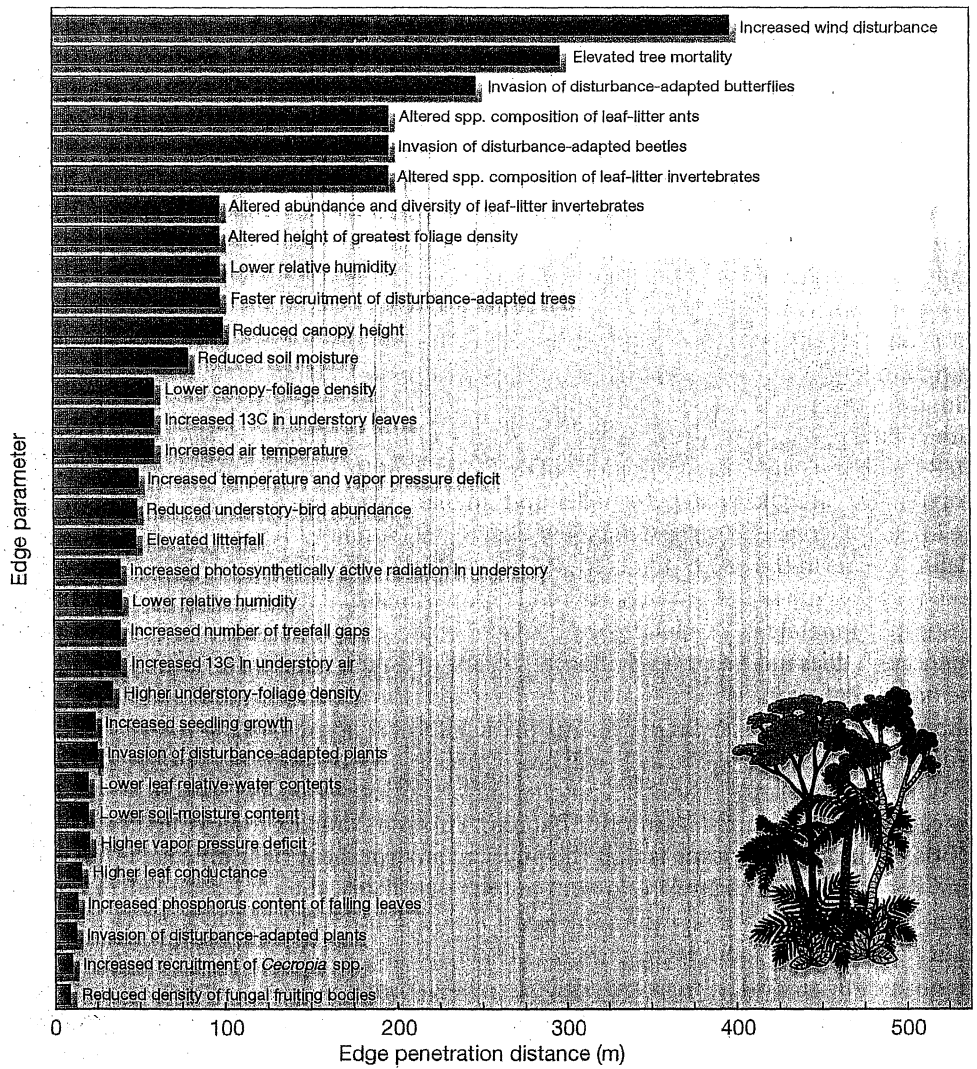

Figure 8.16 Penetration distances of different edge effects into forest remnants of the Biological Dynamics of Forest Fragments Project in the Brazilian Amazon. (From Laurance et al. 2002.)

either case, virtually all types of ecosystems are highly degraded today, and less than 25% of the island remains in forests and woodlands (Dufils 2003). Presumably, the loss of forests and resulting siltation has also affected freshwater and coastal ecosystems (which include many mangrove swamps and coral reefs), but this has been little studied. We do know that Madagascar's unique freshwater fish fauna is severely threatened by deforestation, overfishing, and exotic species (Benstead et al. 2000). One port, Mahajanga, was lost after 100 million m^3 of sediment was deposited in 25 years. Many of Madagascar's most striking species – elephant birds, giant lemurs, and giant tortoises – disappeared after humans inhabited much of the island (Burney et al. 2004). The fact that many of the species were relatively large suggests that overhunting played a role in their demise too, and we will return to this issue in the next chapter. The bottom line in all of this is that the growing numbers of Malagasy people and cattle have made ecosystem degradation and loss almost inevitable. (There were about 2.5 million people in 1900, 4 million in 1950, and 18 million in 2005; it is generally estimated that the Malagasys keep about one head of cattle per person.)

Conservationists throughout the world have set their sights on Madagascar because the stakes are so high (we have so many unique taxa to lose) and the threats so enormous. Here lies some ground for optimism. Ambitious projects to protect key examples of various ecosystems by more than tripling the size of the protected area system (1.7 million km^2 to 6 million km^2), to foster ecotourism and other forms of sustainable development, and to improve land-use practices throughout the island are under way with sponsorship from a diverse array of national and international organizations.

1 This case study is primarily based on Jolly (1980), Jolly et al. (1984), Groombridge (1992), Quammen (1996), Goodman and Patterson (1997), Goodman and Benstead (2003, 2005), and personal communication with Eleanor Sterling.

Summary

Ecosystems and habitats (the physical and biological environment used by a particular species) are routinely degraded, and sometimes destroyed, by human activities. These activities are the most critical threat to biodiversity. Contamination of air, water, soil, and organisms by pollutants is a major form of degradation. Pollution can range from relatively innocuous materials such as sediment that smothers the bottom of a stream to extraordinarily toxic chemicals that are lethal at small doses. Sometimes, populations are eliminated outright by pollution, especially by pesticides; more often, pollution represents a stress that reduces population fitness. People also construct many physical structures that may degrade habitat quality for certain species. Roads are the best known examples; they impede the movement of some organisms, and, worse still, some organisms are run down by vehicles. Moreover, dams and fences are likely to be absolute barriers to the movements of some species. Ecosystems can also be degraded by altering physical processes. For example, people commonly: (1) accelerate soil erosion, which causes silt pollution and decreases site productivity; (2) decrease the frequency of fire in ecosystems where it is a natural event, or increase the frequency of fire where it is uncommon; and (3) remove too much water from ecosystems where it is needed.

Deforestation is a major form of ecosystem destruction that has profound consequences for biodiversity because forests cover less than 6% of the earth's total surface area yet are habitat for a majority of the earth's known species. Deforestation has slowed in many temperate regions, but tropical deforestation continues at an alarming pace and threatens an incredibly diverse biota. Many arid and semiarid ecosystems are being degraded and even destroyed by a process called desertification, primarily the product of overgrazing by livestock and unsound cultivation. Myriad species occur in these environments and are at risk because of desertification. Many aquatic ecosystems have been destroyed by profound changes in their hydrologic

regime imposed by filling, draining, dredging, damming, channelizing, and diking. Rivers and wetlands have been especially vulnerable to these alterations. For this reason, and because they represent a small portion of the earth's area, the species tied to these ecosystems are in considerable jeopardy.

Fragmentation is the process by which a natural landscape is broken up into small parcels of natural ecosystems isolated from one another in a matrix of other ecosystems, usually dominated by human activities. Fragmentation can diminish biodiversity because small, isolated patches of habitat have fewer species than larger, less-isolated patches. This is true because: (1) small patches have less environmental heterogeneity than large patches; (2) some area-sensitive species and uncommon species are unlikely to be found in small patches; (3) small patches have small populations that are more vulnerable to local extinction; (4) immigration into populations occupying isolated patches is limited; and (5) isolated patches are less likely to be used by species that routinely travel among patches. Besides affecting biodiversity by reducing patch size and increasing isolation, fragmentation also creates more edges between different types of ecosystems. These edge zones represent degraded habitat for many species.

FURTHER READING

Many books review the various ways the earth has been degraded by pollution; one of the popular textbooks is Miller (2005a). For statistics and an overview, see the periodic reviews published by the World Resources Institute and its collaborators and their web-based service, Earthtrends (accessible at www.wri.org), a United Nations assessment of the state of the planet (www.millenniumassessment.org), and the Atlas of the Human Footprint (www.wcs.org/Footprint). For books on the degradation and destruction of various types of ecosystems, see Mainguet (1994) on desertification, Williams (2003) on deforestation, Mitsch and Gosselink (2000) on wetlands, Boon et al. (2000) on rivers, and Norse and Crowder (2005) on marine ecosystems. Forman et al. (2003) reviews road impacts; for the effects of fragmentation see Rochelle et al. (1999). Quammen (1996) is a very readable account of island biogeography and fragmentation.

TOPICS FOR DISCUSSION

1. Do you think that, whenever people significantly change an ecosystem from its natural state, this constitutes ecosystem degradation? Recall one example of ecosystem degradation: a power plant warming a river, causing temperature-sensitive species to disappear. Would you consider this ecosystem degradation if all the species that disappeared were common and they were replaced by a larger number of species, all of them native, including one that is an endangered species?
2. Habitat loss for one species often leads to habitat gain for another species; for example, removing a dam may increase habitat for riverine species while decreasing habitat for lake species. How do you balance these out, especially if you are comparing two species that are of equal concern to conservationists and neither habitat is particularly natural?
3. Describe some reasonable thresholds at which habitat degradation can be considered habitat destruction, or ecosystem degradation can be considered ecosystem destruction.
4. Why are some species more sensitive to contamination than others?
5. Discuss the fundamental similarities and dissimilarities between deforestation and desertification.
6. Why are lakes less vulnerable to ecosystem destruction than rivers?

© 2007 by Malcolm L. Hunter, Jr., and James P. Gibbs

BLACKWELL PUBLISHING
350 Main Street, Malden, MA 02148-5020, USA
9600 Garsington Road, Oxford OX4 2DQ, UK
550 Swanston Street, Carlton, Victoria 3053, Australia

The right of Malcolm L. Hunter, Jr., and James P. Gibbs to be identified as the Authors of this Work has been asserted in accordance with the UK Copyright, Designs, and Patents Act 1988.

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, except as permitted by the UK Copyright, Designs, and Patents Act 1988, without the prior permission of the publisher.

First edition published 1995
Second edition published 2002
Third edition published 2007 by Blackwell Publishing Ltd

1 2007

Library of Congress Cataloging-in-Publication Data has been applied for

ISBN-13: 978-1-4051-3545-0 (hardback)
ISBN-10: 1-4051-3545-x (hardback)

A catalogue record for this title is available from the British Library.

Set in 10/12pt Photina MT
by SPi, Pondicherry, India
Printed and bound in Singapore
by C.O.S. Printers Pte Ltd

The publisher's policy is to use permanent paper from mills that operate a sustainable forestry policy, and which has been manufactured from pulp processed using acid-free and elementary chlorine-free practices. Furthermore, the publisher ensures that the text paper and cover board used have met acceptable environmental accreditation standards.

For further information on
Blackwell Publishing, visit our website:
www.blackwellpublishing.com

333.9516
H946f
2007

1616277

Fundamentals of Conservation Biology

Third Edition

Malcolm L. Hunter, Jr.
Department of Wildlife Ecology,
University of Maine

James P. Gibbs
College of Environmental Science and Forestry,
State University of New York