

# Lag times and exotic species: The ecology and management of biological invasions in slow-motion<sup>1</sup>

Jeffrey A. CROOKS, Tijuana River National Estuarine Research Reserve, Southwest Wetlands Interpretive Association, 301 Caspian Way, Imperial Beach, California 91932, USA, e-mail: jcrooks@tijuanaestuary.org

**Abstract:** Time lags can be found throughout the invasion process, including in the arrival, establishment, and impacts of invaders. While we often lack the information necessary to generate quantitative expectations of invader performance, some types of lags are not surprising. For example, populations often grow exponentially in the early phases of invasion, and this will give rise to an inherent lag. More broadly, early rates of anthropogenic invasion were much slower than what we are now witnessing, but as the vectors of invasion have also increased dramatically over time, this early lag is not unexpected. Many other lags, however, appear dramatically prolonged, and can come to an end with changes to the invader or its environment. For example, exotics can exist in relatively low numbers for decades before exploding, or invaders can become more aggressive over time and increase their impacts on native species. Invasion-related lags are critical for our efforts to manage invaders, as they may lead us to make inaccurate assessments of the risks posed by invaders as well as miss critical windows for action. Recognition of the phenomenon of long lags before sudden changes in invader dynamics also suggests that we adopt a strict precautionary principle: we should assume that any invader has the potential for undesirable effects and that long periods of seemingly consistent behaviour can be poor predictors of what invaders will do in the future.

**Keywords:** biological invasions, management, risk assessment, time lags.

**Résumé :** On observe parfois des décalages lorsqu'on étudie une invasion biologique, que ce soit au moment de l'arrivée d'une espèce envahissante, pendant son établissement ou lorsqu'on tente d'en mesurer les impacts. Il n'est guère surprenant d'observer de tels décalages compte tenu du peu d'informations dont disposent les chercheurs pour prévoir de façon quantitative les performances d'une espèce envahissante. Par exemple, les populations croissent souvent de façon exponentielle pendant les premières phases d'une invasion, ce qui entraîne l'apparition d'un décalage inhérent à cette invasion. Dans le passé, la vitesse des invasions anthropiques était bien inférieure à ce que l'on constate maintenant, mais comme les vecteurs propageant les invasions sont bien plus nombreux et efficaces de nos jours, les décalages observés naguère ne risquent plus de se reproduire. Cela dit, plusieurs autres types de décalage semblent se prolonger grandement et ne se terminent que lorsque des changements affectent l'envahisseur ou son environnement. Par exemple, des espèces exotiques peuvent persister en très petits nombres pendant des décennies avant de se répandre. Des espèces envahissantes peuvent aussi devenir plus agressives avec le temps et avec plus d'impacts sur les espèces indigènes. Les décalages liés aux invasions doivent être pris sérieusement en considération par les gestionnaires des espèces envahissantes. Ils peuvent en effet conduire à de fausses évaluations des risques associés à ces espèces. Les gestionnaires peuvent aussi mal circonscrire le moment propice aux actions de contrôle. Le fait de reconnaître qu'il existe parfois de longs décalages entre l'introduction d'une espèce envahissante et un changement soudain dans la dynamique de ses populations suggère également que nous devons être prudents et assumer dès le départ que toute espèce exotique a le potentiel de créer des effets indésirables dans son nouvel environnement. Il ne faut surtout pas se fier aux longues périodes pendant lesquelles les espèces exotiques se comportent d'une manière particulière pour prédire ce qu'elles feront dans le futur.

**Mots-clés :** décalage, évaluation des risques, gestion environnementale, invasion biologique.

**Nomenclature:** Kartesz, 1994.

## Introduction

While prediction is important in any scientific discipline, it is particularly relevant in applied sciences like invasion biology (Elton, 1958; National Research Council, 2002; Heger & Trepl, 2003). Given the magnitude of the exotic species problem, predictions are needed to prioritize management efforts and assess risks and benefits of invasives-related actions. Recognizing the limits of predictive ability also is critical (Ellstrand & Schierenbeck, 2000). Although invasions have proven to be "irritatingly

idiosyncratic" (Richardson *et al.*, 2000), some progress has been made in knowing what to expect from invaders. Forecasting relationships between vector activities (such as trade) and invasions has yielded promising results (Levine & D'Antonio, 2003). There also have been attempts to predict potential effects of invaders, such as those that affect the complexity of habitats (Crooks, 2002).

One of the more recalcitrant aspects of invasion predictability relates to temporal dynamics. Although the timescales of some aspects of biological invasions are becoming better understood, such as those related to the population growth and range expansion of well-established

<sup>1</sup>Rec. 2004-10-26; acc. 2005-05-03.  
 Guest Editor: Ladd Johnson.

invaders (Hengeveld, 1989; Shigesada & Kawasaki, 1997), the timing of many invasion-related events and processes is renowned for being difficult to forecast (Crooks & Soulé, 1999; Simberloff, 2003). For example, the time course of invasions often can involve long initial periods of relative inactivity followed by seemingly sudden changes in invader dynamics. This phenomenon of lag times has become an increasingly recognized aspect of invasions (Baker & Stebbins, 1965; Hobbs & Humphries, 1995; Kowarik, 1995; Crooks & Soulé, 1999; Binggeli, 2001). Most of the attention related to lags has focused on the population dynamics of invaders, but lags are possible during any stage of the invasion process, including in the arrival of species, the impacts of already established invaders, or even our management of the growing invasion crisis (Table I).

Examining why lags occur and when they end will help improve predictive ability as well as point to limitations in our efforts to decide what invaders will do in the future. This in turn has important ramifications for invader management (Hobbs & Humphries, 1995; Simberloff, 2003). In general, there is often a mismatch between the timescales of ecological processes and those needed for effective decision-making and management. While increasing evidence suggests that ecological and even evolutionary processes can occur relatively rapidly (Stockwell, Hendry & Kinnison, 2003), researchers and resource managers often need to make decisions much more quickly.

### What is a lag?

The term lag is employed in ecology in ways that reflect its more general usages. Broadly, it can mean a relative slowness, and it is used to compare the rates of two different processes. For example, species accumulation over time might be slower in one patch than another, and the rate in the former might be considered to lag behind that in the latter (Figure 1a). More specifically, a lag can be “an interval between phenomena considered together” (American Heritage Dictionary, 2004). For example, two related events might be separated by a dis-

crete time step, or two processes might start at different points in time, even though the rates of the processes themselves may be similar (Figure 1b). It is in this context that the term lag is often used in ecological modeling, representing the interval between cause and effect, such as that caused by ontogenetic delays in the onset of density-dependent effects (Pielou, 1974; MacDonald, 1978; Erb, Boyce & Stenseth, 2001). One might also compare the dynamics or behaviour of a single process at different points in time (Figure 1c). A lag in this case would arise when initial rates are slower than those that occur later. This is the most common use of lag in relation to invasion dynamics, and the term lag time often refers to the duration of initial, relatively slow rates of population density increase or geographic spread. It should be noted that as this lag is defined in relation to later events, it may not be recognized as such until it is over.

A key point related to lags is that they, in and of themselves, do not necessarily decrease predictive ability. If the lag results from some understood intrinsic process, such as those that occur when an established population is in the early stages of exponential growth, then lags can be expected and incorporated into ecological and management considerations. Where lags become more problematic is when they become prolonged and deviate from these expectations, such as an invader existing in low numbers for decades before exploding (Crooks & Soulé, 1999). More fundamentally, lags also become problematic if an expectation cannot be derived in the first place, and the infancy of the field of invasion biology has led to a relatively undeveloped understanding of the temporal dynamics of invasion.

Despite these potential difficulties, it is useful where possible to try to distinguish between lags that are inherent or expected and those that are prolonged or unexpected. In some cases, it is possible to make simple yet quantitative models of expected invasion dynamics and compare them to observed behaviour, such as those related to population growth or range expansion (Hengeveld, 1989). Generating *a priori* expectations of how fast populations

TABLE I. Lags in the different phases of a biological invasion, showing possible categorizations as inherent or expected lags *versus* prolonged or unexpected ones.

Lag type	Inherent or expected lag	Prolonged or unexpected lag	Potential causes of prolonged lags
Appearance of invaders	Increasing vector activity over time	Changes in invasion rate without changes in vector activity	Changing species attributes or distributions; Increasing vulnerability of receiving environment
Population growth	Exponential growth at a constant intrinsic rate of increase ( <i>r</i> )	Increasing intrinsic rates of increase ( <i>r</i> ) over time	Changes in the invader ( <i>e.g.</i> , genetics); More receptive abiotic environment; Relaxation of biotic pressures
Range expansion	Lagged increase in area with constant rate of spread	Increasing rates of spread over time	Changes in the invader; More receptive abiotic environment; Relaxation of biotic pressures
Invader impact	Increase in population density or areal extent of invader	Increase in <i>per capita</i> impact of invader	Evolutionary increase in invader aggressiveness; Increasing vulnerability of resident species

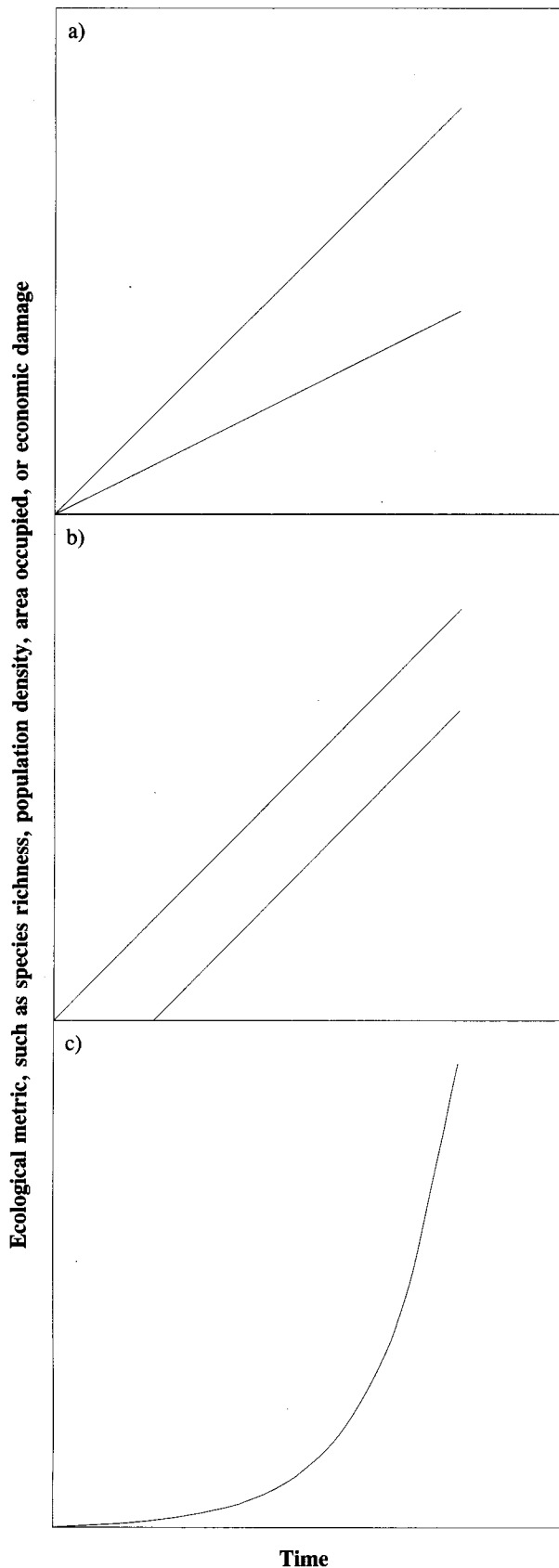


FIGURE 1. General conceptualizations of three types of lags related to ecological processes. a) Lag in one rate compared to another. b) Lag in terms of a discrete time step between events or processes. c) Lag in the rate of a single process over time.

should grow and spread, however, is more difficult than extrapolating forward from extant data or examining historical datasets for evidence of prolonged lags (but see Hengeveld, 1992). For many other invasion dynamics, it is not yet possible to develop clear models. For example, we expect that the number of successful invaders will increase as vector activity ramps up, but we do not know the exact parameters of this relationship or how it will change temporally (Ruiz & Carlton, 2003a). Similarly, we generally expect that the cumulative impact of an invader will relate to its population size and extent (Parker *et al.*, 1999), but do not know the shape of this curve over time.

In this paper, I will review the phenomenon of invasion-related lags by highlighting case histories and showing the potential importance and causes of lags. I will try to distinguish between what might be considered lags that are inherent or expected and those that are prolonged or more unexpected, although in some cases this can be done only in broad terms (Table I). These distinctions are somewhat subjective (ideally we should strive to have the data and forecasting ability to make all lags “expected”). As mentioned earlier, lags in the population explosions of exotics have received the most attention (see Crooks & Soulé, 1999, and references therein), and herein I will provide additional consideration of lags in this phase of invasion. In addition, I will highlight lags in the initial appearance, impacts, and management of invaders. I will focus primarily on lags in terms of initial slow rates followed by increases (Figure 1c), but will address other types of lags (Figure 1 a and b) as any phenomenon that is unpredictable or slow to manifest itself could lead to wrong conclusions and ineffective action related to the ecology and management of invaders.

### Lags in the rate of invader appearance

#### LAGS IN DETECTION

For an invader to appear in a system, it first must arrive there via a transport vector (*e.g.*, a ballast tank, canal, or airplane wheel well), and then it must be documented. In a limited number of cases, such as with intentional introductions or the invasion of large, conspicuous species, it is possible that the detection of a new invader will be virtually simultaneous with its entry into a system. In most cases, however, it is likely that some time will lapse between the initial invasion and subsequent discovery of the invader, as there is a strong bias for noticing invaders only after they become an abundant nuisance (Lewin, 1987; Crooks & Soulé, 1999). These lags in detection are critical as they affect our ability to estimate the prevalence of other types of lags. For example, it is assumed that the zebra mussel first invaded the Great Lakes in the mid-1980s and rapidly experienced a population explosion (Nalepa & Schloesser, 1993). It is possible, however, that the mussel went undetected in very low densities for years and that there was an unrecognized lag in the population explosion of this invader.

In general, lags in detection might arise from “cryptic invasions,” where the invader is noticed but not recognized as an exotic (Carlton, 1996a; Saltonstall, 2002).

Such is the case for the marsh grass *Phragmites australis*, an introduced genotype of which is now expanding its range into more saline marshes of North America (Saltonstall, 2002; 2003). It is also likely that many entirely distinct species of invaders are not documented at all. For a recent survey of alien arthropods in Hawaii, 490 exotics were found, and there were 145 new records for Maui (Loope & Howarth, 2003). However, 40% of these have been in Hawaii at least 50 y and had probably gone undetected on Maui for long periods of time. A similar pattern has been seen in the marine systems of San Diego County. As of the late 1990s, there were 57 recognized invaders in the region (Crooks, 1998). A short field expedition in 2000 by a team of experts, consisting of approximately one hour of field collection at each of 7 sites, increased the species list by almost one-third (Cohen *et al.*, 2002). It is possible that some of these were recent invaders, but it is likely that most either had not been encountered before because of inadequate monitoring or had not been recognized as new species because of lack of taxonomic expertise.

#### VECTOR ACTIVITY

Aside from the issues associated with invader detection, the rate of appearance of new species in ecosystems will be related to vector activity, the amenability of the receiving environment, and invader characteristics (Table I). Most directly, lags might result from an increase in the actual transport of species over time. In general, we expect positive relationships between invader appearance and vector activity. The more ballast water is moved, for example, the more species should invade. If we have information on ship traffic and ballast discharge over time, we can then infer temporal patterns in invasion rates and determine whether observed patterns depart from expectations. The problem, however, is that we have a relatively poor understanding of the fundamental relationship between the strength of the vector and the invasion of exotics (Ruiz & Carlton, 2003a), although some progress is being made in this regard (Levine & D'Antonio, 2003). It is only possible, therefore, to address the relationship between vector activity and invasion rate in the broadest terms, thus limiting our ability to detect any prolonged lags that may have occurred.

Despite the lack of a quantitative understanding of these patterns, increasing vector activity has clearly played a role in driving the pattern of overall invasion rates (both natural and anthropogenic) over time. In this age of globalization, trade is increasing rapidly (Levine & D'Antonio, 2003). The number of transported shipping containers doubles every 10 y (Loope & Howarth, 2003), and it is estimated that 7,000 species are on the move in ballast tanks at any instant (Carlton, 1999). Also, because of advances in the way in which we move around the world, the transport process itself is becoming less of a filter. In the case of ballast water, increasing speed of ship voyages has made it more likely that invaders will survive to be released into foreign ecosystems (Carlton, 1985).

If one would (and could) make a curve of invasion rate over geologic time, it likely would be relatively flat for eons, driven by natural invasions that have been occurring since the inception of life on earth. In recent

centuries, however, there would be a massive spike caused by the advent of anthropogenic invasions (Ewel *et al.*, 1999; Ruiz & Carlton, 2003b; Crooks & Suarez, in press). Historical evidence for the invertebrate colonization of the Hawaiian islands, for example, suggests that approximately one species arrived every 50,000 to 100,000 y. The current rate of invasion is one species every 18 d (Holt, 1999). Similarly, it is estimated that the current rate of invasion of cladoceran crustaceans into the Great Lakes is now 50,000 times higher than it was without human-aided movement of species (Hebert & Cristescu, 2002).

A similar pattern of slow early rates of invasion followed by a quickening pace is seen when considering invasions due only to human activities (Figure 2; also see Ruiz & Carlton, 2003b). This pace of invader appearance across many systems is continuing to increase with little sign of any let-up. Although it is certain that some of this pattern has been driven by an increased interest and ability to find and identify exotics (Costello & Solow, 2003), it is likely that the general patterns are robust and that we are experiencing an ever-quickening onslaught of invaders due to increased human-aided transport (Cohen & Carlton, 1998).

#### CHANGES IN INVADER CHARACTERISTICS OR THE ENVIRONMENT

Although the increases in vector activity have played a major role in increasing rates of invasion, changes in the characteristics of the invaders and the environment will also contribute to this pattern. There may be changes in the distribution or abundance of a potential invader within its native range that makes it more likely for it to become associated with a vector in the first place. For example, many planktonic marine organisms display diel changes in distribution due to activities such as vertical migration, and filling ballast tanks at night rather than during the day will tend to entrain more organisms (Rigby & Taylor, 2000).

In order to address the importance of non-vector causes of lags, one would ideally formulate a precise relationship between vector strength, invasion rate, and time and look for deviations from this. Although this is difficult to do, one can consider cases where vector strength does not change over time to look for unexpected lags.

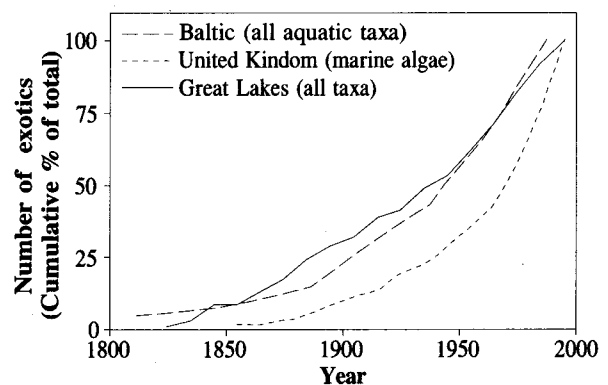


FIGURE 2. Cumulative number of invasive species established in the wild for different geographic regions (adapted from Ricciardi, 2001; Leppäkoski *et al.*, 2002; Ribera Siguan, 2003). Note the concave curves and increasing invasion rates over time.

Canal construction, for example, should provide a relatively constant means of transit over time. Therefore, we might expect a linear increase in the accumulation of invaders over time, or perhaps even a decaying relationship over time as the pool of potential invaders dwindles (Levine & D'Antonio, 2003). In the relatively well-studied Suez Canal, however, the number of invaders found per 20-y period has actually been steadily increasing over time (Figure 3). The potential reasons for this are varied, but include changing conditions in the Canal and in the water bodies on either end and the possibility of some delays in documenting invaders (Boudouresque, 1999).

Although difficult to quantify, increasing ecosystem vulnerability to invasion is a potentially important driver of the recent invasion phenomenon. Anthropogenic modification of habitat quality will affect ecosystem vulnerability to invasion, and it is commonly noted that disturbed or polluted areas tend to have more invaders than pristine sites (Hobbs & Huenneke, 1992; D'Antonio, Dudley & Mack, 1999). Thus, deterioration of environmental conditions might increase invasion rate over time. It should be noted, however, that improved environmental conditions might actually benefit invaders if conditions are initially so degraded that few biota can survive. For example, improving water quality in the Los Angeles / Long Beach Harbor allowed the ecological release of destructive, invasive bioeroders (Reish, Soule & Soule, 1980). At broader scales, climate change will undoubtedly cause shifts in both spatial and temporal patterns of invader appearance (Kowarik, 1995; Mooney & Hobbs, 2000).

Invasibility of systems also will be affected by resident biota (Elton, 1958; Levine & D'Antonio, 1999; Crooks & Suarez, in press). Decreasing the number or diversity of potential enemies in the recipient system will make invasions more likely, and, at small-scales at least, negative relationships between diversity and invader success have been noted (Shea & Chesson, 2002). Positive interactions also play a role in invader success, and increasing the potential for mutualistic relationships can pave the way for more rapid invasions. For example, invasional meltdown is hypothesized to occur when one invader changes conditions in the recipient ecosystem such that it makes the ecosystem more vulnerable to future invasion, and this could generate positive feedbacks

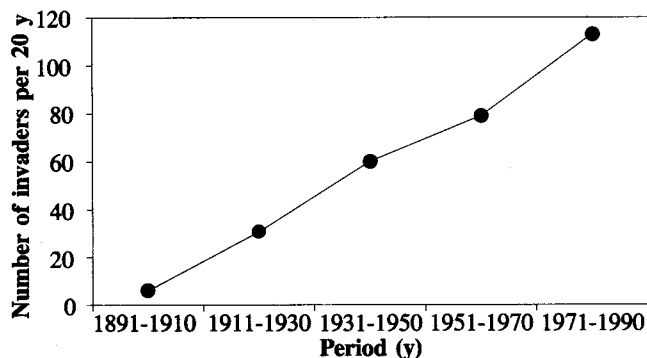


FIGURE 3. Accelerating rates of invasion through the Suez Canal, demonstrated by the steady increase in the number of invaders per 20-y period (adapted from Boudouresque, 1999).

that allow increasing susceptibility to invasion (Simberloff & Von Holle, 1999). Also, ecosystems throughout the world are accumulating invasive plant mutualists, such as generalist pollinators, mycorrhizal fungi, and rhizobia, and because of this newly introduced plants will find increasingly hospitable environments upon their arrival (Richardson *et al.*, 2000).

### Lags in population growth and range expansion

#### INITIAL SPREAD INTO THE WILD

After initial arrival into ecosystems, successful invaders establish themselves, and their populations begin to grow. For unintentionally introduced species, a successful invasion entails that those individuals that survive transit must survive to reproduce. For intentionally introduced species, such as ornamental or cultivated plants, some time can pass between the original planting of the species and its subsequent spread into the wild. Interestingly, there is evidence that this interval can be quite long. For trees in Brandenburg, Germany, it was found that the average time between first introduction and first appearance of an unplanted seedling was a remarkable 147 y (Kowarik, 1995). Lags of over 350 y were found for some species. A smaller dataset exists for trees in the tropics, where lags were appreciably shorter (Binggeli, 2001). The average lag was less than 30 y, and the longest interval between first planting and first record of spread was 50 y. It has been suggested that the shorter lags found in the tropics relate, at least in part, to the faster times to first flowering found in warm-climate species, although there is likely a wide variety of factors involved (Binggeli, 2001).

#### INHERENT LAGS IN THE GROWTH AND SPREAD OF POPULATIONS

As highlighted above, the population growth and range expansion of established invaders represent some of the better-understood dynamics in invasion biology (Okubo, 1988; Hengeveld, 1989; Andow *et al.*, 1993; Shigesada & Kawasaki, 1997). Because of some general but fairly robust models, we have reasonable expectations of what populations should do in terms of increasing in both numbers and areal extent (Table I). This allows the distinction between intrinsic and prolonged lags to be relatively sharp (Hengeveld, 1989; Crooks & Soulé, 1999). Inherent lags arise from dynamics early in the invasion process, when population sizes and area occupied are small. The classic model for the growth of incipient populations is that of exponential increase, and this undoubtedly accounts for many observed lags. In the case of collared doves invading the Netherlands, there appears to have been a rapid increase in density after an early lag (Figure 4a). However, the linear relationship observed when plotting this on a log scale (Figure 4b) demonstrates a clear exponential pattern of increase (a prolonged lag would be evidenced by a concave curve).

For range expansion of populations, another simple model gives rise to early lags. If populations are introduced into a small area and subsequently spread at a constant rate outwards in all directions, the area occupied

will be a circle with the spread in any one direction forming its radius. Therefore, the area occupied will be a squared function of time (Hengeveld, 1989). In order to easily visualize whether this spread rate is constant, a straight line would be expected when time is plotted *versus* the square root of area (Crooks & Soulé, 1999). Such is the case for the spread of the muskrat in Europe in the early 1900s (Figure 5a). Prolonged lags would occur when the curve is concave, as was seen for the spread of starlings in the United States (Figure 5b).

CAUSES OF PROLONGED LAGS IN GROWTH AND SPREAD OF POPULATIONS

There are many, non-mutually exclusive mechanisms that can account for prolonged lags (Baker & Stebbins, 1965; Kowarik, 1995; Crooks & Soulé, 1999). In some cases, demographic processes more complex or stochastic than exponential growth or circular expansion of populations might cause unexpected behaviour. For example, simple models that examine spread of populations on a lattice of points can exhibit spontaneous, prolonged lags (Hastings, 1996). Also, while the spread of populations as a diffusion-like expanding front is a reasonable expectation in some cases, such as when there is one primary dispersal mode, it will not hold in other cases, such as when there are more than one means by which organisms expand their ranges (Suarez, Holway & Case, 2001). Invader spread via "jump-dispersal" can establish foci of invasion well ahead of the expanding front and thus rapidly

increase invader range (Johnson & Carlton, 1996; Johnson & Padilla, 1996). Similarly, while the leading edge of the invasion is often the focus of much attention, the dynamics of spread behind the front can be complicated and considerable lags can occur in the colonization of specific sites (Kraft & Johnson, 2000).

Intraspecific interactions also can lead to changes in invader dynamics, and one factor that has received increasing attention related to lags in invasions is the Allee effect, where there are disproportionately low population growth rates at small population sizes (Lewis & Kareiva, 1993; Veit & Lewis, 1996; Drake, 2004; Leung, Drake & Lodge, 2004; Parker, 2004). A variety of mechanisms giving rise to initial slow growth of invasive populations have been proposed, such as difficulty in finding mates when there is undercrowding (Veit & Lewis, 1996) and increased ability to suppress natives at high invader densities (Cappuccino, 2004). Pollen limitation in small, low-density patches also can cause prolonged lags in plants, such as that seen for the spread of exotic cordgrass (*Spartina alterniflora*) in Willapa Bay, Washington (Figure 6; Davis *et al.*, 2004; Parker, 2004).

Genetics is another potentially important cause of early lag phases preceding rapid population increases, in that time might be needed for organisms to adapt to their new environments (Baker, 1965; Crooks & Soulé, 1999; Petit, 2004). Although direct confirmation of the genetic basis of lags has been slow in coming, the evidence is mounting. It is thought that introduction to novel environ-

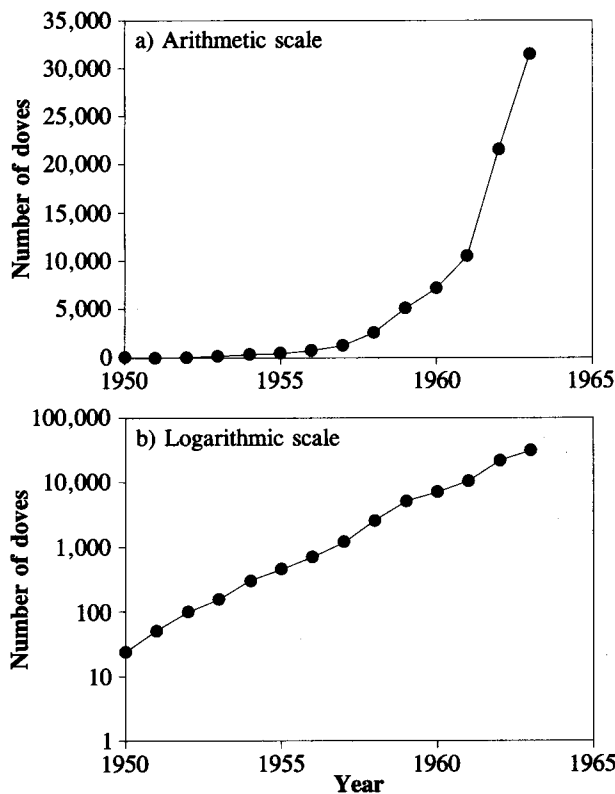


FIGURE 4. Population increases in collared doves in the Netherlands. Data are presented on arithmetic (a) and logarithmic scales (b) to emphasize how exponential growth can account for the early lag observed in a) (adapted from Hengeveld, 1992).

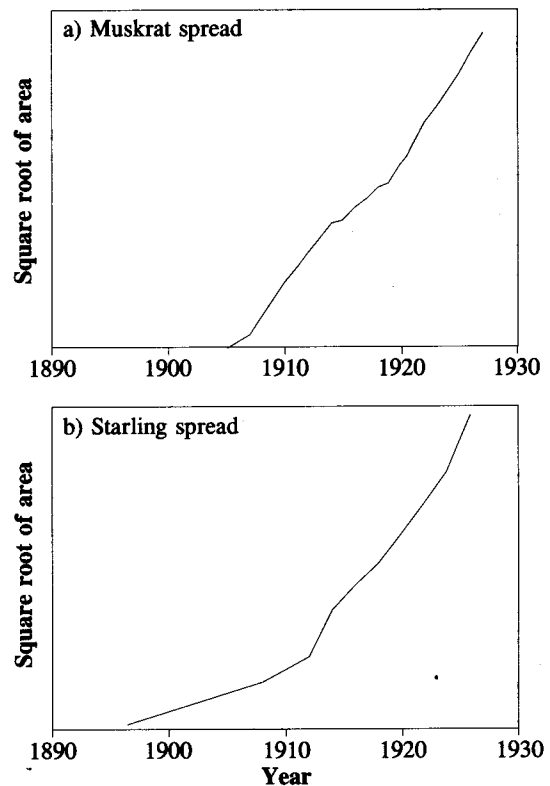


FIGURE 5. Areal spread of muskrats (a) and starling (b). Muskrats show the expected linear increase in the square root of area with time, and starlings show a prolonged lag early in the invasion (adapted from Hengeveld, 1989).

ments is the most important factor related to rapid adaptation (Reznick & Ghalambor, 2001), and recent evidence suggests that evolutionary change can be observed on time-scales of years or decades (Stockwell & Ashley, 2004). While this is quite fast by conventional standards, it is slow in terms of the decisions that are often made in terms of invader ecology and management.

It is possible that even small genetic changes might influence invasion success (Lee, 2002). For example, a mutation in one nucleotide has been demonstrated to cause a host switch and new invasion potential in cucumber mosaic virus (Sleat & Palukaitis, 1992). It is also likely that the cumulative effects of subtle quantitative changes in phenotypic traits (such as metabolic rate and toxin resistance) will also enhance invasive potential of organisms (Crooks & Soulé, 1999). Plants might undergo other genetic changes that may delay rapid establishment. For example, the evolution of polyploidy has been suggested to be important in invasions; it has occurred multiple times in introduced plants (Cook *et al.*, 1998). Evolution of selfing would also benefit invading populations (Daehler, 1998).

Additional examples of evolution within invader populations suggest that directional selection can make species better invaders over time (Mooney & Cleland, 2001; Lee, 2002; Cox, 2004). The case of the velvetleaf plant is a good example, as it was introduced to North America in the 1700s but has only become a pest in the last century. Since its introduction, this plant has evolved different life history strategies depending on the species it is competing with (Weinig, 2000). This is an example of what has been termed evolution of improved competitive abilities (EICA). Having left behind its natural enemies, genotypes that improve competitive success will be selected for, and this will come at the expense of herbivore defence (Blossey & Notzöld, 1995; Siemann & Rogers, 2003; Rogers & Siemann, 2004, but see Coluatti *et al.*, 2004). Additional examples of evolutionary change in invaders include wingsize change in fruitflies in North America (Gilchrist, Huey & Serra, 2001; Mooney & Cleland, 2001), adaptive clines in North American popula-

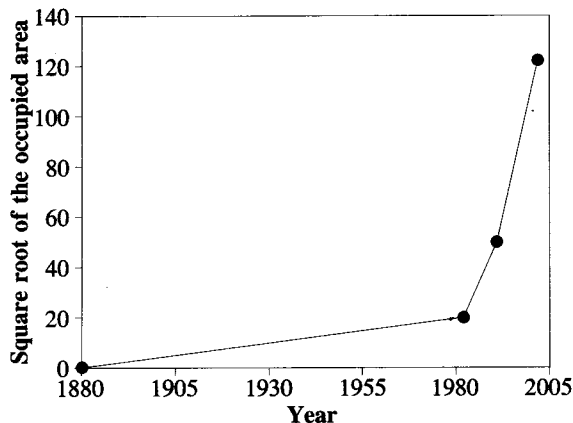


FIGURE 6. Prolonged lag in the population increase of exotic cordgrass, *Spartina alterniflora*, in Willapa Bay, Washington. Note that as the y-axis is the square root of area, a straight line would be expected if cordgrass was spreading at a constant rate (adapted from Parker, 2004).

tions of English sparrows (Johnston & Selander, 1964), and longer ears in rabbits introduced to Australia (Williams & Moore, 1989).

Population size also plays an important role in the genetics of invaders. In general, there is a feedback between population size and chance of beneficial mutation, so as invader populations grow larger there is an increasing chance of adaptations that will increase invasiveness (Crooks & Soulé, 1999). Although the typical cause of increased invader numbers is local population growth, it also might occur by repeated invasions adding individuals over time. Further, such unchecked immigration is important in that it can increase genetic diversity and counteract founder effects by means other than mutation (Crooks & Soulé, 1999; Mooney & Cleland, 2001). For example, within-population genetic variation in North American cheatgrass is higher than that within its native range, and this species has likely been introduced multiple times (Novak & Mack, 1993; Novak, Mack & Soltis, 1993). Similarly, the relatively high genetic diversity of a crustacean invader (*Bosmina coregoni*) in the Great Lakes suggests multiple introductions due to ballast water (Demelo & Herbert, 1994).

Changing interactions between invaders and the biotic and abiotic environment also can cause population explosions of exotics (*e.g.*, by changing carrying capacity). Altered trophic relationships, such as the removal of a native predator or herbivore, might cause the containment of an invader to suddenly end; there are a number of cases where removal of exotic grazers has caused explosions of formerly controlled weeds (Beatty & Licari, 1992; Simberloff, 2003). Changes in competitive abilities also might cause the abrupt end of lag phases. This might arise from relaxation of competition from residents (similar to the removal of predators or herbivores) or the evolution of increased competitive abilities (as discussed above). As was discussed for initial establishment, mutualistic relationships also mediate post-invasion rates of population increases (Richardson *et al.*, 2000). Figs, for example, have close associations with pollinating wasps, and the introduction of these insects into Florida and New Zealand has caused dramatic increases in fig invasions (Richardson *et al.*, 2000). Organisms also can biogenically modify habitat through ecosystem engineering (Jones, Lawton & Shachak, 1994; Crooks, 2002), and changes in resident engineers might cause subsequent responses in exotics. In the Mediterranean, there was a 120-y lag in the population explosion of an invasive mussel, and this might have arisen through increased space availability caused by the loss of native reef-building molluscs (Rilov, Benayahu & Gasith, 2004).

Similarly, shifts in abiotic factors such as habitat quality, climate, and patterns of vector operation also will be important in affecting temporal dynamics of invader abundance and diversity (Crooks & Soulé, 1999). For instance, differences in the lag phases before the spread of riparian plants in Europe have been attributed to interactions between habitat preference and propagule dispersal (Pyšek & Prach, 1993). In a more bellicose example, the sudden spread of several long-contained weeds occurred in Britain during World War II, and this has

been attributed to bombings that increased the availability of rubble sites and perhaps even aided the airborne spread of propagules (Baker, 1965). As highlighted above, climate change also will undoubtedly affect the distribution and abundance of invaders (Mooney & Hobbs 2000; Kriticos *et al.*, 2003).

#### POPULATION CRASHES

A phenomenon related to lags in population explosions is the seemingly spontaneous population crashes of invaders (Simberloff & Gibbons, 2004). The “boom and bust” cycle is an often-reported property of invasions, where, after increases, invader populations decrease and tend to stabilize at lower densities (Williamson, 1996). Although this overshoot and stabilization is clearly an oversimplification, it does have a basis in theory related to rapid growth surpassing carrying capacity and a return to equilibrium. As with prolonged lags, however, there are examples of seemingly persistent and successful invaders that suddenly experience rapid population decreases (Simberloff & Gibbons, 2004). It appears that these population decreases remain quite unpredictable, and in terms of management, it would be unwise to wait for invaders to disappear on their own (Simberloff & Gibbons, 2004).

#### Lags in impact on other species

##### TIMESCALES OF INVADER IMPACT

The effects of invaders are the primary factor motivating interest in the ecology and control of exotics. When considered in totality, and given that invasions are fundamentally natural events, a list of the possible effects of invaders is simply the list of the role of any species in an ecosystem. Invaders can be consumers, competitors, parasites, disease carriers, ecosystem modifiers, facilitators, behaviour modifiers, or agents of evolutionary change. Given that these interactions are quite complex and difficult to model (but see Shigesada & Kawasaki, 1997), it is hard to generate quantitative predictions of invader impact. Overall, the cumulative impact of an invader will be generally related to its abundance, range, and per capita effect (Parker *et al.*, 1999). Therefore, any lag in impact that corresponds with lags in density or areal increase would not be surprising. We expect a relatively small total impact when there are only a few, confined invaders. Prolonged lags would arise, then, when the per capita effect of invaders increases over time (Table I).

Given the importance of invader impacts, however, it is also worth considering situations where per capita effect, range, and abundance may not necessarily change, but the effects may take some time to manifest themselves. This represents lags in the more general sense, in terms of the relative slowness of processes (Figure 1a). This issue is critical as decisions are often made on what an invader is doing here and now, and long response times can lead us into a false sense of security (Duffy, 2003).

Of the ecological impacts of invaders, those involving the direct consumption of natives by exotics will often occur on the fastest timescales. There are, unfortunately, plentiful examples of introduced predators on islands quickly extirpating indigenous species (Williamson, 1996;

Bright, 1998), such as the devastating effects of brown tree snakes on ground-nesting birds (Savidge, 1987). Predation also can lead to indirect impacts that will take longer to develop. For example, there is concern about the effects of introduced trout on native frog populations in California lakes. In these systems, the virtual elimination of frogs from the many trout lakes will likely result in a loss of gene flow in the highly fragmented remnant populations (Bradford, Tabatabai & Graber, 1993). Also, the threat of predation by introduced species can induce behavioural changes in resident populations (Townsend, 1996). In an interesting case in Yellowstone National Park, the reintroduction of (native) wolves has caused elk to avoid browsing along stream margins, where they are more vulnerable to predation. This has led to increased tree growth along the river margins, providing dam material for beavers and an increase in pond habitats within the system (Ripple & Beschta, 2004).

A wide variety of other invader effects also may proceed at relatively slow rates. Invaders can disrupt mutualistic relationships between natives and this has been seen with exotic Argentine ants in South Africa displacing native ants (Bond & Slingsby, 1984). As only the latter disperse *Protea* seeds, this loss of dispersal ability could lead to negative effects on the native plant. Slow-motion effects also might emerge from the results of habitat alteration, such as has been observed related to the dramatic decline of acorn woodpeckers in parts of New Mexico. These birds need old, dead trees for acorn storage, and a historical period of intense cattle grazing essentially removed an age class of trees, making them unavailable to serve as granary trees years later (Ligon & Stacey, 1996). Examples such as this emphasize the importance of considering the timescales between cause and effect, impacts throughout the life-cycle of the species involved (*e.g.*, ontogenetic delays), and the complex nature of invader-induced changes in systems.

Evolutionary effects of invaders will tend to be the slowest to emerge and hardest to predict, although there has been increasing interest in these types of invader impacts (Mooney & Cleland, 2001; Hanfling & Kollmann, 2002; Lee, 2002; Cox, 2004). It is known that invaders may cause morphological changes in native populations, such as the evolution of beak lengths in soapberry bugs using invasive plants (Carroll *et al.*, 2001). Invaders also might affect induced defences, there is evidence for the evolution of plastic responses in shell thickening in populations of intertidal snails with histories of exposure to invasive green crabs (Trussell & Smith, 2000).

Another evolutionary consequence of invasion that will take time to develop is the creation of entirely new species. Invasions themselves can be viewed as speciation events (Lee, 2002), with invaders evolving to become new species (Reznick & Ghalambor, 2001; Stockwell & Ashley, 2004). Invaders also can induce speciation in natives. It appears that there is now an incipient species of apple maggot responding to introduction of the domesticated apple in the mid-1800s (Filchak, Roethele & Feder, 2000). On longer time scales, five species of host-specific moths have developed in response to banana introduction to Hawaii 1,000 y ago (Zimmerman, 1960).



Another common concern is that exotics will hybridize with natives, this has been shown to occur in many instances (Ellstrand & Schierenbeck, 2000). *Spartina anglica*, for example, is an aggressive plant invader that was created when exotic and native species hybridized and later underwent chromosome doubling (Thompson, 1991). There has also been a recent suggestion that the current increase in human cases of West Nile Virus in the United States is caused by a hybrid mosquito that tends to feed on both people and birds. Although the hybridization appears to have happened only recently, its parent species have both long been in the US, and one tends to feed primarily on birds and the other on humans (Fonseca *et al.*, 2004). Hybridization also can lead to extinction of the native forms: McMillan and Wilcove (1994) state that hybridization was the cause of extinction of 3 of 24 now-extinct US species that were formerly listed as endangered.

#### CHANGES IN PER CAPITA EFFECT

Prolonged lags in invader impact can be considered to occur when there is an increase in the invader's ability to affect resident species over time. Such changes in per capita effect could conceivably arise from shifts in the responses of native biota to invaders (where they become more vulnerable), but at present there is little information on this. There is evidence for the invaders themselves changing, however. Predators can switch prey during the course of an invasion, such as when a preferred prey population declines or when there are evolutionary changes in the invader. The biocontrol literature provides examples of these changes (Secord & Kareiva, 1996), such as an introduced caterpillar that switched from introduced to native parsnips (Berenbaum & Zangerl, 1991). Lag times are also possible when invaders serve as a food for natives. In response to the invasion of Eurasian watermilfoil, a native beetle has increased its importance in the trophic structure of North American freshwater systems (Creed, 2000). This shift took over 30 y, due in part, it has been suggested, to the time needed for the introduced plant to increase in abundance (an expected lag) and the time needed for the beetle to switch preferred species (a prolonged lag).

As described earlier, the implications of EICA are that the invaders will become more successful as they evolve in their new environments, such as was seen for velvetleaf. This invasive plant has evolved different life-strategies, specialization *versus* plasticity, depending on whether it is competing in a homogeneous corn culture or a patchy, weedy environment (Weinig, 2000). Also, invaders can evolve novel weapons, such as through increased allelopathy (Callaway & Ridenour, 2004). The biocontrol literature offers a rather extensive discussion of the potential for lagged evolutionary changes in invaders, given the need to consider the long-term impact of intentionally introduced predators or parasites (Onstad & McManus, 1996; Secord & Kareiva, 1996). There has been some controversy surrounding this topic, particularly as related to biocontrol species with high degrees of host specificity (Secord & Kareiva, 1996; Hoddle, 2004; Louda & Stiling, 2004). As discussed above, it is clear that there has been a range of unintended consequences

of biocontrol species. An additional example is the European weevil *Rhinocyllus conicus*, which was introduced to North America for control of exotic thistles but later switched to native thistles. This reduced seed production and indirectly impacted native insects (Louda *et al.*, 1997).

#### Lags in the human dimension of biological invasions

Lags associated with invaders and their impacts can impact decision-making processes and the implementation of invasion control. They can lead to underestimates of the potential consequences of a particular invasion and can impair accurate risk assessment (Drake, 2004). Lags can even undermine legal responses to invasions, which typically need to show demonstrable harm (Courtney, 2004). Above and beyond lags associated with the actual invasions, delayed reactions on our part represent another critical category of lags (Binggeli, 2001). There are lags associated with appreciating the importance of biological invasions, recognizing specific invasion threats, and taking steps toward invasion management.

#### CHANGING PERCEPTIONS

Biological invasions deal with living organisms; this is a fundamentally different type of ecological problem than issues such as toxic waste, sewage pollution, or habitat loss (Bright, 1998). Sentiments about invaders vary widely and have changed over time. Historically, there was much effort expended in blithely translocating species (Lever, 1992), but intentional introductions are now typically (but not uniformly) treated with more care. In terms of communication about invasions, Reichard and White (2001) document an early slow pace in lay articles (*e.g.*, in newspapers) about invasions, followed by a rapidly increasing publication rate (Figure 7a). A similar early lag can be seen in publications in the scientific literature (Figure 7b; Pyšek, 1993). These lags in publication undoubtedly reflect the increased pace of invasion, but the topic of biological invasions has taken time to garner widespread interest. Thoughts about specific invaders also can change with time. For example, the black cherry tree in Europe has over time been considered a valuable timber tree, a useful non-timber resource, a pest, a controllable weed, and finally a tolerated component of a now-changed ecosystem (Starfinger *et al.*, 2003).

#### IMPLEMENTATION OF MANAGEMENT ACTION

By far the most effective way of dealing with invasions is to not let them happen in the first place (Ruiz & Crooks, 2002; Ruiz & Carlton, 2003b). This is easier said than done, however, and there are often substantial delays in instituting effective vector control. As many vectors are associated with trade, commerce, and travel, intense underlying economic pressures make it impossible to simply halt these flows. However, as lags in perception of the invasion problem are now waning, there is increasing pressure to deal with this issue. Solutions to vector management are being developed, but this takes time (Ruiz & Carlton, 2003b). Ballast water has long been recognized as a major vector, transporting countless organ-

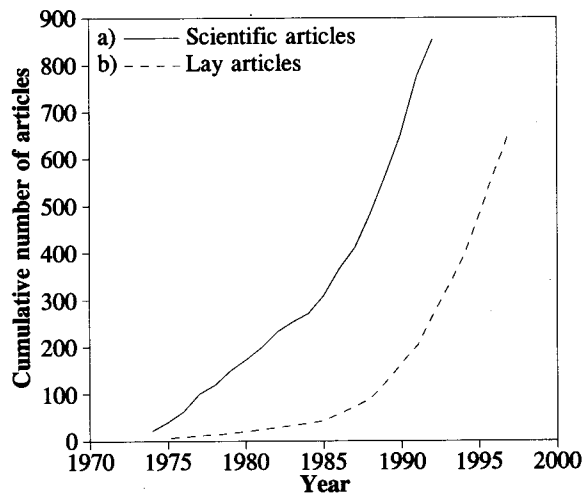


FIGURE 7. Lags in publications of scientific (a) and lay (b) articles about biological invasions (adapted from Pyšek, 1993, and Reichard & White, 2001).

isms: a single litre of ballast water might have millions of individual planktonic plants and animals and billions of bacteria (Ruiz & Carlton, 2003a). Ballast dumping regulations, if they exist at all, principally consist of the relatively crude method of exchanging water on the open sea. Although other solutions are being developed, they are still years away from implementation. Furthermore, even if movement of species from foreign origins stops, invasions will still continue as species spread outwards from their initial points of invasion through both natural and anthropogenic means (the hub-and-spoke model, Carlton, 1996b). Similarly, completely effective vector control will not stop the lagged emergence of new impacts of already established invaders (Kowarik, 1995; Loope & Howarth, 2003).

When attempting to manage established invaders, such as through eradication efforts, it is typically best to act at the earliest possible stages of invasion, when population densities are low (Hobbs & Humphries, 1995; Simberloff, 2003). For example, the invasive tree tamarisk (*Tamarix* spp.) has invaded and severely degraded large portions of high salt marsh in the Tijuana River Estuary (San Diego County, California), and a control effort costing over a million dollars is underway (Crooks, pers. observ.). This relatively large tree is a conspicuous invader in the low-lying salt marsh, and it had been first noticed in low numbers approximately 20 y ago, but lags in quantifying the actual extent of invasion and implementing eradication have dramatically increased the cost and difficulty of necessary management action.

In general, recognition of the possibility of lags in invader dynamics actually suggests that there may be relatively large windows of opportunity, as long as we have mechanisms in place to overcome detection lags (for inconspicuous species) and manage incipient invaders. This highlights the need for early warning and rapid response systems (Simberloff & Gibbons, 2004). Anything that delays our responses will compound problems associated with invader management, and, as with the tamarisk example above, it is necessary to avoid complacency at the stage when species are vulnerable (Cappuccino,

2004). A paradox arises, however, in that the best chances for success occur when we know the least about a particular invader (Kriticos *et al.*, 2003), although continued work on invasions should serve to generate important guiding principles.

Even when invader control is instituted, the potential for a wide array of lags continues. On the positive side, recognition of factors such as Allee effects suggests that it may not be necessary to eradicate entire populations (Liebhold & Bascombe, 2003). However, it is important to realize that removing invaders will often take considerable time, and this tends to be unpopular in management and funding circles, where a premium is placed on achieving demonstrable results in a short timeframe (Bissonette & Storch, 2002). Even when an invader is removed, there may be long-term legacies of the invasion due to biological inertia (Von Holle, Delcourt & Simberloff, 2003). Invader-induced extinctions of native species are irreversible, and the presence of allelopathic chemicals or other types of habitat alterations might persist for years (Hiero & Callaway, 2003). Also, native species might be slow to respond to invader removal, such as has occurred in slow-growing lichens after the abatement of reindeer grazing pressure (Scheffer, 1951; Simberloff, 2003). Great care also must be taken in removing an exotic that is keeping other invaders in check, such as eradicating grazing animals and thus allowing the release of exotic weeds (Crooks & Soulé, 1999; Simberloff, 2003). In terms of biocontrol, we need to consider long-term changes in both the invader and control agent (Onstad & McManus, 1996; Secord & Karieva, 1996; Müller-Scharer, Schaffner & Steinger, 2004). Recognition of unpredictable lag times also makes it difficult to determine the appropriate length of time to wait in assessing the risks and benefits of invader management actions (Ewel *et al.*, 1999). Insight into issues such as these will require detailed information on specific systems and a general understanding of invasion dynamics, although some element of unpredictability will undoubtedly persist.

## Conclusion

Even with a growing interest in invaders and increased funding for invasions research, the field of invasion biology is still in its infancy and there are many lessons to learn. There is a variety of invasion-related "non-linearities and synergisms" that make prediction difficult (Richardson, Cowling & Lamont, 1996), and lags represent a clear example of just such a challenge. At the very least, we should expect inherent lags related to factors such as exponential growth and be wary of prolonged lags that are at present difficult to predict. This should provide ample support for employing the precautionary principle with regard to invasion (Williamson, 1996). While not all invasions are necessarily bad (and it might be deemed that some are desirable), the burden of proof needs to be on demonstrating a lack of negative effects, with recognition that those effects may not manifest themselves for many years. Recognizing lags also highlights the need for researchers, the public, resource managers, and decision-makers to work together and form long-term

commitments to address one of our most pressing environmental problems.

### Acknowledgements

I thank L. Johnson for the opportunity to contribute to this volume and for his helpful comments on the manuscript. I also thank two anonymous reviewers, whose comments substantially improved the paper, as well as M. Soulé and A. Suarez, who have helped shape these ideas about lags and invasion biology. This work was supported in part by the National Sea Grant College Program of the US Department of Commerce's National Oceanic and Atmospheric Administration under NOAA Grant #NA04OAR4170038, project #R/CZ-190A, through the California Sea Grant College Program, and in part by the California State Resources Agency. The views expressed herein do not necessarily reflect the views of these organizations.

### Literature cited

- American Heritage Dictionary of the English Language, 2004. Houghton-Mifflin Company, Boston, Massachusetts.
- Andow, D. A., P. M. Kareiva, S. A. Levin & A. Okubo, 1993. Spread of invading organisms: Patterns of spread. Pages 219-242 in K. C. Kim & B. A. McPheron (eds.). *Evolution of Insect Pests*. John Wiley & Sons, New York, New York.
- Baker, H. G., 1965. Characteristics and modes of origins of weeds. Pages 147-172 in H. G. Baker & G. L. Stebbins (eds.). *The Genetics of Colonizing Species*. Academic Press, New York, New York.
- Baker, H. G. & G. L. Stebbins, 1965. *The Genetics of Colonizing Species*. Academic Press, New York, New York.
- Beatty, S. W. & D. L. Licari, 1992. Invasion of fennel (*Foeniculum vulgare*) into shrub communities on Santa Cruz Island, California. *Madroño*, 39: 54-66.
- Berenbaum, M. R. & A. R. Zangerl, 1991. Acquisition of a native hostplant by an introduced oligophagous herbivore. *Oikos*, 62: 153-159.
- Binggeli, P., 2001. Time-lag between introduction, establishment and rapid spread of introduced environmental weeds. *Proceedings of the III International Weed Science Congress*, MS no 8. International Weed Science Society, Oxford.
- Bissonette, J. A. & I. Storch, 2002. Fragmentation: Is the message clear? *Conservation Ecology*, 6: 14 [online] URL: <http://www.ecologyandsociety.org/vol6/iss2/art14/>
- Blossey, B. & R. Notzöld, 1995. Evolution of increased competitive ability in invasive nonindigenous plants: A hypothesis. *Journal of Ecology*, 83: 887-889.
- Bond, W. & P. Slingsby, 1984. Collapse of an ant-plant mutualism: The Argentine ant (*Iridomyrmex humilis*) and Myrmecochorous Proteaceae. *Ecology*, 65: 1031-1037.
- Boudouresque, C. F., 1999. The Red Sea-Mediterranean link: Unwanted effects of canals. Pages 213-235 in O. T. Sandlund, P. J. Schei & A. Viken (eds.). *Invasive Species and Biodiversity Management*. Kluwer Academic Press, Dordrecht.
- Bradford, D. F., F. Tabatabai & D. M. Graber, 1993. Isolation of remaining populations of the native frog *Rana muscosa* by introduced fishes in Sequoia and Kings Canyon National Parks, California. *Conservation Biology*, 7: 882-888.
- Bright, C., 1998. *Life Out of Bounds*. W. W. Norton and Co., New York, New York.
- Callaway, R. M. & W. M. Ridenour, 2004. Novel weapons: Invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment*, 2: 436-443.
- Cappuccino, N., 2004. Allee effect in an invasive alien plant, pale swallow-wort *Vincetoxicum rossicum* (Asclepidaceae). *Oikos*, 106: 3-8.
- Carlton, J. T., 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: The biology of ballast water. *Oceanography and Marine Biology: An Annual Review*, 23: 313-371.
- Carlton, J. T., 1996a. Biological invasions and cryptogenic species. *Ecology*, 77: 1653-1655.
- Carlton, J. T., 1996b. Pattern, process, and prediction in marine invasion ecology. *Biological Conservation*, 78: 97-106.
- Carlton, J. T., 1999. The scale and ecological consequences of biological invasions in the world's oceans. Pages 195-212 in O. T. Sandlund, P. J. Schei & A. Viken (eds.). *Invasive Species and Biodiversity Management*. Kluwer Academic Press, Dordrecht.
- Carroll, S. P., H. Dingle, T. R. Famula & C. W. Fox, 2001. Genetic architecture of adaptive differentiation in evolving host races of the soapberry bug, *Jadera haematoloma*. *Genetica*, 112-113: 257-272.
- Cohen, A. N. & J. T. Carlton, 1998. Accelerating invasion rate in a highly invaded estuary. *Science*, 279: 555-558.
- Cohen, A. N., L. H. Harris, B. L. Bingham, J. T. Carlton, J. W. Chapman, C. C. Lambert, G. Lambert, J. C. Ljubenkov, S. N. Murray, L. C. Rao, K. Reardon & E. Schwindt, 2002. Project Report for the Southern California Exotics Expeditions 2000. A Rapid Assessment Survey of Exotic Species in Sheltered Coastal Waters. California Department of Fish and Game, Sacramento, California.
- Coluatti, R. I., A. Ricciardi, I. A. Grigorovich & H. J. MacIsaac, 2004. Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, 7: 721-733.
- Cook, L. M., P. S. Soltis, S. J. Brunsfeld & D. E. Soltis, 1998. Multiple independent formations of *Tragopogon tetraploids* (Asteraceae): Evidence from RAPD markers. *Molecular Ecology*, 7: 1293-1302.
- Costello, C. J. & A. R. Solow, 2003. On the pattern of discovery of introduced species. *Proceedings of the National Academy of Sciences of the USA*, 100: 3321-3323.
- Courtney, A., 2004. Fighting invasive species in the courts: The potential applicability of United States tort law (nuisance and trespass) to address invasive species issues and how such efforts can be strengthened through the use of statutory law. Page 46 in *International Conference on Assessment and Control of Biological Invasion Risks*, Yokohama, Japan.
- Cox, G. W., 2004. *Alien Species and Evolution*. Island Press, Washington, DC.
- Creed, R. P. J., 2000. Is there a new keystone species in North American lakes and rivers? *Oikos*, 91: 405-408.
- Crooks, J. A., 1998. The effects of the introduced mussel, *Musculista senhousia*, and other anthropogenic agents on benthic ecosystems of Mission Bay, San Diego. Ph.D. thesis. Scripps Institution of Oceanography, University of California San Diego, San Diego, California.
- Crooks, J. A., 2002. Characterizing the consequences of biological invasions: The role of introduced ecosystem engineers. *Oikos*, 97: 153-166.
- Crooks, J. A. & M. E. Soulé, 1999. Lag times in population explosions of invasive species: Causes and implications. Pages 103-125 in O. T. Sandlund, P. J. Schei & A. Viken (eds.). *Invasive Species and Biodiversity Management*. Kluwer Academic Press, Dordrecht.
- Crooks, J. A. & A.V. Suarez, in press. Hyperconnectivity, invasive species, and the breakdown of barriers to dispersal. in K. R. Crooks & M. A. Sanjayan (eds.). *Connectivity Conservation: Maintaining Connections for Nature*. Cambridge University Press, Cambridge.

- Daehler, C. C., 1998. Variation in self-fertility and the reproductive advantage of self-fertility for an invading plant (*Spartina alterniflora*). *Evolutionary Ecology*, 12: 553-568.
- D'Antonio, C. M., T. L. Dudley & M. Mack, 1999. Disturbance and biological invasions: Direct effects and feedbacks. Pages 429-468 in L. R. Walker (ed.). *Ecosystems of Disturbed Ground*. Elsevier, Amsterdam.
- Davis, H. G., C. M. Taylor, J. G. Lambrinos & D. R. Strong, 2004. Pollen limitation causes an Allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). *Proceedings of the National Academy of Sciences of the USA*, 101: 13804-13808.
- Demelo, R. & P. D. N. Hebert, 1994. Founder effects and geographical variation in the invading cladoceran *Bosmina (Eubosmina) coregoni* Baird 1857 in North America. *Heredity*, 73: 490-499.
- Drake, J. M., 2004. Allee effects and the risk of biological invasion. *Risk Analysis*, 24: 795-802.
- Duffy, J. E., 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters*, 6: 680-687.
- Ellstrand, N. C. & K. A. Schierenbeck, 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences of the USA*, 97: 7043-7050.
- Elton, C. S., 1958. *The Ecology of Invasions by Animals and Plants*. John Wiley and Sons, New York, New York.
- Erb, J., M. Boyce & N. C. Stenseth, 2001. Population dynamics of large and small mammals. *Oikos*, 92: 3-12.
- Ewel, J. J., D. J. O'Dowd, J. Bergelson, C. C. Daehler, C. M. D'Antonio, L. D. Gomez, D. R. Gordon, R. J. Hobbs, A. Holt, K. R. Hopper, C. E. Hughers, M. LaHart, R. R. B. Leakey, W. G. Lee, L. L. Loope, D. H. Lorence, S. M. Louda, A. E. Lugo, P. B. McEvoy, D. M. Richardson & P. M. Vitousek, 1999. Deliberate introduction of species: Research needs. *BioScience*, 49: 620-630.
- Filchak, K. E., J. B. Roethele & J. L. Feder, 2000. Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. *Nature*, 407: 739-742.
- Fonseca, D. M., N. Keyghobadi, C. A. Malcom, C. Mehmet, F. Schaffner, M. Mogi, R. C. Fleischer & R. C. Wilkerson, 2004. Emerging vectors in the *Culex pipiens* complex. *Science*, 303: 1535-1538.
- Gilchrist, G. W., R. B. Huey & L. Serra, 2001. Rapid evolution of wing size clines in *Drosophila subobscura*. *Genetica*, 112-113: 273-286.
- Hanfling, B. & J. Kollmann, 2002. An evolutionary perspective of biological invasions. *Trends in Ecology and Evolution*, 17: 545-546.
- Hastings, A., 1996. Models of spatial spread: Is the theory complete? *Ecology*, 77: 1675-1679.
- Hebert, P. D. N. & M. E. A. Cristecu, 2002. Genetic perspectives on invasions: The case of the Cladocera. *Canadian Journal of Fisheries and Aquatic Sciences*, 59: 1229-1234.
- Heger, T. & L. Trepl, 2003. Predicting biological invasions. *Biological Invasions*, 5: 313-321.
- Hengeveld, R., 1989. *Dynamics of Biological Invasions*. Chapman and Hall, New York, New York.
- Hengeveld, R., 1992. Potential and limitations of predicting invasion rates. *Florida Entomologist*, 75: 60-72.
- Hierro, J. L. & R. M. Callaway, 2003. Allelopathy and exotic plant invasion. *Plant and Soil*, 256: 29-39.
- Hobbs, R. J. & L. F. Huenneke, 1992. Disturbance, diversity, and invasion: Implications for conservation. *Conservation Biology*, 6: 324-337.
- Hobbs, R. J. & S. E. Humphries, 1995. An integrated approach to the ecology and management of plant invasions. *Conservation Biology*, 9: 761-770.
- Hodde, M., 2004. Restoring balance: Using exotic species to control invasive exotic species. *Conservation Biology*, 18: 38-49.
- Holt, A., 1999. An alliance of biodiversity, agriculture, health, and business interests for improved alien species management in Hawaii. Pages 65-75 in O. T. Sandlund, P. J. Schei & A. Viken (eds.). *Invasive Species and Biodiversity Management*. Kluwer Academic Press, Dordrecht.
- Johnson, L. E. & J. T. Carlton, 1996. Post-establishment spread in large-scale invasions: The relative roles of leading natural and human-mediated dispersal mechanisms of the zebra mussel, *Dreissena polymorpha*. *Ecology*, 77: 1686-1690.
- Johnson, L. E. & D. K. Padilla, 1996. Geographic spread of exotic species: Ecological lessons and opportunities from the invasion of the zebra mussel, *Dreissena polymorpha*. *Biological Conservation*, 78: 23-33.
- Johnston, R. F. & R. K. Selander, 1964. House sparrows: Rapid evolution of races in North America. *Science*, 141: 548-550.
- Jones, C. G., J. H. Lawton & M. Shachak, 1994. Organisms as ecosystem engineers. *Oikos*, 689: 373-386.
- Kartesz, J. T., 1994. *A Synonymized Checklist of the Vascular Flora of the United States, Canada and Greenland*. 2<sup>nd</sup> Edition. Timber Press, Portland, Oregon.
- Kowarik, I., 1995. Time lags in biological invasions with regard to the success and failure of alien species. Pages 15-38 in P. Pyšek, K. Prach, M. Rejmánek & M. Wade (eds.). *Plant Invasions - General Aspects and Special Problems*. SPB Academic Publishing, Amsterdam.
- Kraft, C. E. & L. E. Johnson, 2000. Regional differences in rates and patterns of North American inland lake invasions by zebra mussels (*Dreissena polymorpha*). *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 993-1001.
- Kriticos, D. J., R. W. Suthers, J. R. Brown, S. W. Adkins & G. F. Maywald, 2003. Climate change and biotic invasions: A case history of a tropical woody vine. *Biological Invasions*, 5: 145-165.
- Lee, C. E., 2002. Evolutionary genetics of invasive species. *Trends in Ecology and Evolution*, 17: 386-391.
- Leppäkoski, E., S. Gollasch, P. Gruska, H. Ojaveer, S. Olenin & V. Panov, 2002. The Baltic - A sea of invaders. *Canadian Journal of Fisheries and Aquatic Science*, 59: 1175-1188.
- Leung, B., J. M. Drake & D. M. Lodge, 2004. Predicting invasions: Propagule pressure and the gravity of Allee effects. *Ecology*, 85: 1651-1660.
- Lever, C., 1992. *They Dined on Eland. The Story of Acclimatisation Societies*. Quiller Press, London.
- Levine, J. M. & C. M. D'Antonio, 1999. Elton revisited: A review of evidence linking diversity and invasibility. *Oikos*, 87: 15-26.
- Levine, J. M. & C. M. D'Antonio, 2003. Forecasting biological invasions with increasing international trade. *Conservation Biology*, 17: 322-326.
- Lewin, R., 1987. Ecological invasions offer opportunities. *Science*, 238: 752-753.
- Lewis, M. A. & P. Kareiva, 1993. Allee dynamics and the spread of invading organisms. *Theoretical Population Biology*, 43: 141-158.
- Liebold, A. & J. Bascompte, 2003. The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters*, 6: 133-140.

- Ligon, J. D. & P. B. Stacey, 1996. Land use, lag times, and the detection of demographic change: The case of the acorn woodpecker. *Conservation Biology*, 10: 840-846.
- Loope, L. L. & F. G. Howarth, 2003. Globalization and pest invasion: Where will we be in five years? Pages 34-39 in *Proceedings of the 1<sup>st</sup> International Symposium on the Biological Control of Arthropods*. SDA-Forest Service, FHTET-03-05. USDA Forest Service, Honolulu, Hawaii.
- Louda, S. M. & P. Stiling, 2004. The double-edged sword of biological control in conservation and restoration. *Conservation Biology*, 18: 50-53.
- Louda, S. M., D. Kendall, J. Conner & D. Simberloff, 1997. Ecological effects of an insect introduced for the biological control of weeds. *Science*, 277: 1088-1090.
- MacDonald, N., 1978. *Time Lags in Biological Models*. Springer, Berlin.
- McMillan, M. & D. Wilcove, 1994. Gone but not forgotten: Why have species protected by the Endangered Species Act become extinct? *Endangered Species Update*, 11: 5-6.
- Mooney, H. A. & E. E. Cleland, 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences of the USA*, 98: 5446-5451.
- Mooney, H. A. & R. J. Hobbs, 2000. *Invasive Species in a Changing World*. Island Press, Washington, DC.
- Müller-Scharer, H., U. Schaffner & T. Steinger, 2004. Evolution in invasive plants: Implications for biological control. *Trends in Ecology and Evolution*, 19: 417-422.
- Nalepa, T. F. & D. W. Schloesser, 1993. *Zebra Mussels: Biology, Impacts, and Control*. Lewis Publishers, Boca Raton, Florida.
- National Research Council, 2002. *Predicting Invasions of Nonindigenous Plants and Plant Pests*. National Academy Press, Washington, DC.
- Novak, S. J. & R. N. Mack, 1993. Genetic variation in *Bromus tectorum* (Poaceae): A comparison between native and introduced populations. *Heredity*, 71: 167-176.
- Novak, S. J., R. N. Mack & P. S. Soltis, 1993. Genetic variation in *Bromus tectorum* (Poaceae): Introduction dynamics in North America. *Canadian Journal of Botany*, 71: 1441-1448.
- Okubo, A., 1988. Diffusion-type models for avian range expansion. Pages 1038-1049 in *International Ornithological Congress* (ed.). Acta: XIX Congressus Internationalis Ornithologici, Ottawa, Canada. University of Ottawa Press, Ottawa, Ontario.
- Onstad, D. W. & M. L. McManus, 1996. Risk of host range expansion by parasites of insects. *BioScience*, 46: 430-435.
- Parker, I. M., 2004. Mating patterns and rates of biological invasions. *Proceedings of the National Academy of Sciences of the USA*, 101: 13695-13696.
- Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers & L. Goldwasser, 1999. Impact: Toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, 1: 3-19.
- Petit, R., 2004. Biological invasions at the gene level. *Diversity and Distributions*, 10: 159-165.
- Pielou, E. C., 1974. *Population and Community Ecology. Principles and Methods*. Gordon and Breach Scientific Publishers, New York, New York.
- Pyšek, P., 1993. Recent trends in studies on plant invasions (1974-1993). Pages 223-236 in P. Pyšek, K. Prach & M. Rejmánek (eds.). *Plant Invasions - General Aspects and Special Problems*. SPB Academic Publishers, Amsterdam.
- Pyšek, P. & K. Prach, 1993. Plant invasions and the role of riparian habitats: A comparison of four species alien to central Europe. *Journal of Biogeography*, 20: 413-420.
- Reichard, S. H. & P. White, 2001. Horticulture as a pathway of invasive plant introductions in the United States. *BioScience*, 51: 103-113.
- Reish, D. J., D. F. Soule & J. D. Soule, 1980. The benthic biological conditions of Los Angeles-Long Beach Harbors: Results of 28 years of investigations and monitoring. *Helgolander Meeresuntersuchungen*, 34: 193-205.
- Reznick, D. N. & C. K. Ghalambor, 2001. The population ecology of contemporary adaptations: What empirical studies reveal about the conditions that promote adaptive evolution. *Genetica*, 112-113: 183-198.
- Ribera Siguan, M. A., 2003. Pathways of biological invasion of marine plants. Pages 183-226 in G. M. Ruiz & J. T. Carlton (eds.). *Invasive Species. Vectors and Management Strategies*. Island Press, Washington, DC.
- Ricciardi, A., 2001. Facilitative interactions among aquatic invaders: Is an invasional meltdown occurring in the Great Lakes? *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 2513-2525.
- Richardson, D. M., R. M. Cowling & B. B. Lamont, 1996. Non-linearities, synergisms and plant extinctions in South African fynbos and Australian kwongan. *Biodiversity and Conservation*, 5: 1035-1046.
- Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. J. Milton & M. Rejmánek, 2000. Plant invasions - The role of mutualisms. *Biological Reviews*, 75: 65-93.
- Rigby, G. R. & A. H. Taylor, 2000. Progress in the management and treatment of ship's ballast water to minimize the risks of translocating harmful nonindigenous aquatic organisms. Pages 344-356 in J. Pederson (ed.). *Marine Bioinvasions: Proceedings of the First National Conference*. Massachusetts Institute of Technology, Cambridge, Massachusetts.
- Rilov, G., Y. Benayahu & A. Gasith, 2004. Prolonged lag in population outbreak of an invasive mussel: A shifting habitat model. *Biological Invasions*, 6: 347-364.
- Ripple, W. J. & R. L. Beschta, 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? *BioScience*, 54: 755-766.
- Rogers, W. E. & E. Siemann, 2004. Invasive ecotypes tolerate herbivory more effectively than native ecotypes of the Chinese tallow tree *Sapium sebiferum*. *Journal of Applied Ecology*, 41: 561-570.
- Ruiz, G. M. & J. T. Carlton, 2003a. Invasion vectors: A conceptual framework for management. Pages 459-504 in G. M. Ruiz & J. T. Carlton (eds.). *Invasive Species. Vectors and Management Strategies*. Island Press, Washington, DC.
- Ruiz, G. M. & J. T. Carlton (eds.), 2003b. *Invasive Species. Vectors and Management Strategies*. Island Press, Washington, DC.
- Ruiz, G. M. & J. A. Crooks, 2001. Marine invaders: Patterns, effects, and management of non-indigenous species. Pages 3-17 in P. Gallagher & L. Bendell-Young (eds.). *Waters in Peril*. Kluwer Academic Publishers, Dordrecht.
- Saltonstall, K., 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proceedings of the National Academy of Sciences of the USA*, 99: 2445-2449.
- Saltonstall, K., 2003. Microsatellite variation within and among North American lineages of *Phragmites australis*. *Molecular Ecology*, 12: 1689-1702.

- Savidge, J. A., 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology*, 68: 660-668.
- Scheffer, V. B., 1951. The rise and fall of a reindeer herd. *The Scientific Monthly*, 73: 356-362.
- Secord, D. & P. Karieva, 1996. Perils and pitfalls in the host specificity paradigm. *BioScience*, 46: 448-453.
- Shea, K. & P. Chesson, 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, 17: 170-176.
- Shigesada, N. & K. Kawasaki, 1997. *Biological Invasions: Theory and Practice*. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford.
- Siemann, E. & W. E. Rogers, 2003. Reduced resistance of invasive varieties of the alien tree *Sapium sebiferum* to a generalist herbivore. *Oecologia*, 135: 451-457.
- Simberloff, D., 2003. Eradication - Preventing invasions at the outset. *Weed Science*, 51: 247-253.
- Simberloff, D. & L. Gibbons, 2004. Now you see them, now you don't! Population crashes of established introduced species. *Biological Invasions*, 6: 161-172.
- Simberloff, D. & B. Von Holle, 1999. Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions*, 1: 21-32.
- Sleat, D. E. & P. Palukaitis, 1992. A single nucleotide change within a plant virus satellite RNA alters the host specificity of disease induction. *The Plant Journal*, 2: 43-49.
- Starfinger, U., I. Kowarik, M. Rode & H. Schepker, 2003. From desirable ornamental plant to pest to accepted addition to the flora? The perception of an alien tree species through the centuries. *Biological Invasions*, 5: 323-335.
- Stockwell, C. A. & M. V. Ashley, 2004. Rapid adaptation and conservation. *Conservation Biology*, 18: 272-273.
- Stockwell, C. A., A. P. Hendry & M. T. Kinnison, 2003. Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution*, 18: 94-101.
- Suarez, A. V., D. A. Holway & T. J. Case, 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: Insights from Argentine ants. *Proceedings of the National Academy of Sciences of the USA*, 98: 1095-1100.
- Thompson, J. D., 1991. The biology of an invasive plant. *BioScience*, 41: 393-401.
- Townsend, C. R., 1996. Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. *Biological Conservation*, 78: 13-22.
- Trussell, G. C. & L. D. Smith, 2000. Induced defenses in response to an invading crab predator: An explanation of historical and geographic phenotypic change. *Proceedings of the National Academy of Sciences of the USA*, 97: 2123-2127.
- Veit, R. R. & M. A. Lewis, 1996. Dispersal, population growth, and the Allee effect: Dynamics of the house finch invasion of eastern North America. *American Naturalist*, 148: 255-274.
- Von Holle, B., H. R. Delcourt & D. Simberloff, 2003. The importance of biological inertia in plant community resistance to invasion. *Journal of Vegetation Science*, 14: 425-432.
- Weinig, C., 2000. Plasticity versus canalization: Population differences in the timing of shade-avoidance responses. *Ecology Letters*, 54: 441-451.
- Williams, C. K. & R. J. Moore, 1989. Phenotypic adaptation and natural selection in the wild rabbit, *Oryctolagus cuniculus*, in Australia. *Journal of Animal Ecology*, 58: 495-508.
- Williamson, M. B., 1996. *Biological Invasions*. Chapman and Hall, London.
- Zimmerman, E. C., 1960. Possible evidence of rapid evolution in Hawaiian moths. *Evolution*, 14: 137-138.