Introduction: Population Biology, Evolution, and Control of Invasive Species

Introduction

Invasion by nonindigenous species has been recognized as second only to loss of habitat and landscape fragmentation as a threat to global biodiversity (Walker & Steffen 1997). The economic impact of these species is a major concern throughout the world. For example, an estimated 50,000 nonindigenous species established in the United States cause major environmental damage and economic losses that total over an estimated U.S.$125 billion per year (Pimentel et al. 2000). Management and control of nonindigenous species is perhaps the biggest challenge that conservation biologists will face in the next few decades.

The six papers in this special section and these introductory remarks consider the role that population biology can play in understanding invasive species through life-history studies, demographic models, genetic considerations, and knowledge of the ecology and evolution of both invasive and native species in a community context. Studies of genetic diversity and the potential for rapid evolution of invasive species may provide useful insights into what causes species to become invasive. Life-history studies may also lead to predictions of which species are likely to become serious pests or identify critical life-history stages during which control will be most successful. Population biology might be useful in identifying the point where containment rather than eradication efforts would be more practical. Demographic models may be useful for examining the spread of invasive species and methods of control. More information about the genetics and evolution of invasive species or native species in invaded communities, as well as their interactions, may lead to predictions of the relative susceptibility of ecosystems to invasion, identification of key alien species, and predictions of the subsequent effects of removal.

Two major themes emerge from the papers in this special section. First, invasive species provide an exceptional opportunity for basic research in the population biology and short-term evolution of species. Many unresolved central issues in the application of genetics to conservation—such as the inbreeding effects of small populations and the importance of local adaptation—can be much better experimentally addressed with introduced species. Second, the management and control of invasive species is a controversial and incredibly complex problem. There may be much to be gained from the study of introduced species, but it is unclear how much this increased understanding of the biology of invasive species will be helpful in their management and control. In addition, the use of biological controls introduces a completely new set of dangers.

Genetic Paradoxes

Two paradoxes emerge from the comparison of the role of genetics in the conservation of species to its role in the invasion of introduced species. Much of the concern in conservation genetics relates to the potential harmful effects of small population sizes. The loss of genetic variation through genetic drift and the inbreeding effect of small populations are thought to contribute to the increased extinction rate of small populations (e.g., Frankham & Ralls 1998). However, colonization of introduced species often involves a population bottleneck because the number of initial colonists is often small. Thus, a newly established population is likely to be much less genetically diverse than the population from which it is derived (Barrett & Kohn 1991). The reduced genetic diversity can have two consequences. First, inbreeding depression may limit population growth and lower the probability that the population will persist. Second, reduced genetic diversity will limit the ability of introduced populations to evolve in their new environments. Thus we face a paradox: If population bottlenecks are harmful, then why are invasive species that have gone through a founding bottleneck so successful?

The presence of genetically based local adaptations is often an important concern in the conservation of threatened species (McKay & Latta 2002). That is, adaptive differences between local populations are expected to evolve in response to selective pressures associated

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with different environmental conditions. The presence of such local adaptations in geographically isolated populations often plays an important role in the management of threatened species (Crandall et al. 2000).

When a species invades a new locality it will almost certainly face a novel environment. However, many introduced species often out-compete and replace native species. For example, introduced brook trout (*Salvelinus fontinalis*) are a serious problem in the western United States, where they often out-compete and replace ecologically similar species of native trout (Adams et al. 2000). The situation is reversed in the eastern United States, where brook trout are native. They are in serious jeopardy because of competition from and replacement by introduced rainbow trout (*Oncorhynchus mykiss*) that are native to the western United States (Krueger & May 1991). Thus, we face a second paradox: If local adaptation is common and important, then why are introduced species so successful at out-competing and replacing native species?

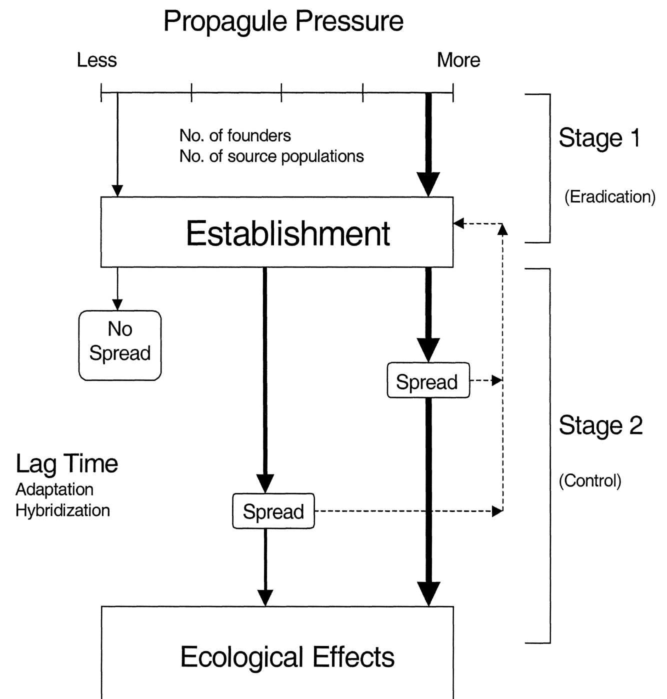

Figure 1. The two stages of invasion that generally coincide with different management responses. Propagule pressure is a continuum, with greater pressure leading to increased chance of establishment and spread with shorter lag times. If spread involves small groups of dispersing individuals, each group must be able to establish itself in a different area. Establishment or subsequent spread may be inhibited where groups reach the limits of particular environmental conditions.

Genetics and Evolution of Biological Invasions

There are two primary stages in the development of a species invasion (Fig. 1). The first stage is the introduction, colonization, and establishment of a nonindigenous species in a new area. In other words, the introduced species must arrive, survive, and establish itself. The second stage is the spread and replacement of native species by the introduced species. The genetic principles that may help us predict whether or not a nonindigenous species will pass through these two stages to become invasive are the same principles that apply to the conservation of species and populations threatened with extinction: (1) genetic drift and the effects of small populations, (2) gene flow and hybridization, and (3) natural selection and adaptation.

Propagule pressure has emerged as the most important factor for predicting whether or not a nonindigenous species will become established (Kolar & Lodge 2001). Propagule pressure includes both the number of individuals introduced and the number of release events. Propagule pressure is expected to be an important factor in the establishment of introduced species on the basis of demography alone. That is, it is unclear what role, if any, genetic effects may play in the effect of propagule pressure.

There are two primary ways in which the genetics of an introduced species may be affected by propagule pressure. First, a greater number of founding individuals would be expected to reduce the effect of any population bottleneck so that the newly established population would have greater genetic variation. Second, and perhaps most important, different releases may have different source populations. Therefore, hybridization between individuals from genetically divergent native populations may result in introduced populations having more genetic variation than native populations of the same species. Hybridization also may play an important role in introduced species becoming invasive (Ellstrand & Schierenbeck 2000).

For example, Baker (1992) reported that Chaffinches (*Fringilla coelebs*) from 8 populations in New Zealand have an average heterozygosity that is 38% greater (0.066 vs. 0.048) than 10 native European populations at 42 allozyme loci. Approximately 400 Chaffinches were imported from England between 1862 and 1877. Overwintering birds from several populations on the European continent could have been included in the birds collected for introduction to New Zealand. Hatchery populations of salmonid fish used for introduction have also generally had a mixed origin, so that populations of nonindigenous trout often have greater amounts of genetic variation than nonindigenous populations (Busack et al. 1979; Allendorf et al. 2001).

One solution to the first of the two genetic paradoxes lies in the strong observed effect of propagule pressure

on the invasiveness of species. That is, the clear association between the greater number of introduced individuals and the number of release events and the probability of an introduced species becoming invasive suggests that many invasive species are not as genetically depauperate as expected.

In addition, plant species can avoid the reduction in genetic variation associated with colonization by their means of reproduction (Barrett & Husband 1990). Many invasive plant species reproduce asexually by apomixis or vegetative reproduction (Baker 1995; Calzada et al. 1996). In both cases, the effects of inbreeding depression are avoided because the progeny are genetically identical to the parental plants. In addition, many invasive plant species are polyploids and can reproduce by selfing. In this situation, genetic variation is maintained in the form of fixed heterozygosity because of genetic divergence between the genomes combined in the formation of the allopolyploid (Brown & Marshall 1981).

A variety of explanations have been proposed to account for the fact that introduced species often outperform indigenous species. First, some species may be intrinsically better competitors because they evolved in a more competitive environment (Callaway & Aschehoug 2000). Second, the absence of enemies (e.g., herbivores in the case of plants) leaves nonindigenous species more resources available for growth and reproduction and thereby allows them to out-compete native species. Siemann and Rogers (2001) found that an invasive tree species, the Chinese tallow tree (*Sapium sebiferum*), evolved increased competitive ability in their introduced range. Invasive genotypes were larger than native genotypes and produced more seeds, but they had lower-quality leaves and invested fewer resources in defending them. Thus, there are a number of reasons why introduced species may fare well even though native species may be locally adapted (paradox 2).

In addition, local adaptation of native populations might be essential only during periodic episodes of extreme environmental conditions such as winter storms, drought, or fire. For example, Rieman and Clayton (1997) suggest that the complex life histories of some fish species (e.g., mixed migratory behaviors) are adaptations to periodic disturbances such as fire and flooding. Thus, introduced species may be able to out-perform native species in the short term (a few generations) because the performance of native species in the short term is constrained by long-term adaptations that may come into play every 50 or 100 years.

Many recently established species often persist at low and sometimes undetectable numbers and then "explode" to become invasive years or decades later (Sakai et al. 2001). Such evolutionary changes may explain the lag time that is seen in many species that become invasive (García-Ramos & Rodríguez 2002). Many of the best examples of rapid evolutionary change come from the study of recently introduced populations (e.g., Williams & Moore 1989; Huey et al. 2000; Carroll et al. 2001).

Overview of Special-Section Contents

The origin of this special section was a symposium held during the 2001 annual meeting of the Society for Conservation Biology in Hilo, Hawaii. The symposium was organized by F. W. A. and grew out of the Collaboratory on the Population Biology of Invasive Species chaired by A. K. Sakai and S. G. Weller, which was sponsored by the Division of Environmental Biology of the U.S. National Science Foundation.

The papers in this section highlight a number of issues in invasion biology. Although the topics are varied, the authors echo a few key points: invasive species are one of the leading causes of loss of biodiversity, prevention of introduction is more effective than eradication of an established non-native species, and more research is needed to develop safe and effective control measures. This final point is an understatement because invasion biology incorporates a number of subject areas, from the study of life histories (including development and physiology) to those of ecosystem dynamics and genetics. These papers demonstrate the potential that the study of the population biology of invasions holds for increasing our knowledge in a number of areas.

Lodge and Shrader-Frechette confront an issue that scientists face trying to gather support for the study and control of invasive species. Although the harmful effects of invasive species are recognized, there are many misunderstandings on the part of the public, sometimes influenced by scientists and the media. These misunderstandings can lessen concern over non-native species, especially when some introduced species are associated with economic gain. Botkin (2001) and others assert that invasions have occurred throughout evolutionary history, so much of the concern over present invasions is unwarranted. Rosenzweig (2001) agrees that invasions may reduce diversity, but he argues that evolution can compensate for this in the long run so that the impact may be exaggerated. Finally, Sagoff (2000) demonstrates that confusion can arise when there are not consistent definitions of invasive as opposed to nonindigenous species. Lodge and Shrader-Frechette counter the arguments of these authors to support the position that the introduction of non-native species should not be accepted. The biggest problem arises when a non-native species provides economic gain for some parts of society. Lodge and Shrader-Frechette propose that scientists need to contribute to risk analysis of the introduction and management of such species. There are many unknowns, but lack of information should not stop scientists from influencing such decisions.

Townsend weaves together a series of long-term studies—from the individual to the ecosystem—of the effects of brown trout (*Salmo trutta*), introduced into New Zealand as a sport fish. Such a long-term study is rare, but the investment of time, effort, and resources goes a long way toward reducing the uncertainty associated with risk assessment. Townsend found that, as a top predator, the trout appear to exert a strong top-down effect on the stream ecosystem. The trout prey heavily on grazing (and predatory) invertebrates, thus allowing primary production by algae to increase. This can cause changes locally and at a distance as a greater amount of biomass sloughs off downstream. The native galaxiid fishes have much less of an effect and are often absent in streams where trout exist. In studies of introductions into previously fishless lakes, trout appear to have a similar influence on primary production. Although this study shows the extent to which an invasive species can change ecosystem processes, it will have little effect on management because the brown trout is a popular sport fish in New Zealand, and there is little support for its eradication.

In contrast, Tsutsui and Suarez studied invasive ants that are recognized as a major problem throughout the world. They show how population biology can be helpful in the prevention of new outbreaks. Introduced Argentine ants (*Linepithema humile*) and red fire ants (*Solenopsis invicta*) have two characteristics not present in their native populations which facilitate their invasive spread, unicolonial organization and polygyny. In native colonies, nest mates can recognize outsiders from different chemical cues and attack them. Because nest mates are related, they share similar chemical phenotypes. Because of bottlenecks, introduced populations have reduced genetic variation, which results in individuals possessing similar chemical phenotypes, even though they may be only distantly related. Thus, colonies are not aggressive toward each other and cooperation makes the populations more prolific than native populations.

The authors suggest that control could be brought about by introducing chemical or genetic variation that would cause intercolony aggression to increase. Also, the features that make the ants successful in the short term may not aid them in the long term. Loss of genetic diversity affects sex determination and can lead to sterility in Hymenoptera. If continued introductions can be checked and intercolony aggression is promoted, perhaps the established populations could be eliminated. The former requirement is difficult to meet, however, because most introductions occur by way of human-mediated transport.

Parker et al. examine the European common mullein (*Verbascum thapsus*), which is one of the few introduced plant species that has invaded high elevations in the Sierra Nevada. They provide a case study of how adaptation and genetic structure may promote or constrain an invader's success. Attempts to predict the success of an invader generally focus on the species in the present and ignore the genetic potential for change, a myopic point of view for biologists. A number of factors may trigger evolution of a non-native species, including founder effects, genetic drift, and rapid evolution sparked by stress and the new environment. But adaptation may not explain the success of all invasive species. Many demonstrate phenotypic plasticity, a characteristic that allows for immediate adjustment to different habitats and that could also make prediction of success difficult (Sakai et al. 2001). If a species is established but has not yet spread, is the delay due to the time required for adaptation, or is spread just a stochastic process, having not yet occurred at a specific point in time?

Tsutsui and Suarez contend that the primary goal of invasion biology should be to construct a predictive framework for prevention of invasions. They show, however, how changes brought about by founding effects and bottlenecks may affect the genetics of introduced species. Although they identify some characteristics possessed by the invasive populations that make them successful, it would have been difficult if not impossible to predict success based on the traits of the native populations. Parker et al. also point out that in cases where genetic changes occur, prediction of success can be difficult. Developing a method to predict success is required primarily if a policy exists allowing non-native species to be imported if they are considered benign. If all non-natives were considered undesirable, there would be little need for prediction of invasiveness (except perhaps to prioritize eradication). Because of difficulties associated with prediction, and the inconsistent philosophy underlying its employment, perhaps less emphasis should be placed on this "goal" of invasion biology.

Louda et al. address the controversial issue of the biological control of invasive species. To illustrate problems with the application of biological control agents, they use two examples in which Eurasian weevils were imported into the United States to control non-native thistles. The research conducted on potential control agents is too often limited, focusing only on a few characteristics. Such studies are often conducted in a laboratory setting, and the conditions are probably not representative of the environment where the agents will be released. In addition, studies from a single region are used to justify their use in a number of regions, even though populations undoubtedly differ from one another.

According to Louda et al., native species have suffered in nearly every case where biological control has been used. Harm can be done not only to native species that resemble or are related to the invasive species but also to species that operate in the same guild as the biological control agent. If biological control is considered, community-level research should be conducted to deter-

mine how species interact and how these interactions may be influenced by the introduction of another species. In the unlikely event that such research supports the introduction of biological control agents, the introduction should be given long-term monitoring, a step that is rarely, if ever, taken.

Simberloff argues strongly for a no-tolerance policy toward non-native species. First, non-native species should not be allowed into the country. Unfortunately this position is often overruled because disallowing imports may threaten trade and economic growth. As a secondary defense, when non-native species are discovered, they should be immediately attacked with whatever means are known to be effective, except biological control. One of the characteristics of species invasion is lag time, the period between the arrival of a non-native species and the point where it begins to spread. This is the period that must be exploited, because here eradication is most effective. Simberloff cites a number of cases where immediate action has been successful and relatively inexpensive. Often, unfortunately, too much time is wasted after non-natives are found: no one wants to claim responsibility (and thus the expense) for the situation; the red tape of bureaucracy adds impediments; or more information is demanded and time must be taken to research the biology. During such delays, the non-native species becomes established and the window of easy opportunity is closed. The remedy is now more involved and expensive than it would have been shortly after the appearance of the non-native species.

Simberloff is concerned that obtaining more information has sometimes been used to delay action. In some of the cases he cites, the eradication effort took anywhere from 2–5 years. Studies could be conducted during eradication, and if more-effective methods of eradication are found, they can be implemented subsequently; at least in the meantime the population is diminishing. Quarantine is always a key step. Then general eradication methods can be applied. Mammals are relatively easy to eradicate with traps, dogs, guns, and poisons. Plants can be somewhat more difficult, requiring herbicides and machines. In some instances, knowledge of the biology aids in the timing of application of poisons or other means but is not essential to the eventual removal. Rarely has the delay taken for study resulted in a silver bullet, and often methods are used that are no different than what could have been used at the beginning. As in the treatment of cancer, early detection is crucial. As soon as cancer is detected, action is immediately taken to remove the cells before they spread. Once it spreads, cancer becomes more difficult to remove. So it is with invasive species. Early removal of non-native species should take on a similar urgency.

Is biological control worth the risk? That is, should we risk the introduction of yet another potentially invasive species for purposes of control in the face of so much uncertainty? Louda et al. and Simberloff both cite the very low percentages of success in cases where biological control was used (<20% of the cases attain complete control, and only 41% of the cases provide some control). Louda et al. demonstrate the risks and uncertainty involved in biological control, and Simberloff makes a strong argument for a no-tolerance policy for introduced species.

In contrast, Strong and Pemberton (2000) have argued that imported natural enemies are the last hope for managing some of the most harmful invasive species. They acknowledge the dangers of biological control and that current regulations dealing with the use of biological control agents are generally inadequate. Nevertheless, they believe that the introduction of species for biological control is an essential tool for management of invasive species that if used carefully is worth the inherent risks.

Management and Control of Invasive Species

As Simberloff argues, understanding the population biology of invasive species is not necessary, and in some circumstances will not even be helpful in their management and control. During his spoken presentation at the symposium, he described this as a policy of "shoot first, ask questions later" (see also Ruesink et al. 1995). This recommendation is in agreement with experience and basic population biology. The best way to reduce the probability that an introduced species will become invasive is to eliminate it before it has time to become abundant and widespread and to evolve adaptations that may allow it to out-compete native species. Nevertheless, understanding population biology, genetics, and evolution may be helpful in identifying introduced species that are most likely to become invasive, in predicting the potential for invasive species to evolve responses to management practices, and in developing policy.

Not all introduced populations of a potentially invasive species have equal potential for becoming invasive. The probability of becoming invasive results from a variety of genetic, demographic, and ecological factors. Genetic differences in these factors have resulted in situations where both invasive and non-invasive populations of an introduced species may occur in the same area (Sakai et al. 2001).

For example, most strains of the marine green algae *Caulerpa taxifolia* are not invasive. However, a small colony of *C. taxifolia* was introduced into the Mediterranean in 1984 from a public aquarium and spread widely, seriously reducing biological diversity in the northwestern Mediterranean (Jousson et al. 2000). The invasive strain differs from native tropical strains in that it reproduces asexually, grows more vigorously, and is resistant to lower temperatures. Colonies of *C. taxifolia* have re-

cently been reported on the coast of California and have raised concerns about the danger of an invasion similar to that in the Mediterranean (Kaiser 2000). Genetic analysis of the California alga has shown that it is the same strain as the one responsible for the Mediterranean invasion (Jousson et al. 2000). Thus, the rapid eradication of this introduced alga should receive high priority to reduce the probability of a new invasion.

Genetics may play an important role in the potential of an established invader to evolve defenses against the effects of a control agent (e.g., evolution of resistance to herbicides or biological control agents). The rate of change in response to natural selection is proportional to the amount of genetic variation present (Fisher 1930). Therefore, the amount of heterozygosity or allelic diversity at molecular markers that are likely to be neutral with respect to natural selection may provide an indication of the amount of genetic variation at loci that potentially could be involved in response to a control agent.

The amount of molecular genetic variation may not be a reliable indicator of the amount of heritable variation for adaptive traits (Frankham 1999; McKay & Latta 2002). However, molecular genetic variation is likely to be a reliable indicator for invasive species of the potential for adaptive change because of the genetic effects of recent colonization. For example, greatly reduced molecular variation in an invasive population relative to native populations of the same species is a good indicator of a small effective population during the founding event; this is expected to reduce the amount of variation at adaptive loci. In addition, greater molecular variation in an invasive population relative to native populations of the same species is a good indicator of introductions from multiple populations. This indicates that the invasive species likely has undergone substantial amounts of adaptive genetic variation to escape the effects of a control agent.

Genetics should play a larger role in the development of policy to manage and control invasive species. Regulations generally have not taken into account the fact that some genotypes may be more invasive than others of the same species. According to the standards set by the International Plant Protection Convention, imports cannot be restricted for species that are already widespread and are not the object of an "official" control program (Baskin 2002). For example, several well-known noxious range weeds (e.g., the yellow star thistle [*Centaurea solstitialis*]) are on the list of permitted imports in Western Australia because they are widespread and the government is not officially trying to control them. However, they are subject to control attempts by landowners for which they are a problem. Allowing the future import of additional strains that could be more invasive seems unwise in situations such as this.

Major challenges in managing and controlling invasive species lie ahead in virtually every ecosystem throughout the world. We hope this special section will provide helpful guidance in the application of the principles of population biology and evolution to invasive biology. We also hope it stimulates further research on these important topics in conservation biology.

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Literature Cited

Adams, S. B., C. A. Frissell, and B. E. Rieman. 2000. Movements of nonnative brook trout in relation to stream channel slope. Transactions of the American Fisheries Society **129:**623-638.

Allendorf, F. W., P. Spruell, and F. M. Utter. 2001. Whirling disease and wild trout: Darwinian fisheries management. Fisheries **26(5):**27-29.

Baker, A. J. 1992. Genetic and morphometric divergence in ancestral European and descent New Zealand populations of chaffinches (*Fringilla coelebs*). Evolution **46:**1784-1800.

Baker, H. G. 1995. Aspects of the genecology of weeds. Pages 189-224 in A. R. Kruckeberg, R. B. Walker, and A. E. Leviton, editors. Genecology and ecogeographic races. Pacific Division of the American Association for the Advancement of Science, San Francisco.

Barrett, S. C. H., and B. C Husband. 1990. The genetics of plant migration and colonization. Pages 254-278 in A. H. D. Brown, M. T. Clegg, A. L. Kahler, and B. S. Weir, editors. Plant population genetics, breeding, and genetic resources. Sinauer Associates, Sunderland, Massachusetts.

Barrett, S. C. H., and J. R. Kohn. 1991. Genetic and evolutionary consequences of small population size in plants: implications for conservation. Pages 3-30 in D.A. Falk and K. E. Holsinger, editors. Genetics and conservation of rare plants. Oxford University Press, New York.

Baskin, Y. 2002. A plague of rats and rubbervines: the growing threat of species invasions. Island Press, Washington, D.C.

Botkin, D. B. 2001. The naturalness of biological invasions. Western North American Naturalist **61:**261-266.

Brown, A. H. D., and D. R. Marshall. 1981. Evolutionary changes accompanying colonization in plants. Pages 351-363 in G. G. E. Scudder and J. L. Reveal, editors. Evolution today: proceedings of sec-

ond international congress of systematic and evolutionary biology. Hunt Institute for Biological Documentation, Carnegie-Mellon University, Pittsburgh, PA.

Busack, C. A., R. Halliburton, and G. A. E. Gall. 1979. Electrophoretic variation and differentiation in four strains of domesticated rainbow trout (*Salmo gairdneri*). Canadian Journal of Genetics and Cytology **21:**81–94.

Callaway, R. M., and E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science **290:**521–523.

Calzada, J. P. V., C. F. Crane, and D. M. Stelly. 1996. Botany—apomixis: the asexual revolution. Science **274:**1322–1323.

Carroll, S. P., H. Dingle, T. R. Famula, and C. W. Fox. 2001. Genetic architecture of adaptive differentiation in evolving host races of the soapberry bug, *Jadera haematoloma.* Genetica **112–113:**257–272.

Crandall, K. A., O. R. P. Binindaemonds, G. M. Mace, and R. K. Wayne. 2000. Considering evolutionary processes in conservation biology. Trends in Ecology & Evolution **15:**290–295.

Ellstrand, N. C., and K. A. Schierenbeck. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Proceedings of the National Academy of Sciences of the United States of America **97:** 7043–7050.

Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford, United Kingdom.

Frankham, R. 1999. Quantitative genetics in conservation biology. Genetical Research **74:**237–244.

Frankham, R., and K. Ralls. 1998. Conservation biology: inbreeding leads to extinction. Nature **392:**441–442.

García-Ramos, G., and D. Rodríguez. 2002. Evolutionary speed of species invasions. Evolution **56:**661–668.

Huey, R. B., G. W. Gilchrist, M. L. Carlson, D. Berrigan, and L. Serra. 2000. Rapid evolution of a geographic cline in size in an introduced fly. Science **287:**308–309.

Jousson, O., J. Pawlowski, L. Zaninetti, F. W. Zechman, F. Dini, G. Di Guiseppe, R. Woodfield, A. Millar, and A. Meinesz. 2000. Invasive alga reaches California. Nature **408:**157–158.

Kaiser, J. 2000. California algae may be feared European species. Science **289:**222–223.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution **16:**199–204.

Krueger, C. C., and B. May. 1991. Ecological and genetic effects of salmonid introductions in North America. Canadian Journal of Fisheries and Aquatic Sciences **48**(supplement 1):66–77.

McKay, J. K., and R. G. Latta. 2002. Adaptive population divergence: markers, QTL and traits. Trends in Ecology & Evolution **17:**285–291.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience **50:**53–65.

Rieman, B., and J. Clayton. 1997. Wildlife and native fish: issues of forest health and conservation of sensitive species. Fisheries **22(11):**6–15.

Rosenzweig, M. L. 2001. The four questions: What does the introduction of exotic species do to diversity? Evolutionary Ecology Research **3:**361–367.

Ruesink, J. L., I. M. Parker, M. J. Groom, and P. M. Kareiva. 1995. Reducing the risks of nonindigenous species introductions: guilty until proven innocent. BioScience **45:**465–477.

Sagoff, M. 2000. Why exotic species are not as bad as we fear. Chronicle of Higher Education 23 June: B7.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics **32:**305–332.

Siemann, E., and W. E. Rogers. 2001. Genetic differences in growth of an invasive tree species. Ecology Letters **4:**514–518.

Strong, D. R., and R. W. Pemberton. 2000. Biological control of invading species: risk and reform. Science **288:**1969–1971.

Walker, B., and W. Steffen. 1997. An overview of the implications of global change for natural and managed terrestrial ecosystems. Conservation Ecology **1**(2): http://www.consecol.org/vol1/iss2/art2.

Williams, C., and R. Moore. 1989. Phenotypic adaptation and natural selection in the wild rabbit, *Oryctolagus cuniculus*, in Australia. Journal of Animal Ecology **58:**495–507.