

# SPECIES INVASIONS

## Introduction

Let's visit Hawaii and review what has happened to the native flora since humans arrived.

- Native flora consisted of 1200–1300 species prior to Polynesian contact, about 90% of which were found nowhere else on earth.
- At the time of European contact — Captain Cook's voyage, 1778 — the flora contained about 30 species introduced by the Polynesians, examples include:<sup>1</sup>
  - breadfruit — *Artocarpus altilis*
  - coconut — *Cocos nucifera*
  - taro — *Colocasia esculenta*
  - yam — *Dioscorea* (3 species)
  - sweet potato — *Ipomoea batatas*
  - banana — *Musa acuminata* hybrids
  - sugar cane — *Saccharum officinarum*

Polynesian immigrants also brought a variety of animals.

- dog
  - a jungle fowl
  - pig
  - rat
- Today the native flora consists of roughly 1000–1100 species, i.e., 100–200 native plant species are already extinct. About 30% of those that remain are considered threatened or endangered.

---

<sup>1</sup>After I. Abbott, as cited in [14]

- One century after Captain Cook’s first contact about 150 introduced species were known from the islands. Today over 800 introduced species are known. Almost one-half of the species of vascular plants found on the Hawaiian Islands are introduced. Moreover, most of the plants that you see when you visit the Hawaiian Islands are not native, especially in the lowlands.

- Kahili ginger — *Hedychium gardnerianum*
- Guava — *Psidium guava*
- Passion flower — *Passiflora mollissima*
- *Lantana camara*
- *Tibouchina urvilleana*

Invasive exotics now pose at least as great a threat to many Hawaiian plants as direct habitat destruction. Goats and pigs disturb the native vegetation, and many invasive exotics capitalize on the disturbances they cause. They also invade undisturbed habitat, some— notably the Kahili ginger and *Tibouchina urvilleana* – forming dense, monospecific stands that exclude native plants.

## Invasives as “ecosystem engineers”

In teaching classical, Clementsian ideas about ecological succession to undergraduates, we often describe how early successional species modify the habitat in ways that make the establishment of other species possible. Vitousek [15] points out that invasives can do the same thing to the ecosystems they invade.

In Hawaii, for example, firetree (*Morella faya*, formerly *Myrica faya*) is native to northern Macaronesia (the Azores, Madeira, and the Canaries), and it was probably introduced to Hawaii in the late 19th century by Portugese immigrants [9], and it is now found on all of the high islands. Firetree is a nitrogen-fixer, meaning that after it invades nitrogen levels in the soil are enhanced. Experiments summarized in [15] show that:

- Growth of koa (*Metrosideros polymorpha*), the dominant native tree is nitrogen limited. Addition of N-fertilizer enhances growth
- Firetree is responsible for fixing about  $18 \text{ kg ha}^{-1} \text{ yr}^{-1}$  of nitrogen, which vastly exceeds nitrogen inputs from others sources. Rainfall adds at most  $5 \text{ kg ha}^{-1} \text{ yr}^{-1}$  and native nitrogen-fixers (cyanobacteria and decomposers) add only about  $0.5 \text{ kg ha}^{-1} \text{ yr}^{-1}$ .

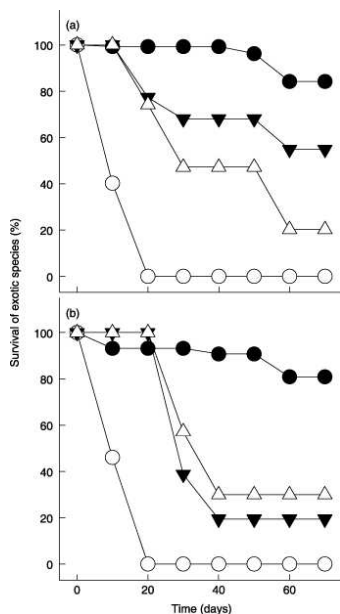


Figure 1: Survival of dandelion (a) and chickweed (b) in cushions of *Azorella monantha* (filled symbols) and in open area (open symbols) and at the lowest (triangles) and highest (circles) elevations (from [1]).

As a result of the substantial changes in nitrogen availability, areas invaded by firetree are more susceptible to invasion by exotics than other areas. Firetree is an “ecosystem engineer.”

Badano et al. [1] show that a native cushion plant in the high Andes, *Azorella monantha*, facilitates the invasion of dandelion (*Taraxacum officinale*) and chickweed (*Cerastium arvense*). The effect is especially pronounced at high altitudes. Survival of transplanted seedlings is enhanced at both the lowest (3200m) and the highest (3600m) elevations, but the effect is especially pronounced at the highest elevation (Figure 1).

## Impacts of invasive exotics

Daehler and Strong [2] suggest that invasive exotic pose the most severe threat to native plant diversity in many nature reserves.

- Exotic plants pose a severe threat to over 7 million hectares of Federal lands in the western U.S.
  - Annual losses to leafy spurge (*Euphorbia esula*) — \$144 million.

- \$20 million needed annually to control hydrilla (*Hydrilla verticillata*) in 35,000 hectares of Florida waterways.
- Mediterranean fruit fly—\$100 million in 1981 to eradicate from San Francisco Bay area. (Helicopters, aerial spraying of malathion.)
- Congressional Office of Technology Assessment report “Harmful Non-Indigenous Species in the United States,” OTA-F-565 (Washington, D.C.: U.S. Government Printing Office, September 1993).
  - Evaluated impacts of 79 non-indigenous species (NIS) introduced from 1906–1991.
  - Cumulative losses estimated to be \$97 billion.
- More recently Pimentel et al. [12] estimated that “the approximately 50,000 nonindigenous species in the United States cause major environmental damage and losses totaling approximately \$137 billion per year.”

## Species invasions and deletions

The way I have just described the situation of the native flora in Hawaii is the way we usually describe the impact of invasive exotics. We implicitly presume that the species composition of communities is static and that all species invasions are “bad.” In fact,

- at least 77% of documented bird species introductions into Britain occurred without human assistance<sup>2</sup> and
- the mesic forests of Wisconsin<sup>3</sup> have had their current species composition for only 2000 years.

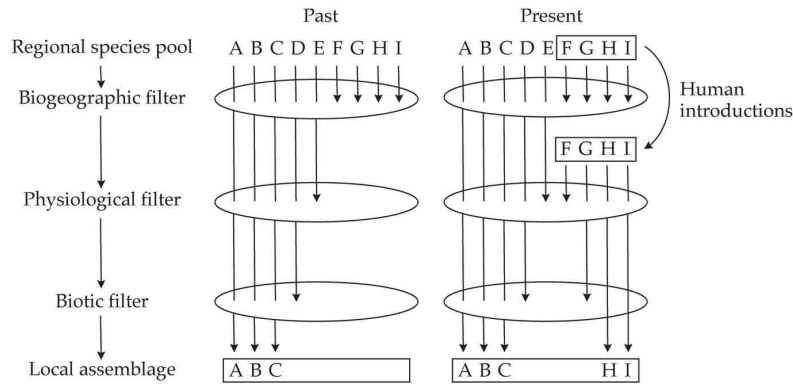
Just as species have come and gone through the course of evolutionary history, so have their ranges expanded and contracted. Why should we care that species formerly restricted to Europe and the Mediterranean are now found in California, South Africa, Chile, Argentina, and Australia?

First of all, species naturally come *and go* from communities. Thus, a focus on *invasions* is too narrow. We should also consider the impact of species *deletions*. Both invasions and

---

<sup>2</sup>Of course, human activities that altered existing habitat in Britain may have made the introductions possible.

<sup>3</sup>And presumably of many other glaciated regions in the North Temperate Zone



PRINCIPLES OF CONSERVATION BIOLOGY, Third Edition, Figure 9.9 © 2005 Sinauer Associates, Inc.

Figure 2: The invasion filter (Figure 9.9 [3]).

deletions are an integral part of natural communities. Human activities alter the frequency of both and, by so doing, greatly affect community structure.

Although these impacts are less well documented than impacts on species extinctions, the case for concern about human impacts on community structure is analogous to that for concern about extinction. The rate at which human activities impose changes in community structure are likely to be far greater than those they have endured in the past (Figure 2). Moreover, the pattern of change, especially in human-dominated, disturbed ecosystems, is for the biota to become more homogeneous. The ease with which we and our associates now travel the globe mean that homogenization is possible to a far greater extent now than it was even a few decades ago.

McKinney and Lockwood (Table 1) point out that biotic invasions are in many respects the flipside of extinctions. There are, however, many more species declining than increasing in number. For example, We are replacing declining species with a small number of widespread species whose abundance is increasing. The result will be a much more biologically homogeneous world.<sup>4</sup>

<sup>4</sup>This is a theme I first touched on early in the course when we talked about the biology of human-caused extinctions.

Taxon (site)	Proportion declining	Proportion increasing
Birds (Californian preserve)	52%	5%
Butterflies (UK)	74%	9%
Bees, wasps, ants (UK)	70%	10%

Table 1: Species invasions and deletions in three selected groups (from [10]).

## The North American Great Lakes

Refer to Figure 3 for a diagram illustrating these changes in the fish community of the Great Lakes.

- Native fish assemblages dominated by lake trout, coregonids (whitefish and chubs), and perch.
- Construction of Welland Canal (1829) allowed lamprey (in the 1920s) and alewives (in the 1930s) (both marine) to colonize. Rainbow trout were introduced in about 1912.
- Overfishing, combined with predation by lampreys, dramatically reduced populations of lake trout, coregonids, and perch.
- Elimination of piscivorous lake trout led to population explosion of *introduced* alewives and smelt, almost eliminating native populations of planktivores (coregonids and perch).
- Lake trout were reintroduced in 1955 after the development of effective chemical control for lampreys.
- Massive stocking of several species of salmonids in the 1970s led to decreased alewife populations. Populations of native planktivores, especially coregonids and perch, rebounded.
- The result is a fish community whose dynamics are dominated by introduced species—lamprey, salmonids, alewives, and smelt.
- Lampreys and alewives were previously anadromous. The Great Lakes populations spend their entire lives in freshwater.

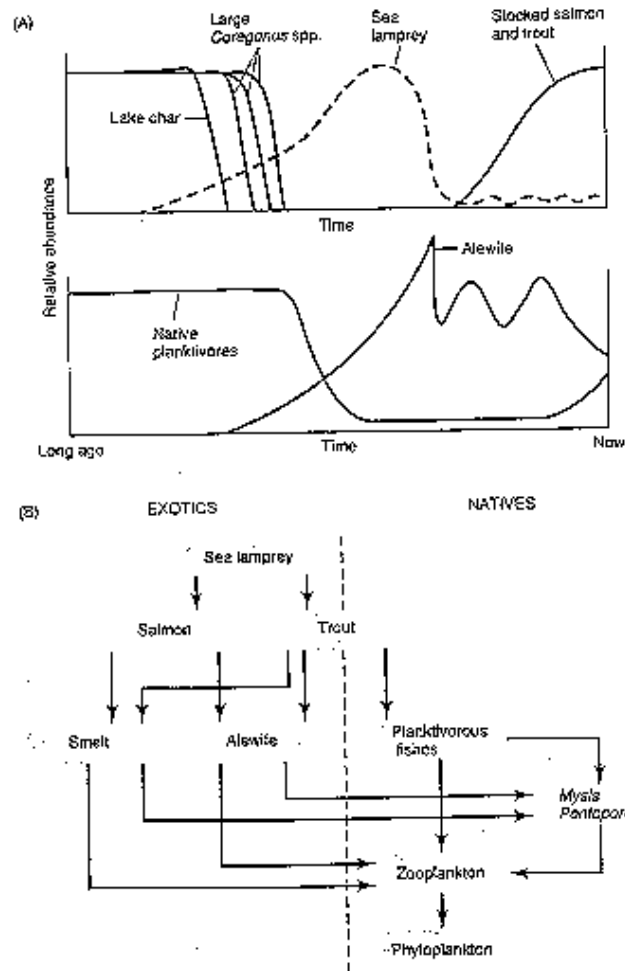


FIGURE 4. (A) Generalized representation of changes in fish populations in the North American Great Lakes. (B) Generalized pelagic food web of the Great Lakes. (From Kitchell and Crowder, 1986.)

Figure 3: (A) Generalized representation of changes in fish populations in the North American Great Lakes. (B) Generalized food web of the Great Lakes. (From [5]).

## Crayfish in northern Wisconsin

Until 1930 *Orconectes virilis* was the most common crayfish in northern Wisconsin lakes. *Orconectes propinquus* arrived around 1950 and *Orconectes rusticus* in the 1960s. *Orconectes propinquus* routinely displaces *Orconectes virilis* from lakes in which both are found, and *Orconectes rusticus* does the same to *Orconectes propinquus*.

The recently introduced *Orconectes rusticus* suffers less predation than its congeners, and it has greater weight-specific feeding rates. As a result, establishment of *Orconectes rusticus* results in reductions of littoral zone macrophytes and invertebrates, possibly even changes in nutrient cycling.

## The zebra mussel — *Dreissena polymorpha*

The zebra mussel provides a particularly scary example of some of the effects Lodge mentions. It is a native of southern Russia. It was introduced into the Great Lakes, apparently in 1985 or 1986 via water ballast from a foreign ship. By 1992 it had been spread throughout the Great Lakes and the St. Lawrence, the Mississippi from St. Paul almost to the Louisiana border, the Illinois River, the Ohio River, the Tennessee River, the Arkansas River, the Susquehanna River, and the Hudson River (Figure 4). Authorities in Connecticut presume that it is only a matter of time before it reaches the Housatonic and the Connecticut Rivers. It has been found in Twin Lakes in northwestern Connecticut. Individual mussels are usually 25–35mm in length, occasionally 50mm.<sup>5</sup>

There are two reasons why the spread of the zebra mussel is of particular concern.

1. It is one of the most notorious biofoulers in the world. By the year 2000, the cost of industrial, utility, and municipal water-use reductions plus the impact of the zebra mussel on navigation, boating, and sport fishing could reach \$5 billion in the Great Lakes alone.
  - Veliger densities in the Saratove Reservoir have reached 550,000 per cubic meter. In other reservoirs consistent densities of 300,000–400,000 per cubic meter have been reported, but a density of 2 million per cubic meter is not uncommon.
  - The Chernobyl intake had a density of 1–2 million adults per square meter; the total biomass in the cooling pond was 1.69 million kg; the greatest density was 19 kg/m<sup>2</sup>.

---

<sup>5</sup>Drawn largely from [8]

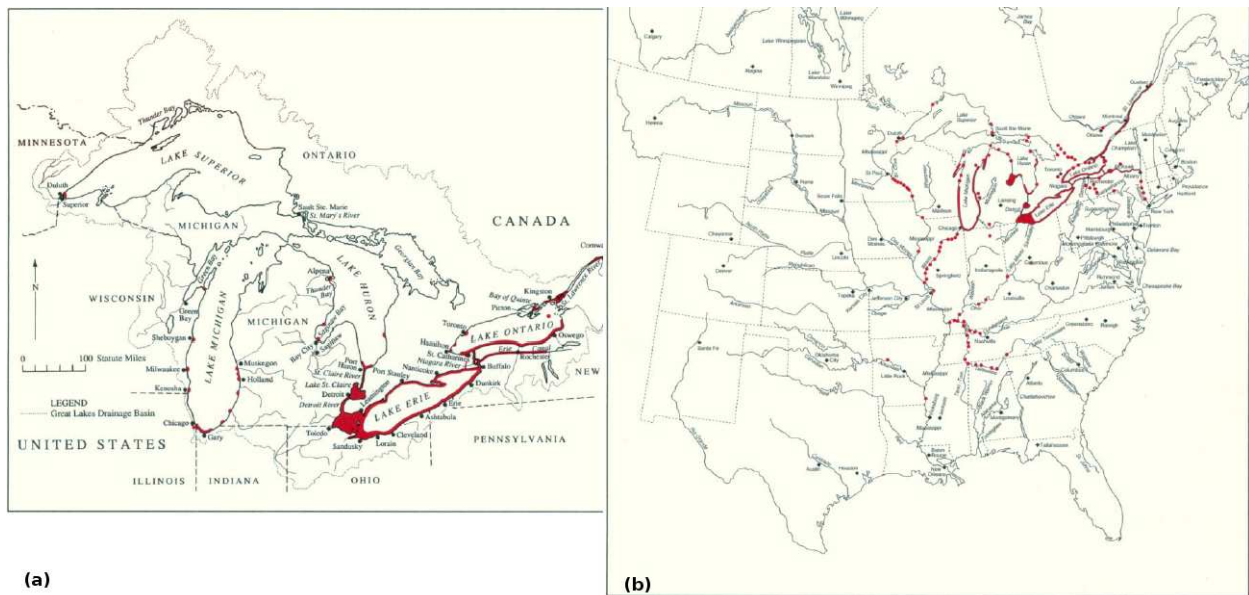


Figure 4: Introduction and early spread of the zebra mussel in North America. (a) Distribution as of 21 November 1990. (b) Distribution as of 15 October 1992. (From [8]).

- The Detroit Edison power plant has densities of up to 750,000 animals per square meter.
  - The opening of water intake tubes is sometimes reduced to as little as 20–30% of its original diameter.
2. It is a *very* efficient filterfeeder. The zebra mussels in Lake St. Clair, for example, can completely filter *all* of its water in 24 days, assuming a density of 10,000/m<sup>2</sup>. A more realistic density is 50,000/m<sup>2</sup>, leading to an expected filtering time of only 10 days. This may have a positive effect on polluted (or eutrophic) aquatic ecosystems, but it may also pose problems for many planktivores and dramatically alter the structure of aquatic communities.
- It removes a large amount of particulate matter from water, promoting a change from a relatively homogeneous environment of turbid water and silty sand substrata to an environment of clearer water with patches of macrophytes. In Lake Erie, Secchi disk transparencies almost doubled and chlorophyll *a* declined 54% between 1988 and 1989.
  - A scenario for Lake St. Claire<sup>6</sup>
    - Biodeposition of most nutrients in the water on the lake floor
    - Decline in primary production
    - Increased development of the benthic community
    - Reduction in biomass and production of zooplankton and fish
  - It removes contaminants from lake water, but it also concentrates them on lake floors and shorelines.
  - Direct threat to other mussels. Unionids with as many as 15,000 zebra mussels on their shell have been found. Often unable to open and close their valves fully.

## Risks of biological control

Biologists have purposely introduced many alien species for the purpose of controlling others that have been accidentally introduced. In some cases these introductions have proved highly successful. Approximately 40% of projects introducing herbivorous insects purposely introduced into the United States to control weeds show some evidence of success, and 20% appear to have exerted some significant control.

---

<sup>6</sup>Lake lying between Lake Huron and Lake Erie.

	percent heads infested
Native	(< 1)16–78%
Introduced	25–100%

Table 2: Results of a 1996 survey in Colorado, South Dakota, and Nebraska for *Rhinocyllus conicus* in thistle (from [7]).

- *Hypericum perforatum*—First reported from California in 1900, by 1944 it occupied more than 800,000ha.
- Four herbivorous insects were released for biological control efforts in 1945.
- Within a decade, it was reduced from an important pest of range lands to an occasional road-side weed.

Biological control is attractive because:

- May allow pests to be controlled *without* use (or with limited use) of chemical pesticides or herbicides.
- Potential for control over a broad geographical region continuously and without additional investment of time or money once control agents are established.

Depends for its effectiveness on:

- Ability of control agent to limit numbers of target species.
- Specificity of control agent for target species.

It's the second of these I want to say a few words about in this context. Consider the case of *Rhinocyllus conicus*, a flowerhead weevil, introduced into North America in 1968 in an effort to control populations of European thistles (*Carduus*).

- Original releases made even after initial feeding tests showed that the weevil's host range included native North American thistles (*Cirsium*, *Silybum*, and *Onopordum*). Stronger oviposition preference for *Carduus* and more successful larval development on *Carduus* were expected to limit use of North American thistles (Table 2).
- Significant increase from 1992 in native infestation.

- Seed production in infested heads 14% that of uninfested heads.
- Threatens persistence of *Cirsium canescens*, a sparsely distributed thistle restricted to the Sandhills prairie of Nebraska. *C. canescens* is presumed progenitor of *C. pitcheri*, which is a federally listed threatened species in the Great Lakes dunes. Foreshadowing of future impact if the weevil makes it to that ecosystem?

A similar study on parasitoids of native Hawaiian moths found that 83% were biological control agents and 14% were accidentally introduced wasps (216 parasitoids collected from 2112 caterpillars) [4].

We also face other difficult choices. In 1999 a biological control project was started in the desert southwest with a Chinese beetle. The control effort's objective is to reduce the abundance of saltcedar (tamarisk), which was originally introduced as a windbreak and to control soil erosion. It now covers almost 500,000 hectares in 15 states. It has crowded out many native species, including cottonwoods and willows that are important resources for desert bighorn. It provides 90% of the nesting habitat for the southwestern willow flycatcher, which is listed as endangered under the Endangered Species Act.<sup>7</sup>

## Conclusions

The story of Hawaii's native flora reminds us what an impact invasive exotics can have on a broad range of species. The story of fish introductions in the Great Lakes shows us how difficult it can be to predict the effects of any of those introductions. The crayfish story cautions us that seemingly minor changes can have unexpectedly large changes. The zebra mussel is perhaps the most sobering story of all. Who would have guessed that a little clam could cause such trouble? What can we do?<sup>8</sup>

- Keep non-indigenous species out until they are known to be safe—an instance of the precautionary principle. Purposeful introductions for biological control efforts need to be carefully examined. Note the possibly conflicting values of reducing chemical use and protective native plants and animals.
- Develop early monitoring programs to detect invasions while they are small enough to be more easily reversed or contained. Take advantage of the problems posed by life in small populations. With endangered species our concern was to prevent extinction. With invasive exotics our concern is to cause it.

---

<sup>7</sup>Its native habitat has been destroyed by past grazing and water-management practices in the parts of Arizona where it occurs.

<sup>8</sup>see [13] for a more complete discussion.

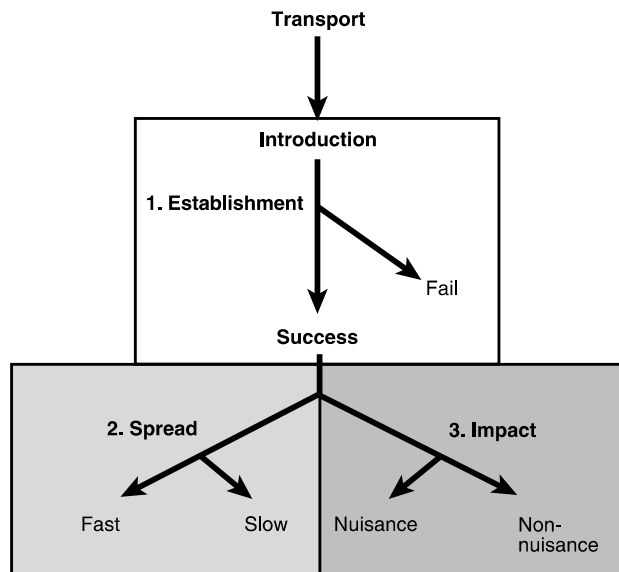


Figure 5: Obstacles to the establishment of introduced, invasive species. From Kolar and Lodge [6]

- In managing endangered species I suggested using a population viability analysis to identify vulnerable life-history stages so that management attention could be directed towards alleviating the passage through difficult life-history transitions.
- In this case a similar analytical approach could be taken. The difference is that we'd try to make those transitions even more difficult than they currently are.
- Develop lists of species known to cause problems elsewhere. They are the most likely to cause problems if introduced in a new habitat.
  - Kolar and Lodge [6] illustrate how it may be possible to do a little better, in at least some cases. First, we must recognize that there are several hurdles that must be crossed before a species can be introduced and cause damage to native ecosystems (Figure 5).
  - Using data on successful introductions and establishment in the Great Lakes, they produced a classification and regression tree (Figure 6) that allowed them to identify life-history variables that affect the chances of success at each stage and used it to identify 22 species from the Ponto-Caspian basin of central Asia

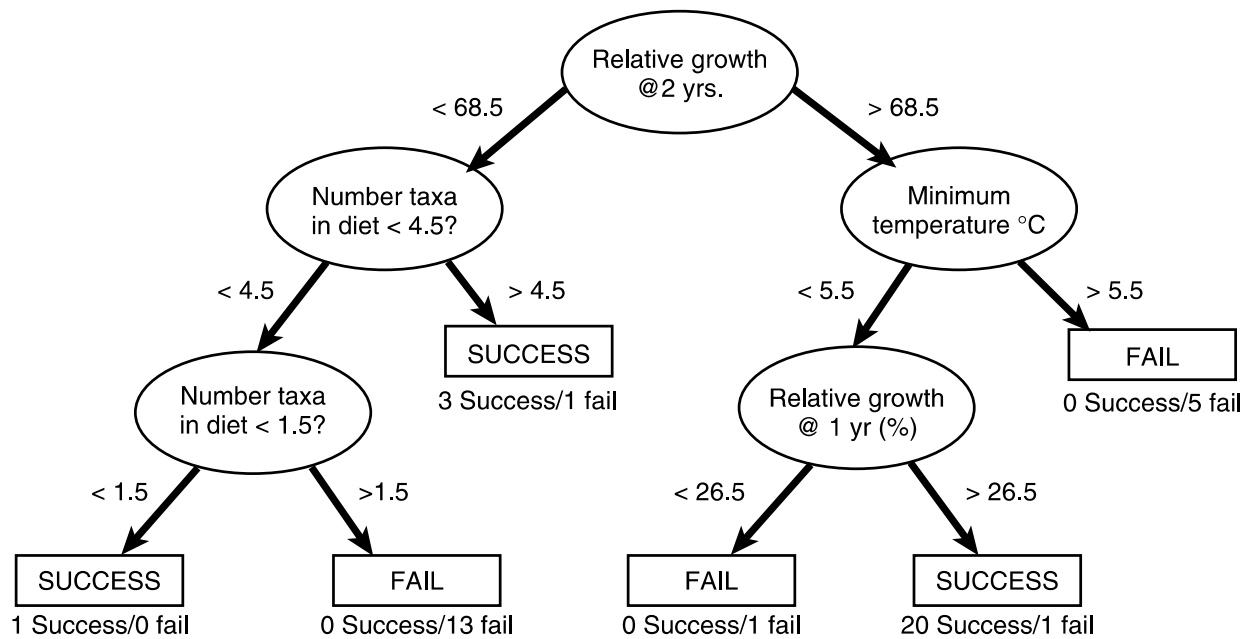


Figure 6: Classification and regression tree for introduction and invasiveness of freshwater fish in the Great Lakes. From Kolar and Lodge [6]

that might become established through unintentional introductions in the Great Lakes. Of those 22 species, only 5 were identified as likely to become a nuisance.

- If a non-indigenous species is consciously introduced, keep a record of the logic used to reach the decision and the consequences of the introduction so that the decision-making process can be improved.
- Be careful about deciding to eradicate a non-indigenous species once it becomes established. As the case of tamarisk shows, non-indigenous species may so change the structure of a community or ecosystem that eradication could have deleterious and unexpected consequences.<sup>9</sup>

This returns us to a theme I mentioned in my first lecture. Conservation biology tests our knowledge of ecological and evolutionary systems in much the same way as a well-designed experiment. To the extent we can predict and manage the impact of changes in a

<sup>9</sup>See [11, 16].

community's species composition, we have understood the dynamics that control it. To the extent we cannot predict and manage those dynamics, we have more to learn. Basic research in genetics, evolutionary biology, ecology, and systematics cannot help but provide us with the knowledge we need to manage ecosystems wisely. And our efforts to manage ecosystems cannot help but provide intellectual challenges for many years to come.

## References

- [1] E. J. Badano, E. Villarroel, R. O. Bustamante, P. A. Marquet, and L. A. Cavieres. Ecosystem engineering facilitates invasions by exotic plants in high-andean ecosystems. *Journal of Ecology*, 95:682–688, 2007.
- [2] C. C. Daehler and D. R. Strong. Native plant biodiversity vs. the introduced invaders: status of the conflict and future management options. In S. K. Majumdar, F. J. Brenner, J. E. Lovich, J. F. Schalles, and E. W. Miller, editors, *Biological Diversity: Problems and Challenges*, pages 92–113. Pennsylvania Academy of Science, Philadelphia, PA, 1994.
- [3] M. Groom, G. K. Meffe, and C. R. Carroll. *Principles of Conservation Biology*. Sinauer Associates, Sunderland, MA, 3rd edition, 2005.
- [4] M. L. Henneman and J. Memmott. Infiltration of a Hawaiian community by introduced biological control agents. *Science*, 293:1314–1316, 2001.
- [5] J. F. Kitchell and L. B. Crowder. Predator-prey interactions in lake michigan: predictions and recent dynamics. *Environmental Biology of Fishes*, 16:205–211, 1986.
- [6] C. S. Kolar and D. M. Lodge. Ecological predictions and risk assessment for alien fishes in north america. *Science*, 298:1233–1236, 2002.
- [7] S. M. Louda, D. Kendall, J. Connor, and D. Simberloff. Ecological effects of an insect introduced for the biological control of weeds. *Science*, 277:1088–1090, 1997.
- [8] M. L. Ludyanskiy, D. McDonald, and D. MacNeill. Impact of the zebra mussel, a bivalve invader. *BioScience*, 43(8):533–544, 1993.
- [9] C. J. Lutzow-Felling, D. E. Gardner, G. P. Markin, and C. W. Smith. *Myrica faya*: Review of the biology, ecology, distribution and control, including an annotated bibliography. technical report 94, cooperative national park resources study unit, university of hawaii at manoa, 1995.

- [10] M. L. McKinney and J. L. Lockwood. Biotic homogenizations: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, 14(11):450–453, 1999.
- [11] J. L. Myers, D. Simberloff, A. M. Kuris, and J. R. Carey. Eradication revisited: dealing with exotic species. *Trends in Ecology & Evolution*, 15:316–320, 2000.
- [12] D. Pimentel, L. Lach, R. Zuniga, and D. Morrison. Environmental and economic costs of nonindigenous species in the United States. *BioScience*, 50:53–65, 2000.
- [13] J. L. Ruesink, I. M. Parker, M. J. Groom, and P. M. Kareiva. Reducing the risks of nonindigenous species introductions: guilty until proven innocent. *BioScience*, 45:465–477, 1995.
- [14] S. M. Sohmer and R. Gustafson. *Plants and Flowers of Hawai‘i*. Univ. of Hawaii Press, Honolulu, HI, 1987.
- [15] P. M. Vitousek. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos*, 57:7–13, 1990.
- [16] E. S. Zavaleta, R. J. Hobbs, and H. A. Mooney. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology & Evolution*, 16:454–459, 2001.

## Creative Commons License

These notes are licensed under the Creative Commons Attribution-NonCommercial-ShareAlike License. To view a copy of this license, visit <http://creativecommons.org/licenses/by-nc-sa/2.5/> or send a letter to Creative Commons, 559 Nathan Abbott Way, Stanford, California 94305, USA.