

# Hyperconnectivity, invasive species, and the breakdown of barriers to dispersal

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## INTRODUCTION

The conservation implications of connectivity arise at many spatial scales. At the regional or landscape level, decreasing connections between natural areas inhibit the movement of species dependent on those habitats. Therefore, current conservation efforts often focus on connecting systems and facilitating the exchange of organisms between otherwise isolated patches. This dispersal of individuals can benefit populations by promoting gene flow and decreasing local extinction risk. Although increasing connectivity at the regional level may have negative consequences, such as altering source–sink dynamics, preventing local adaptation, accelerating the transport of pathogens, and facilitating the localized spread of invaders (Simberloff *et al.* 1992), it is typically considered that the benefits of restoring connectivity outweigh the risks (Crooks and Sanjayan Chapter 1). Much of the current volume addresses the topic of maintaining or increasing connectivity of this type.

At a larger spatial scale, such as between continents, a different connectivity-related conservation concern arises. Because of the long distances involved, natural movement at these scales should be relatively rare. Species can naturally traverse long distances both passively (e.g., via ocean currents or air masses: Scheltema 1986; Censky *et al.* 1998; Ritchie and Rochester 2001; DiBacco *et al.* Chapter 8) and actively (e.g., through

migration: Møller *et al.* 2003), and those few species that do make long-distance treks are often the target of conservation efforts (Harrison and Bjorndal Chapter 9; Marra *et al.* Chapter 7). Currently, however, the majority of global species movement does not occur naturally. Rather, a vast array of anthropogenic transport mechanisms has arisen, allowing for rampant species invasions. This has resulted in systems with greatly inflated connectivity relative to natural, background levels.

This rapid expansion of invasion vectors has promoted an explosion of problems associated with the introduction of species. It is estimated that invasions in six countries (the USA, Britain, Australia, South Africa, India, and Brazil) cost over \$300 billion per year in control efforts and damages (Pimentel 2002). Alien predators, parasites, competitors, and habitat modifiers have penetrated and wreaked havoc in ecosystems throughout the world (Bright 1998; Cox 1999; Baskin 2002; J. A. Crooks 2002). Africanized bees (*Apis mellifera*), gypsy moths (*Lymantria dispar*), brown tree snakes (*Boiga irregularis*), fire ants (*Solenopsis invicta*), zebra mussels (*Dreissena polymorpha*), and kudzu (*Pueraria montana*) are a familiar, but albeit small, sampling of the invaders that now abound throughout the world's ecosystems.

The global swapping of a few successful species is also leading to biotic homogenization of the world's ecosystems (Lockwood and McKinney 2001; Olden *et al.* 2004), resulting in an anthropogenic "New Pangaea" (Rosenzweig 2001). Contemporary times even have been referred to as the "Homocene," an age of homogenization. Because invasions erode the uniqueness of systems, diversity at large spatial scales has been diminished. For example, invasions and urbanization in California promotes the success of a few human-associated bird species (~20%), at the expense of many sensitive species of high conservation value (>50%) (Blair 1996). More striking is the homogenization of fish faunas across the USA due to introductions. On average, US states now have 15 more fish species in common than during pre-European settlement (Rahel 2000). Interestingly, however, invasions can actually have neutral or positive effects on diversity at smaller spatial scales (Sax *et al.* 2002). Across the Pacific region as a whole, for example, avian species richness and endemism have been greatly reduced, but the average number of bird species on a per-island basis remains similar due to the successful establishment of a few widely dispersed introduced species (Steadman 1995; Case 1996). In places like San Francisco Bay, species extinctions appear not to have kept up with the remarkable pace of invasions, and it is very likely that more species are in that system

now than were there 200 years ago (Cohen and Carlton 1998; Carlton *et al.* 1999).

Connectivity and invasions also intersect at the landscape level. In general, both habitat fragmentation and invasions represent major threats to the integrity and diversity of natural ecosystems, are increasing due to human activities, and are difficult to remedy once they have occurred (Wilcove *et al.* 1998). A tighter link also exists between invasions and habitat fragmentation. Relatively large numbers of invaders are typically found in smaller, more fragmented patches of natural habitats when compared to larger, more connected fragments. Similarly, highly modified habitats (such as the urban matrix) tend to support more invaders than less-developed areas (Hobbs and Huenneke 1993; Suarez *et al.* 1998; K. R. Crooks *et al.* 2004). This is commonly attributed to factors such as disturbance, habitat requirements of natives, and the relative increase in edge in small patches.

In this chapter, we examine increased connections caused by anthropogenic activities, and call this phenomenon hyperconnectivity. In terms of biological invasions, hyperconnectivity can result from both the provision of artificial vectors of species transport and the creation of expansive human-modified habitats that facilitate invaders. We first discuss the transport of invaders, including characterizations of invasion vectors, rates of invasion over time, and the effect of continued immigration on already established populations. We next consider how connectivity of habitats within recipient ecosystems influences invasion success, and conclude with a discussion of management implications related to hyperconnectivity and invasion.

## HYPERCONNECTIVITY AND THE TRANSPORT OF INVADERS

### The proliferation of invasion vectors

We live in an age of globalization. Changing economies and politics have meant new trading partners and the opening of world markets (Mack 2003). People and goods now move around the world with unprecedented ease. These connections by land, air, and sea move vast numbers of organisms in a global “ecological roulette” (Carlton and Geller 1993). Although the long-distance dispersal of species into a new locale can be a natural biological event, the manner and rate at which species now move around the globe is wholly unprecedented. Mosquitoes have been transported in used tires, brown tree snakes (*Boiga irregularis*) have hitched rides in airplane wheel wells, “killer algae” (*Caulerpa taxifolia*)

have been dumped with aquarium water into the sea, lampreys (*Petromyzon marinus*) swam through canals to enter the Great Lakes, and kudzu (*Pueraria montana* var. *lobata*) was intentionally planted for ornamental purposes (Cox 1999; Ruiz and Carlton 2003). Here we consider the processes involved in the actual transport of invasive species.

In broad terms, organisms can be intentionally or unintentionally transported across natural barriers and released into the environment (Table 18.1). Intentional introductions occur for many different reasons, including food, sport, biological control, landscaping, and esthetics. An infamous example of intentional introduction is the millions of starlings (*Sturnus vulgaris*) in North America that owe their existence in the New World to the 60 birds released in 1890 by the first President of the North American Acclimatization Society (Lever 1992). Motivated by such factors as introducing all the birds mentioned by Shakespeare (in the case of the aforementioned starlings) and making foreign landscapes more familiar, acclimatization societies are responsible for the establishment of many invasive species in North America, Australia, and New Zealand (Lever 1992).

Biological control of pest organisms, achieved through the introduction of natural enemies, is another example of purposeful introductions, and it represents an entire subdiscipline of biology (DeBach 1974; Van Den Bosch 1982; Van Dreische and Bellows 1996). There are many examples of successful biological control (Flint and Dreisadt 1999), and standard practice dictates that the release of these agents receives intense scrutiny. There are, however, many examples of negative, non-target effects of biological control (Howarth 1991; Follett and Duan 1999). For example, the European weevil *Rhinocyllus conicus*, introduced to North America for control of exotic thistles, switched to native thistles where they reduce seed production and indirectly impact native insects through competition for food resources (Louda *et al.* 1997).

Biological control efforts on islands can be even more problematic. Host switching by parasitoids introduced to control non-native moths in Hawaii has led to parasitism rates of about 20% across 54 endemic moth species (Henneman and Memmott 2001). Introductions of generalist predators provide even more stark examples of intentional releases gone awry, including a series of misguided attempts to control exotic rats (*Rattus* spp.) on Pacific islands (Laycock 1966). To deal with the rat problem, top predators such as monitor lizards (*Varanus indicus*) and mongoose (*Herpestes javanicus*) were intentionally introduced. However, rats are primarily nocturnal while the introduced predators are diurnal.

**Table 18.1.** *Vectors of invasion into ecosystems****Intentional introductions of target species***

Escape of species from containment

- Zoos and botanical gardens
- Landscaping and ornamentals
- Pets
- Farmed species
- Agriculture
- Aquaculture and mariculture
- Research

Release directly into the environment

- Forestry plants
- Plants for soil improvements (e.g., stabilization)
- Ornamental plants
- Animals for hunting and fishing
- Biological control
- “Freed” pets
- “Enrichment” of native biota (e.g., through acclimatization societies)
- Disposal of living packing material (e.g., seaweed for bait)
- Bait
- Research
- Reintroductions of natives

***Release of non-target species (“accidental” releases)***

Contaminants or hitchhikers associated with goods

- Produce
- Nursery plants
- Cut flowers
- Seed stock
- Soil
- Timber
- Aquaculture and mariculture species
- Packing material
- Mail and cargo

Contaminants or hitchhikers associated with transportation

- Cars, trucks, airplanes, etc.
- Machinery, equipment
- Dry ballast in ships
- Ballast water
- Ballast sediments
- Ship hull fouling (e.g., barnacles and mussels)
- Tourists, luggage
- Canals
- Roads

Hitchhikers associated with artificial structures

- Movement of maritime superstructures (e.g., oil rigs)
- Floating debris

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*Source:* Adapted from Wittenburg and Cock (2001).

Subsequently, native species often became primary prey items, leading to the decline of many local birds and lizards (Case and Bolger 1991). Problems were compounded even further when other species were introduced to divert the predators' attention from natives. For example, the giant toad (*Bufo marinus*) was introduced to act as alternate prey for monitor lizards, but as the toads are poisonous, they have led to declines in species that eat them, including pet dogs and cats (Laycock 1966; Atkinson and Atkinson 2000).

Despite many examples of intentional introductions, the bulk of invasions result from "unintentional" introductions. A cautionary note about terminology is warranted here, however. Although many types of introductions are often called "accidental" or "unintentional," we know enough about their vectors to assess the relative likelihood of release of at least some potential invaders. There is little accidental about unloading a cargo of timber that is sure to be laden with foreign insects. This has management implications that rise above semantics, and it should be assumed that the operation of known vectors can release organisms. Therefore, the "unintentional" release of organisms through such activities should no longer be considered "accidents" (Moyle 1999).

Terminology aside, for an organism to successfully arrive in a recipient ecosystem by means other than targeted releases, a number of steps must occur. First, an organism must associate itself with a means of transport — an invasion vector. This often involves a species being moved in association with a physical mode of transportation (e.g., a boat or airplane), but man-made changes in the landscape, such as roads or canals, also can facilitate biological invasions. The likelihood of utilization of a vector by a species is affected by the abundance of an organism in its native range, its habitat preferences, and the characteristics of the vector. In the case of ballast water (used to maintain ship stability during ocean crossings), for example, those species most likely to be entrained are small organisms floating in the water column near ports. Second, the invader must survive during transit, where it will be subjected to a variety of biotic and abiotic pressures. In the ballast tank, a species is likely to encounter competitors and predators, and will be subjected to environmental conditions that may include the presence of toxins and lack of light. Finally, the transported organism must survive upon release into the new environment. This survival involves matching of conditions in source and recipient areas. A planktonic organism in ballast water from Guam will likely find disagreeable environmental conditions upon release in an Alaskan harbor.

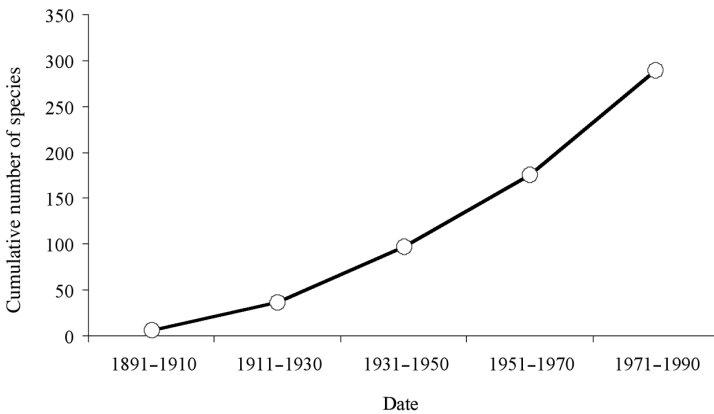
The vectors that move organisms across biogeographic boundaries vary widely in size and efficacy. Among all vectors, ballast tanks appear to be the champion species movers (Carlton 1985, 1987; Carlton and Geller 1993). A single tank can hold many millions of liters of water, with astonishing densities of associated organisms. Densities per single liter of ballast water have been estimated at tens to hundreds for zooplankton, thousands to millions for phytoplankton, and billions for bacteria and viruses (Ruiz and Carlton 2003). This tremendous density translates into high species richness. Carlton and Geller (1993), studying ships entering Coos Bay, Oregon, conservatively identified 367 planktonic species in the ballast water. It has been estimated that at any one time, over 7000 species may be on the move in ballast tanks of ships plying the world's waters (Carlton 1999).

Patterns of vector operation often will vary markedly with time (Ruiz and Carlton 2003). These changes are primarily associated with technological and socio-economic advances and can strongly influence the composition of species being transported. Kiritani and Yamamura (2003) have examined temporal patterns of invasion in Japanese insects. Japan first opened to external influences in 1868, and from then until World War II, invasions were characterized by scale insects and mealybugs associated with a large-scale effort to import fruit trees. The 20 years after World War II saw an invasion of beetles associated with grains moved into the country to prevent food shortages. The third phase of invasion, from 1966 to 1985, was characterized by weevils that infest crops, turfs, vegetables, and ornamental trees, and the most recent wave by greenhouse pests such as thrips, aphids, and whiteflies.

Similar shifts have been seen in west coast marine systems of the USA (Carlton 1979; Ruiz and Crooks 2001; Wonham and Carlton 2005). The first primary vector of invasion was fouling, the transport of organisms living in or on the hulls of ships. The current practice of using metal hulls and antifouling paints has limited spread by this means, although it certainly continues and its impact may be underestimated (Fofonoff *et al.* 2003). The second wave of invasion came from the movement of commercially important animals, and more importantly, species associated with these intentionally transported organisms. Starting in the late nineteenth century, there were large-scale movements of both Japanese and Virginia oysters (*Crassostrea* spp.) onto the west coast, and many invasions can be traced to the mud, packing materials, and shells associated with the movement of live oysters (Miller 2000). The most recent wave of invasion is due to transport with ballast water, and although this may be

decreasing due to current regulations requiring ballast exchange, data for tracking invasion rates in response to management actions is limited (but see Drake and Lodge 2004). It also should be noted that there are many other vectors that have brought invasive species to this region (Carlton 1979; Chapman *et al.* 2003), such as the aquarium trade (Semmens *et al.* 2004) and algal packing material used for live seafood and bait (Carlton and Cohen 2003).

Despite our ability to detect broad patterns in species arrivals, predicting the precise timing of invasion via a particular vector is difficult. Many species likely utilize a vector soon after it becomes operational, but it is also possible that there are long lags in between the commencement of new means of invasion and successful use by invaders (J. A. Crooks 2005). In the case of species invading the Mediterranean Sea via the Suez Canal (Boudouresque 1999), the rate of appearance of new invaders has risen steadily since the time of opening in 1869 (Fig. 18.1). This may be due in part to changing conditions in the canal and Mediterranean, but stochastic factors are also likely at work. Another example is the zebra mussel in the Great Lakes. Despite ballast water being dumped into these lakes for decades, it was not until the 1980s that the mussel was first detected (Nalepa and Schloesser 1993). A potential problem with such cases, however, is that it is difficult to distinguish whether a lag was actually in the arrival phase (i.e., the species never utilized the vector) or in the establishment phase (i.e., the species arrived well before it got noticed) (J.A. Crooks and Soulé 1999; Costello and Solow 2003). Determining



**Fig. 18.1.** Cumulative number of species invading the Mediterranean Sea via the Suez Canal, which opened in 1869. (Adapted from Boudouresque 1999.)



where the lag actually occurred is typically difficult, but it is important to recognize that the failure of a species to utilize a given vector does not indicate that it is incapable of doing so.

### **Anthropogenic influences on invasion rates**

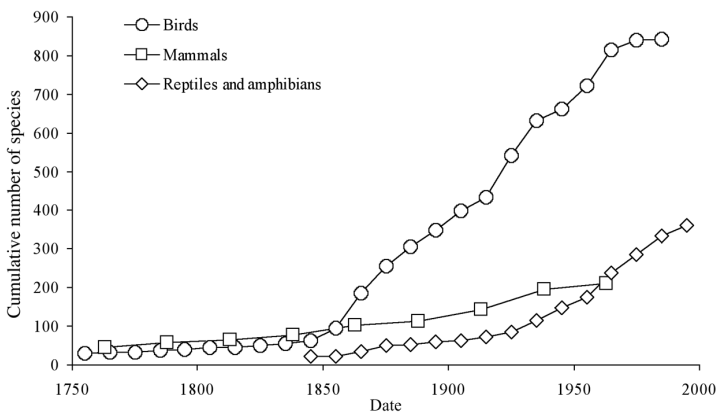
General principles suggest that probability of invader establishment should increase with (a) increased abundances of released organisms, (b) increased frequency of release, (c) increased numbers of released species, and (d) faster transfers (Ruiz and Carlton 2003). However, quantifying any of these relationships remains a great challenge in invasion biology because most of what we know about invasions comes from examination of already established invaders – ones that have successfully arrived as well as formed reproductive populations. These species have been subjected to the rigors associated with both the vector and the receiving environment, thus confounding the arrival and establishment phases of invasion. Despite this challenge, some patterns of invasion related to vector activity have emerged.

The first key question is the relationship between arrival and establishment, and determining what proportion of the inoculant pool will become successful invaders (e.g., Wonham *et al.* 2000, 2001). This number will be highly variable depending on the species transported, the vector, and the receiving environment (e.g., Cowie and Robinson 2003; Kraus 2003), but Williamson (1996) has suggested that approximately an order of magnitude fewer species will establish than arrive. There have been some attempts to quantify this. For intentionally introduced biological control agents, estimated success rates range between 13% and 34% (Hall and Ehler 1979; Ehler and Hall 1982). However, the success rate of unplanned, non-target invasions may be lower. In Japan, over 250 longhorned beetle species have been discovered by agricultural inspection, but only seven (3%) of those are considered established (Kiritani and Yamamura 2003). In the Yeayama Islands of Japan, 71 species of naturally migrating butterfly species have been observed, but only 10 (14%) are considered established (Kiritani and Yamamura 2003).

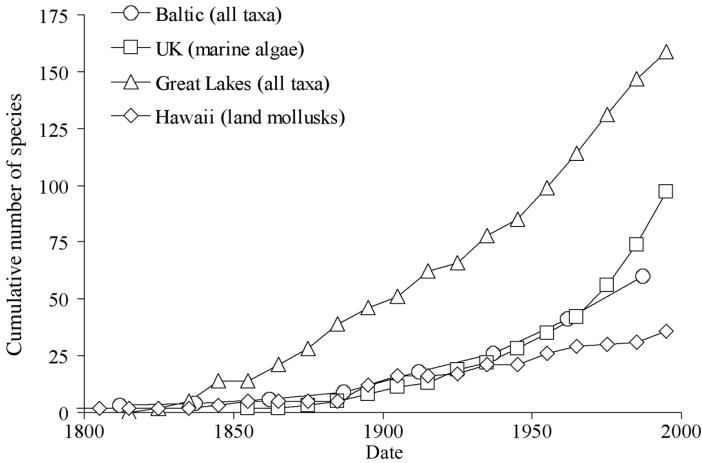
We can also ask how the rate of (successful) invasion has changed over time. There is no doubt that the total rate of invasion over the last few centuries far surpasses any rate seen previously, and estimated magnitudes of this difference are remarkable. For example, in Hawaii, it is estimated that one successful invertebrate colonization occurred every 50 000–100 000 years under natural conditions (Holt 1999). Currently, this anthropogenically inflated rate is estimated at one invasion every

18 days (Holt 1999). For ants specifically, despite winged dispersal of reproductives, no species naturally colonized the Hawaiian Islands. However, over 40 exotic ants are now established, most since World War II (Krushelnycky *et al.* 2005). For cladoceran crustaceans (“water fleas”) in the Great Lakes, genetic evidence suggests that the anthropogenic rate of invasion is 50 000 times greater than the natural rate (Hebert and Cristescu 2002).

On more recent timescales, a wide variety of empirical data support constant or accelerating rates of both introduction of exotic species to the wild (Fig. 18.2) and establishment of successful invasive populations (Fig. 18.3). For example, recent syntheses of global reptile, amphibian, bird, and mammal invasion data demonstrate steadily increasing rates of release of these taxa (Kraus 2003) (Fig. 18.2). Similar patterns have also been seen for the introduction of terrestrial mollusks in Hawaii, with successful establishment rates that track those of introduction rates (Cowie and Robinson 2003). In aquatic systems, dramatic increases in successful invasions have been seen in many systems, including San Francisco Bay (Cohen and Carlton 1998), San Diego (J.A. Crooks 1998), the USA in general (Ruiz *et al.* 2000; Fofonoff *et al.* 2003; Fuller 2003), European coastlines (Ribera Siguan 2003), Port Phillip Bay in Australia (Thresher *et al.* 2000), and the Great Lakes (Ricciardi 2001). Although such patterns are undoubtedly affected by increased search effort and better taxonomy in recent years (Cohen and Carlton 1998), and perhaps by



**Fig. 18.2.** Cumulative number of species introduced to the wild (globally). Data include both successful and unsuccessful invasions. (Adapted from Kraus 2003.)

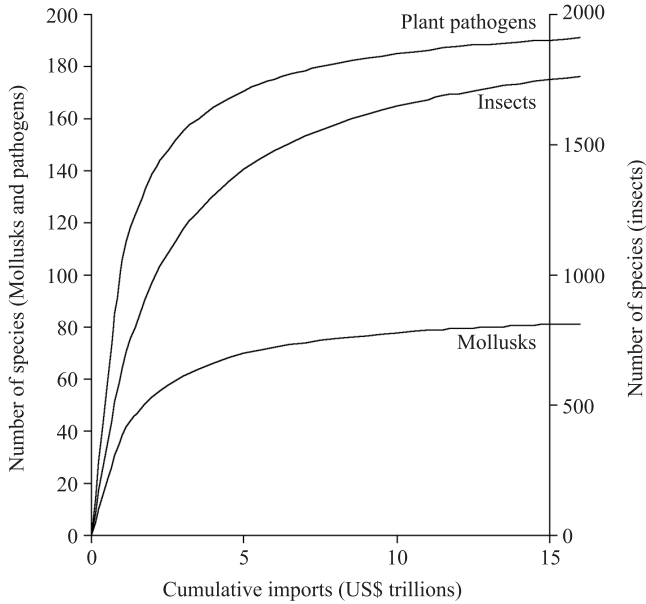


**Fig. 18.3.** Cumulative number of invasive species established in the wild for different geographic regions. Data from Ricciardi (2001), Leppäkoski *et al.* (2002), Cowie and Robinson (2003), and Ribera Siguan (2003).

the intrinsic dynamics of invasive populations (Costello and Solow 2003), there is little doubt that the rate of invader appearance in systems worldwide is on the rise (J. A. Crooks 2005).

There are several factors driving this increased invasion rate. Paradoxically, even though invaders are often associated with disturbance (see below), it has been suggested that improving environmental conditions in some highly degraded systems (such as urbanized bays) may have contributed to the increasing invasion rate (Great Lakes Environmental Research Laboratory 2002). For example, improving water quality in polluted and largely azoic parts of the Los Angeles/Long Beach Harbor allowed the invasion of crustacean bioeroders (gribbles) that destroyed wooden docks (Reish *et al.* 1980). The main force underlying the trend of increasing invasion rate, however, is clearly the frantic pace at which trade now occurs (Office of Technology Assessment 1993; Ruiz and Carlton 2003; Drake and Lodge 2004). In the USA, trade has been increasing exponentially, and over the next two decades it is expected to grow at about 6% per year (Levine and D'Antonio 2003).

Levine and D'Antonio (2003) discuss the relationship between invasions and trade, relating past imports to numbers of biological invaders and forecasting future invasion rates in the USA. The accumulation of successful invaders resulting from the operation of a specific vector turns out to be a problem similar to that of encountering new species when



**Fig. 18.4.** Predicted relationship between cumulative imports and the accumulation of invaders. (Adapted from Levine and D’Antonio 2003.)

examining a series of samples from a community. In the case of species arriving on a ship, the per-ship probability of moving a new species declines as the number of ships increases. There is a limited pool of available species in the source region, and each ship is repeatedly sampling from the same pool. Thus, as more and more ships move, it is decreasingly likely that a new species will be sampled. The authors also modeled number of established exotic mollusks, plant pathogens, and insects as functions of cumulative imports since 1920, and used these models to forecast future invasions with projected increases in foreign imports (Fig. 18.4). The models conservatively predicted the establishment of three new terrestrial mollusks, five new plant pathogens, and 115 new insects in the USA over the next 20 years.

The dynamics of invasion also suggest that the rate of local appearance of new species can increase even without a concomitant increase in trade and vector activity. The “hub-and-spoke model” (Carlton 1996) demonstrates that as species get transported to new trade centers (the hubs), there will be an increased number of source regions from which invasions can radiate (the spokes). Unfortunately, this positive feedback suggests

that new invasions will continue to be a problem even if vector activity levels off.

### **Vector activity and the population dynamics of established invaders**

Hyperconnectivity is at the core of species initially arriving in a new location, but hyperconnectivity and the movement of individuals remains important as invasive populations grow and spread around the inoculation site. The process of utilizing an invasion vector, whether passively (e.g., on a boat) or actively (e.g., swimming through a canal), is likely to put checks on invasive populations. The decline in number of individuals caused by mortality incurred during transit and upon release are particularly important, and can result in relatively few individuals forming the new populations. Theory suggests that this likely will have genetic consequences related to population bottlenecks and founder effects, and the resulting restrictions in genetic diversity tend to negatively impact incipient populations (Mayr 1963; Soulé 1980; Mooney and Cleland 2001; Frankham Chapter 4).

The genetic factors associated with founding populations of invaders have important implications that highlight the need to consider invaders and their management on levels other than that of simply species presence and absence (Petit 2004). For example, just because an invader has already arrived in a system does not suggest that additional introductions of the same species are of no concern. Repeated inoculations will increase genetic flow and work against the inherent checks of small population size and low genetic diversity, thus increasing invasion success (J.A. Crooks and Soulé 1999; Mooney and Cleland 2001). Theory suggests that just one migrant per generation is sufficient to guard against losses in genetic diversity (Mills and Allendorf 1996), and thus there is a direct link between continued connectivity between systems and the potential for expansion of invasive populations. This should provide strong motivation for vector control above and beyond that related to the appearance of new species.

Despite this positive relationship between size of the founding colony and probability of successful establishment, very small numbers of individuals can eventually form large populations. Elephant seals, for example, were nearly exterminated and it is believed that a population of less than 20 individuals eventually recovered to over 100 000 seals (Hoelzel 1999). For invasive ants, evidence suggests that new populations can be founded with a single queen and as few as 10 workers (Tsutsui and Suarez 2003). There are also exceptions to the typical negative effects associated with

small founding populations. For Argentine ants in North America, it has been suggested that a loss of genetic diversity resulting from the invasion process led to a decrease in the expression of intraspecific aggression in introduced populations (Holway *et al.* 1998; Tsutsui *et al.* 2000, 2003). This promotes the formation of expansive, competitively dominant supercolonies that have severe ecological impacts on natural communities (Holway *et al.* 2002a).

Connectivity also plays a role in the post-introduction range expansion of invaders. Species often spread via expanding fronts, and simple passive diffusion models have improved our understanding of this aspect of spread (Hengeveld 1989; Hastings *et al.* 2004). Invaders also can traverse long distances and over natural barriers by a process known as jump dispersal. The importance of this mode of movement has recently been highlighted by both theoretical and empirical work. Higgins and Richardson (1999) used simulations to demonstrate that long-distance dispersal by as little as 0.001% of propagules (seeds in this example) could increase the overall rate of spread by an order of magnitude. Suarez *et al.* (2001) reconstructed the spread of Argentine ants in the continental USA and determined that human-mediated jump-dispersal events accounted for a majority of the spread of this species. Natural rates of dispersal through a diffusion-like process averaged only around 200 m per year, yet this ant spread to over 275 counties in the USA within 50 years of its establishment.

In zebra mussels, human-mediated dispersal can consist of both advective (i.e., within-watershed), and jump dispersal (i.e., across-watershed) events (Johnson and Carlton 1996; Johnson and Padilla 1996). In an attempt to quantify the potential for spread through a primary vector for this species, Buchan and Padilla (1999) measured the rates and distances that recreational boaters traveled in Wisconsin. While a great majority of boaters traveled only short distances, primarily within watersheds, a small number of boaters traveled large distances among watersheds, providing ample opportunity for zebra mussels to establish new, distant foci from which to spread. Also, the extent to which species spread by human-mediated jump dispersal may influence the success of control strategies. For example, preventing the establishment of new infestations can greatly enhance control efforts relative to preventing spread from currently established populations (Moody and Mack 1988). In this light, human-derived hyperconnectivity among formerly isolated areas can greatly influence invasion rates and dynamics at wide-ranging spatial scales.

## HABITAT CONNECTIVITY WITHIN INVADED LANDSCAPES

### Ecosystem quality and invasion success

One of the most discussed topics in invasion biology has been the ecosystem characteristics that confer ecological resistance to invasion (Levine and D'Antonio 1999; Lonsdale 1999). The general idea, espoused by Elton (1958), is that species-poor, disturbed systems should be particularly vulnerable to invasion. The recent literature shows substantial debate on the relationship between diversity and invasibility (and ecosystem properties in general: Kaiser 2000; Loraue *et al.* 2001; Naeem and Wright 2003). An emerging picture is that there is often a negative relationship between diversity and the success of invaders, but only when considered within a similar set of environmental conditions at relatively small spatial scales (Kennedy *et al.* 2002; Shea and Chesson 2002). Integrating over different habitat types at larger spatial scales, it appears that areas that are good for natives are also good for exotics, leading to positive correlations when a range of ecological conditions are considered (Stohlgren *et al.* 1999; Shea and Chesson 2002).

There have been similar discussions about the relationship between disturbance and invasion (Hobbs and Huenneke 1992; D'Antonio *et al.* 1999; Alpert *et al.* 2000). There has been much less experimental focus on this topic (but see Hobbs and Atkins 1988; Burke and Grime 1996; White *et al.* 1997), but a large body of empirical evidence supports the idea that disturbed habitats have more invaders (Elton 1958; D'Antonio *et al.* 1999). It is a common observation that degraded areas have a relative preponderance of invaders. For example, studies along roadsides show that the number of alien plants decreases with increasing distance from the road (Tyser and Worley 1992; Gelbard and Belnap 2003). In California, the invasive Argentine ant increases its abundance with elevated moisture, such as in urban areas and areas with runoff from development (Holway *et al.* 2002b). Also, the densities of non-native and human-commensal birds and mammals often rapidly decline away from urban or agricultural development (Blair 1996; Bolger *et al.* 1997; K.R. Crooks 2002; K.R. Crooks *et al.* 2004). Marine bays and estuaries, which tend to be characterized by anthropogenically reduced habitat quality relative to the open ocean, typically have more invaders than the open coast (e.g., Carlton 1979; Wasson *et al.* 2005).

It is difficult to attribute such patterns to environmental conditions alone, however. It is tempting to say that these areas are more invaded because they are more disturbed, but invasion patterns are confounded by

the spatial distribution of vector operation (Cohen and Carlton 1998; Lonsdale 1999; Ruiz *et al.* 2000). It is expected that roadsides would have more invaders because more propagules would be transported there, such as on passing vehicles or through intentional plantings of ornamentals. Similarly, in the oceans, most of the transport mechanisms operate between one bay and another. Ships with their ballast and fouling move from port to port, and many intentional introductions and unintentional introductions of tag-along species occurred in protected coastal water bodies (Carlton 1979; Fofonoff *et al.* 2003). This would greatly favor the transport of estuarine rather than open-coast species.

### **Fragmentation is in the eye of the beholder**

If we broadly accept that vectors and environmental conditions interact to make disturbed areas more vulnerable to invasion, then exotics and natives may tend to “view” an ecosystem differently. In essence, the establishment and spread of exotic organisms may be facilitated by the hyperconnected, degraded habitat that has resulted from expansion of urban and agricultural areas. What represents a very loosely connected, fragmented system to a native species depending on natural habitats may seem a highly connected, extensive system to an exotic associated with disturbed, urban, or agricultural settings. Smaller, more fragmented patches of remnant natural habitat appear particularly vulnerable to invasion. Moreover, the actual urban/agricultural matrix is suitable and perhaps even preferred habitat for invaders, while in many cases these heavily modified areas do not support large numbers of natives (Suarez *et al.* 1998; K.R. Crooks *et al.* 2004). Therefore the remnant natural patches that remain are truly isolated for these native species.

The well-studied scrub habitat remnants in urban San Diego, California, USA, provide an excellent example of how a system can be highly connected for some species but isolated for others. Many studies show that these habitat fragments are islands for many species of area-sensitive animals including scrub-specialist birds, mammals, and insects (Soulé *et al.* 1988; Bolger *et al.* 1997; Suarez *et al.* 1998; K.R. Crooks and Soulé 1999). For taxa as diverse as birds, mammalian carnivores, and ants, introduced species are much more common in the urban matrix than they are within the remnant patches of native vegetation (K.R. Crooks 2002; Holway *et al.* 2002b; K.R. Crooks *et al.* 2004). Their abundance therefore appears as an edge effect with densities peaking in urban sites and along urban edges and declining with distance into natural vegetation. In effect, the urban matrix, normally thought to decrease connectivity among



isolated patches of habitat, is acting as continuous habitats and corridors for invasive species.

There is also some evidence to suggest that once invaded, ecosystems can be modified by established exotics to pave the way for further invasions. This process has been termed “invasional meltdown” (Simberloff and Von Holle 1999), and it suggests that positive feedbacks may develop that progressively decrease habitat quality for natives. For example, within an Argentinean national park, exotic plants more readily invade areas heavily browsed by exotic livestock than they do more intact areas (Veblen *et al.* 1992).

### IMPLICATIONS OF HYPERCONNECTIVITY FOR CONSERVATION AND MANAGEMENT

Hyperconnectivity is homogenizing the world’s biota and facilitating the invasion of species that are dramatically altering the structure and function of ecosystems. The best opportunities to develop sound management strategies that address this crisis will arise from understanding the process of invasion, characteristics of invaders, vectors of transport, and factors that influence vulnerability of ecosystems. Some important management principles that arise from a consideration of hyperconnectivity have been highlighted above. For example, invasions at the level of the gene emphasize that continued reintroductions of establishing invaders will serve to counter the natural factors working to limit invasion success. Also, the lag effect suggests that there may be long periods of time before a vector gets utilized or populations explode after successful invasion. These delayed responses hamper predictions regarding invader identity and invasion timing (J. A. Crooks 2005).

Above all, the overriding principle of invasion management should be that prevention is the best medicine, as it is notoriously difficult to deal with invaders after they have become established. A recent volume published as a result of a Global Invasive Species Programme conference (Ruiz and Carlton 2003) represents a comprehensive resource detailing specific characteristics and management of many different terrestrial and aquatic vectors. Therein, Ruiz and Carlton (2003) offer a useful framework for vector management. The first step in their management scheme is vector analysis, representing an assessment of how the actual transfer mechanisms work. This analysis should be done regionally, and will provide an indication of propagule supply on a location-by-location basis. The next phase is a vector strength assessment, which gauges the relative

importance of a vector in causing invasions. This represents a key measure because in practice the number of actual invaders is more critical than the number of potential invaders (although the potential for lagged appearance of invaders should not be underappreciated). The next phase of management is vector interruption, representing the imposition of actual action. This can take a variety of different forms, including decreasing the probability of uptake, decreasing survival during transit, and/or preventing release, and can be accomplished through measures such as screening, cleansing and quarantine. Also, in order to ensure effective interruption, stringent guidelines should be established and enforced to prevent the introduction of new species unless it can be demonstrated that the relocation will have a net benefit when economic, societal, and ecological factors are weighed. The last phase in this iterative management process is an assessment of the efficacy of the vector interruption. This can be evaluated in terms of both effects on propagule supply (through vector analysis) and ultimately successful invasions (using vector strength assessment). Again, the latter represents the more important proximate measure for management.

Monitoring programs are an essential component of vector management, as they provide the information needed to assess efficacy of the vector interruption and guide future management actions. Detecting decreases in invasion rates in the field, achieved through thorough monitoring and sound taxonomy, is the only way to gauge success of invasion prevention efforts (Ruiz and Carlton 2003). In addition, a good monitoring program may act as an early-warning system by detecting species before they become established or when they are at low enough densities that eradication remains a possibility (Wittenburg and Cock 2001).

A variety of constraints present themselves when undertaking vector management. The international nature of the invasion problem means that solutions should cut across national borders (Reaser *et al.* 2003). The potential conflict between environmental protection and economics also represents a major challenge to invasion management. Although approaches to some types of vector control will require technological and logistical advances (e.g., physical treatment of tremendous volumes of ballast water), it is often economic considerations that represent a major obstacle for even conceptually simple approaches. For example, considering ballast water as wastewater that would have to undergo treatment similar to that of sewage is a seemingly straightforward approach (Cohen and Foster 2000). However, the costs associated with treating large volumes of water at existing or new facilities make it an unpopular choice

in the business sector, and there has been administrative reluctance to adopt this approach. Overall, truly effective invasion management will only be achieved when we adopt the precautionary principle and shift the burden of proof to those responsible for moving species in the first place (Mack *et al.* 2000). Such leaps, however, are typically very slow in coming (Dayton 1998).

Once an exotic has successfully invaded, any necessary regulatory action needed to initiate management action should be subject to a “rapid review and approval” process. The actual control measures to be employed will vary depending on the invader and the invaded ecosystem, and because control is often very costly and labor-intensive, only the most problematic of species are typically targeted (thus the emphasis on preventing invasions). Control often requires a brute-force approach and the “nasty necessity” of eradication (Temple 1990). The introduction of natural enemies represents another possible control measure, although this rarely achieves full elimination of an invader. Also, as biological control typically involves the intentional introduction of yet another invader, any such efforts should proceed with an abundance of caution.

Another potential means of controlling invader impact is managing the environment to promote natives at the expense of exotics. Despite the ample debate about the mechanisms of ecological resistance, we believe that observed negative relationships between habitat quality and invader success provide (yet another) reason to conserve and restore natural areas. Increasing connectivity of fragmented natural habitats may increase invasion resistance by improving habitat quality and increasing the size of natural areas. This will, however, present risk of spread of invasive species between otherwise separated patches (Simberloff and Cox 1987). This is apparent in riparian areas where connectivity is essential for upstream movement of fish, but aqueducts also may facilitate the spread of exotics to otherwise isolated watersheds (Pringle Chapter 10). Restoring lost connections also will minimize the influence of the surrounding urban/agricultural matrix on remnant natural areas by decreasing the overall contact of urban associates with the natural habitats via the edge.

Increasing public awareness of the problem of invasive species remains absolutely necessary in minimizing future introductions. Specifically, more effective education measures are necessary to teach the public of the economic costs associated with invasions and how exotics can undermine the structure and function of natural areas. Additional research on the ecology of biological invasions is also needed, although advances are being made. We are still a long way from determining what

makes a species a successful invader – a necessary step in making invasion biology a more predictive science (Holway and Suarez 1999; Kolar and Lodge 2002). In addition, basic research assessing the current distribution and identity of exotic (as well as native) species, which will require high-resolution monitoring and careful taxonomy, is also urgently needed. Continued investigations on topics such as these will offer a more complete picture of mechanisms underlying invasion success and impacts, as well as maximize the efficacy of management efforts.

Despite the need to develop better tools for detecting and controlling exotics, it is clear that at its broadest level managing invasions will require managing connectivity. Human activities have artificially inflated connectivity and facilitated the current onslaught of invasions at different spatial scales. Globally, the abundance and efficiency of invasion vectors have begun to erode natural biogeographic boundaries, and to remedy this we must address the difficult issue of decreasing these connections in the face of ever-increasing globalization. At the landscape level, destruction and fragmentation of natural habitats have created hyperconnected urban and agricultural areas that promote invasion. Only by reversing this trend and increasing the size and connectivity of natural habitats will we be able to reconstitute systems that no longer favor exotics at the expense of natives.

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