

## An Introduction to Invasion Ecology

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### Overview

Public and academic recognition of the problems associated with biological invasions has grown exponentially over the past few decades. The reasons for this growth are threefold. First, the negative effects of some non-native species have grown too large to ignore. Second, over time the number of species transported into novel locations has grown, so that the overall number of identified problems has also grown. And lastly, with so many invasive species, it is very hard to do ecological field research without encountering non-native species and potentially including them in investigations even if those investigations are for basic research. Non-native species offer new interactions with the potential for new insights, and curious scientists rarely pass up the opportunity to explore such new avenues. Thus, increasing numbers of scientists are managing and studying non-native species to minimize the effects of biological invaders, to satisfy basic ecological curiosity, or both. In this introductory chapter we precisely define what we mean by a non-native species, settle on a general terminology for use throughout the book, and provide some exploration of what we mean by the “invasion process.”

## What are invaders and why do we care about them?

One of the principal ways in which speciation occurs is through geographic isolation (i.e., vicariance speciation; Mayr 1963). Physical features such as oceans, mountains, ice sheets, and river valleys represent boundaries to the movement of individuals between populations of the same species. Over time these separated populations diverge via drift and selection, with each population eventually forming a unique species. This process generally happens on long, geological time scales. On those same time scales, we also see climatic and geological events that remove barriers and allow individuals to disperse over long distances and into previously unreachable areas. During these events, some species expand their ranges to intermingle with new communities and sample new habitats. For example, during the Miocene when the isthmus of Panama emerged from the sea to link North and South America, North American mammals moved south while birds and plants of the South American rainforests tended to move north (i.e., the Great American Interchange; Marshall *et al.* 1982). Such relatively rapid expansion of species groups is unusual enough to deserve special recognition, and paleontologists and ecologists have long been interested in why some species expand their ranges successfully in these events (while others do not) and have given these species a whole host of names (e.g., immigrants, waifs, colonizers; see Table 1.1).

As long as humans have had the ability to disperse across continents, they have also helped many other species breach geographic boundaries. Domesticated animals and plants have trailed along as human settlers have moved into novel territory (Crosby 1986). Almost certainly, representatives of non-domesticated species have hitched a ride in clothes, on boats or wagons, and within or on domesticated animals. Like the groups of mammals, birds, and plants that expanded their geographical ranges in the Great American Interchange, species moving with humans encountered locations that were previously out of their reach, and some of them successfully colonized these novel environments. These successful colonizers, however, achieved this new distribution with the help of humans. In the same way that ecologists distinguish between human-mediated and natural extinction of species, they also distinguish between natural and human-mediated rapid range expansion. This book concentrates exclusively on those species that found their way out of their native range and into a novel location via human actions.

There is ongoing discussion within the scientific community as to whether range expansions aided by humans are substantively different from range expansions that follow shifts in the earth's paleoclimate (e.g., Vermeij 2005). We address this debate in Chapter 2. Suffice it to say here that, compared with natural range expansion, humans have massively increased the rate at which species colonize new areas, and they have substantially changed the geographic patterns of invasion. This is not to say that there is little to be learnt from examining invasion patterns in the paleontological record. It is never wise to ignore the lessons of history.

One of the reasons for the debate about natural and human-aided colonization and range expansion is to determine whether invasion, like extinction, deserves

special attention or is a natural process. As with extinction, the answer is that the natural and human-aided processes share many characteristics. While examining the natural process may inform our understanding, there is no doubt that the human-aided process deserves and demands additional attention. There is ample evidence that non-native species can cause serious ecological and economic problems (Mooney *et al.* 2005). Invasive species eat, compete, and hybridize with native species often to the detriment of the natives. Invasion can result in the loss of native species and the loss of ecosystem services such as water filtration, soil stabilization, and “pest” control. More directly, most agricultural pests are non-natives, and many new human diseases are “emerging,” meaning they are non-native with us as novel hosts (Pimentel 1997). Invasive species clog waterways, impede navigation, destroy homes, and kill livestock and fisheries (Mooney *et al.* 2005). Whether or not we think modern invasions are historically unique, they demand our attention.

The motivation for this book comes as much from this practical concern as it does from the more esoteric interest in invasion as an ecological fact of life. This approach follows directly from the seminal work of Charles Elton (Box 1.1), who was one of the first to consider biological invaders as key drivers of ecosystem change and specifically of detrimental change (Davis 2006). The next seminal work on invasions, an edited volume by Baker and Stebbins (1965), took a more neutral stance. We (the authors) believe that biological invaders can act as useful “probes” into the inner workings of nature. Often we know the origins of non-native species, can document their arrival, and can directly collect information on their activities in their new community. This information allows the study of non-native species to become a powerful tool in our ecological and evolutionary arsenal (Sax *et al.* 2005; Cadotte *et al.* 2006a,b). Invasion ecology has swung back and forth through the years between an Eltonian view focused on invaders as problems and a less judgmental view, more oriented toward basic science. Interestingly though, the ascendancy of the field has mirrored the rise in prominence

### Box 1.1 Unknown legend

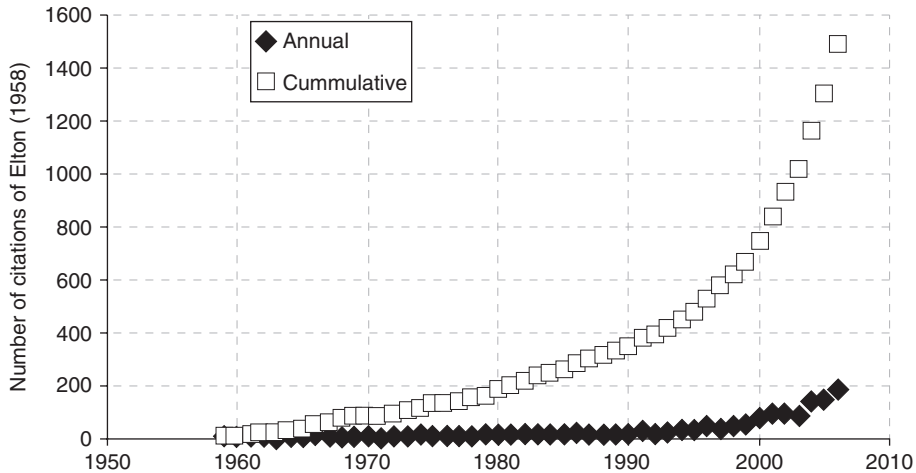
Charles Sutherland Elton (1900–1991) produced the foundational book on biological invasions, *The Ecology of Invasion by Animals and Plants*, in 1958, just less than 10 years before his retirement from Oxford University in 1967. This classic book grew out of a series of three radio lectures Elton made for the British Broadcasting Corporation (BBC) under the title “Balance and Barrier.” Within the book, Elton summarized a relatively obscure literature on the impact and spread of non-native species that, at that time, was largely confined to the disciplines of entomology and plant pathology (Southwood & Clarke 1999). Perhaps because the original intent of the lectures was to reach a larger non-academic audience, *The Ecology of Invasion by Animals and Plants* is a pleasure to read. Elton manages the nearly impossible task of melding scientific rigor with an engaging and often witty writing style.

**Box 1.1** *Continued*

As Dan Simberloff relates in his Foreword to the 2000 reprinted edition, “A writer who can describe oysters as ‘a kind of sessile sheep’ and characterize advances in quarantine methods by the proposition that ‘no one is likely to get into New Zealand again accompanied by a live red deer’ is more than just a scientist pointing out an unrecognized problem.” Because of his ability to communicate effectively in writing, Elton’s book has today become the most cited source in invasion biology (Richardson & Pyšek 2008).

The predominant feeling one gets after reading *The Ecology of Invasion by Animals and Plants* is that Elton presaged nearly all the arguments within the field, and indeed there are very few topics that we cover in this text that were not originally discussed by him. Due to the era in which he wrote, he could not have explored some currently hot topics (e.g., genetic diversity), was disinclined to pursue others (e.g., mathematics of population growth and range expansion), and given the rate at which global transportation has grown in 50 years, he could not have anticipated some emerging elements of the field (e.g., vector analysis; Richardson 2011). Nevertheless, one could argue that we are all simply putting mechanisms behind many of the patterns Elton noticed a half century ago. Of course, one could also make that argument for the majority of community and population ecology theories because Elton also wrote *Animal Ecology* (1927), *Voles, Mice and Lemmings: Problems in Population Dynamics* (1942), and *The Pattern of Animal Communities* (1966). Within these volumes Elton laid out the foundation for population cycles, food chains, pyramids of numbers, and the structure of communities. The first of these books was written in 85 days when Elton was in his late twenties (Southwood & Clarke 1999). If only we could all be so productive so early in our careers!

Presaging where ecologists stand today (especially as our work relates to biological invasions), Elton embraced the sociopolitical implications of his work and often steered his research agenda toward solving fundamental societal problems. He founded the Bureau of Animal Populations in Oxford during World War II in part to satisfy the need to reduce the loss of stored grains from over-abundant rodent populations (Southwood & Clarke 1999). He helped found The Nature Conservancy and sat on its Scientific Advisory Board until 1957 despite the fact that he was “allergic to committees” (Nicholson 1987 as quoted in Southwood & Clarke 1999). Elton made the critical connection between population cycles of mammals and human health concerns such as the plague, and, in an early example of cross-disciplinary collaboration, spent several years exploring the population cycles and parasites of voles and mice. Thus, perhaps his most lasting contribution was his recognition that ecology was a distinct discipline in biology, and that ecologists had a large role to play in how society dealt with the problems it faced. In this sense, and in several other ways, the book you are reading is clearly infused with the spirit of Charles Elton.



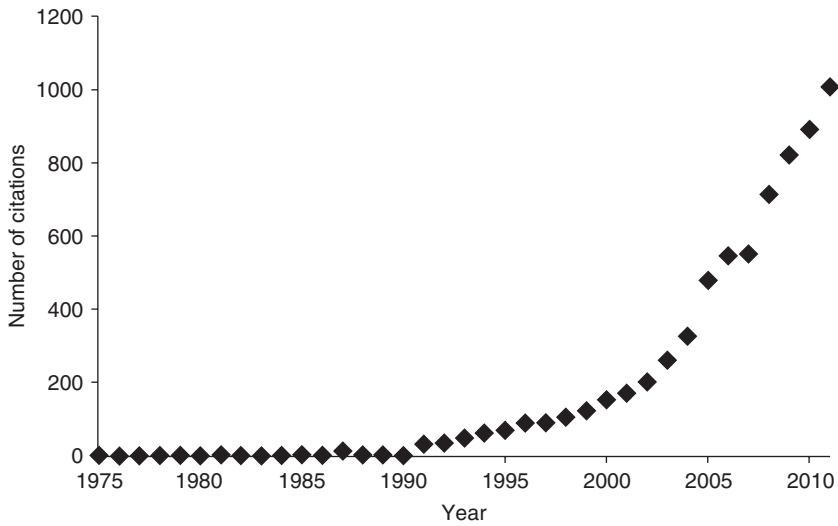
**Figure 1.1** Cumulative number (white squares) and annual number (black diamonds) of citations of Charles S. Elton's (1958) book *The Ecology of Invasions by Animals and Plants* between 1960 and 2006. From Richardson D. and Pyšek, P. (2008) Fifty years of invasion ecology: the legacy of Charles Elton. *Diversity and Distributions* **14**, 161–167.

of Elton's classic book (Fig. 1.1) (Davis 2006; Richardson & Pyšek 2008). As ecologists, we (the authors) recognize the value of non-native species as unique sources of ecological and evolutionary knowledge and have conducted research from this point of view (e.g., Mathys & Lockwood 2011), but we also lean toward the Eltonian view that non-native species can drive change in ways that may be detrimental. Indeed the one thing that separates this text from a basic overview of ecology is its focus on how non-native species interact with human society, and how we can use ecological knowledge to thwart the influx and impacts of invasive species.

## A brief history of invasion ecology

As Mark Davis points out in his work on the history of invasion ecology, the topic “would be a dream dissertation ... for some history of science graduate student” (Davis 2006). The rapid rise of the discipline over the last decade continues a rather long history of scientific interest in non-native species that goes back at least to the publication of Elton's book in 1958 (Richardson 2011). In addition, the list of scientists that have dabbled in invasion ecology over the decades reads like an all-star ecology roster, including such famous names as Ernst Mayr, E.O. Wilson, and Rachel Carson (Davis 2006).

Much like other modern disciplines, invasion ecology grew out of a variety of much older research foci including agriculture, forestry, entomology, zoology, botany, and pathology (Davis 2006). Within each of these disciplines there were scientists grappling with the effects of non-native species. Foresters were concerned about non-native species that decimated natural and managed forested lands. Agricultural scientists (e.g., plant pathologists) were concerned about non-native



**Figure 1.2** The number of citations returned from a search of the Science Citation Index using the search terms “invas\*” and “ecolog\*” over the search period from 1975 to 2011. Republished with permission of Ecological Society of America, from Simberloff *et al.* (2012) *The natives are restless, but not often and mostly when disturbed. Ecology* 93, 598–607; permission conveyed through Copyright Clearance Center, Inc.

species that reduced crop yields. Animal scientists were concerned about non-native species that killed or caused disease in livestock and wild populations. Botanists were concerned about non-native species that transformed native plant communities. But some of the interest arose because scientists found the growing number of novel species in their location noteworthy and documented their presence and sometimes their interactions with native species. There was substantial and somewhat simultaneous work on non-native species occurring among European, North American, South African, and Australian biologists and natural resource managers throughout the 1950s and 1960s (Davis 2006). Because English has grown to be the language of science over the decades, much of the early work not published in English has unfortunately escaped notice by contemporary biologists (Davis 2006).

A rising interest in invasion ecology is manifest in the increasing number of contemporary publications related to invasive species. For a quick view of how interest in invasion ecology has changed through time we did a search in the Science Citation Index® for articles published between 1975 and 2011 that included as keywords “invas\*” and “ecolog\*” and the results are shown in Fig. 1.2. From 1975 to 1985 there were no articles that utilized variations of “invasion ecology” in their keywords. This almost certainly reflects the inconsistent use of the term “invasion” prior to the mid-1980s, but it also indicates a somewhat scattered and diffuse interest in the field during this time (Davis 2006; Richardson & Pyšek 2008). After 1990 there was an exponential growth in such articles. Indeed an exponential line fits the data depicted in Fig. 1.2 nearly perfectly ( $R^2 = 0.9028$ ).

There is a tiny blip in Fig. 1.2 around the mid-1980s that corresponds with the publication of the Scientific Committee on Problems of the Environment (SCOPE) volumes. This committee, founded by the International Council for

Science in 1969, is an amalgamation of environmental scientists that seeks to develop syntheses and reviews on various environmental issues. SCOPE pulled together a large group of ecologists from around the world between 1982 and 1989 to document the problems that invasive species posed (Mooney 2005). From the SCOPE focus, a series of books and journal articles on invasive species emerged, as well as a generation of newly minted PhDs who saw biological invasions as a significant component to global change (Vitousek *et al.* 1996). Arguably, the SCOPE volumes may signal the gelling of the study of non-native species into a coherent field (Davis 2006). The language used in these volumes marks a move toward viewing invasions as a conservation concern, much like the Eltonian view, and such usage continues in today's literature (Davis 2006). We count ourselves among the academic "children" of SCOPE and suggest that the need to produce this textbook comes from the expansion of research in invasive species generated by these early SCOPE publications.

### The wicked terminological web we weave

In many ways the exponential growth of invasion ecology is one of the joys of working within the field, as it is inherently a rapidly changing, interdisciplinary science that focuses squarely on applied problems. On the other hand, early scientists working on non-native species developed individual sets of terminology for their disciplines. Once the interdisciplinary conversations started, these scientists discovered they often had very little overlap in language and terminology. The terminological morass is still challenging. On the surface, much of the difference in terms appears to be semantics, but there are some important distinctions in use between fields that can cause confusion when collating and synthesizing results (Richardson *et al.* 2000a) or producing management recommendations (Shrader-Frechette 2001). We take a close look at terminology here, so readers can clearly identify the limits to our use of various terms and can place the semantic traditions of their respective fields within our framework. This discussion of terminology also sets the stage for understanding ongoing debates.

Table 1.1 is a list of terms in the English literature on invasion ecology. Some of these terms are used interchangeably to describe the same concept. For example, "non-indigenous," "exotic," and "alien" are often used to signify that a species is not native to a particular location. In other cases, one term is used to represent a variety of slightly different things. For example, Richardson *et al.* (2000a) identified four unique applications for the term "naturalized." These are (i) non-native species that are reproducing outside of human cultivation, (ii) the set of non-native species that are reproducing in natural or semi-natural settings, (iii) species that are found outside their native range but that may or may not be successfully reproducing, and (iv) non-native species that have expanded their geographic ranges. The lack of a consistent meaning for the term "naturalized" represents a real problem when trying to assemble lists of species that demonstrate a particular trait (i.e., established but not expanding its range vs. established and spreading), and thus for subsequent analyses based on this trait (Richardson *et al.* 2000a; Daehler 2001a). Table 1.1 and compendiums of definitions such as those found in Colautti and MacIsaac (2004)

**Table 1.1** Terminology commonly used for non-native species in the English language.

	Native	Non-native	Transported	Established	Spread	Impact	Invasive
Adventive	*	*		*	*		
Alien		*	*	*	*	*	*
Casual		*	*				
Colonizing		*	*	*	*		
Cryptogenic		*	*	*			
Escaped	*	*	*	*	*		
Established		*		*	*		
Exotic		*	*	*	*	*	*
Foreign		*	*	*			
Immigrant		*	*	*	*		
Imported		*	*	*	*		
Introduced	*	*	*	*	*		
Invasive	*	*	*	*	*	*	*
Naturalized		*	*	*	*		*
Non-indigenous		*	*	*	*	*	*
Noxious	*	*				*	*
Nuisance	*	*				*	*
Pest	*	*				*	*
Ruderal	*	*		*	*		*
Tramp		*	*	*	*		
Transformer		*				*	*
Transient		*	*				
Translocated	*	*	*	*			
Transplanted	*	*	*	*			
Transported	*	*	*				
Waif		*	*	*			
Weed	*	*	*	*	*	*	*

*Note:* The list was compiled from the authors' readings of the invasion ecology literature. Other scientists may categorize the terms differently. This inconsistency of usage creates problems for synthesis and management. The columns indicate types of species and invasion stages to which the words apply. See Figure 1.3.

and Richardson *et al.* (2011) go a long way toward alleviating some of this confusion related to terminology. However, debates about term usage foreshadow some more substantive issues within the field that are well worth reviewing before we delve into the rest of the book. We deal with two linguistic/philosophic issues in the following sections.

### Natives, non-natives, and loaded language

There is a persistent charge that the language of invasion ecology evokes anthropocentric concepts that are militaristic and pejorative (see Davis 2006 for historical roots of this argument). For example, a standard thesaurus gives the



following synonyms for “invasion”: attack, assault, incursion, raid, foray, and offense. Of course it is unwise to assume that words co-opted by scientists have the same meaning in and out of the profession (Daehler 2001b). For example, physicists have divided the subatomic particles called quarks into six types or flavors: up, down, strange, charm, bottom, and top. These words are different in physics than when applied to ice cream or jewelry. Nevertheless, the connotations of such terms as “invasion” are less neutral and have opened the field to criticism (Simberloff 2003a; Brown & Sax 2004). The vast majority of invasion ecologists have responded to criticisms of language by adopting militaristically neutral terms such as non-indigenous and non-native (Young & Larson 2011). We adopt this approach here with the use of “non-native” to describe species that have been moved outside their normal geographic ranges via human actions, regardless of their eventual impact on native ecosystems. Even this language is not socially neutral, though. Non-native is perhaps more neutral than “alien” but perhaps less linguistically appealing than “exotic,” both terms frequently used to identify species outside their native range. Some authors have taken issue not just with the language but also with the distinction between native and non-native (see more below), pointing out that the distinction draws into question how we value things “not from here,” however defined (Chew & Carrol 2011). We would recommend Simberloff (2003a, 2011a), Brown and Sax (2004), and Cassey *et al.* (2005) for thoughtful discussions of both the scientific applications and the sociological implications of invasion terminology.

An important element of this debate lies in the definitional boundaries between “native” and “non-native.” An assessment of the definition is useful for clarity and reveals nuanced ecological details that are worth exploring. To the casual observer, the definitions of native and non-native make intuitive sense; natives are from “here” and non-natives were transported by humans to “here” from “over there.” Usually “here” and “there” are defined as clear biogeographical units like continents or islands (Preston 2009). For the most part, this *ad hoc* definition works reasonably well (Preston 2009). But, like many reasonably useful concepts in biology (e.g., species), a deconstruction of these definitions reveals the extent of the gray area. This gray area can be divided along two axes, space and time.

Once we reduce our spatial scale from continents and islands, the distinction between native and non-native becomes more difficult to draw. For example, there are several species that have expanded beyond the geographical limits of their native range via human actions yet have never left their native continent or island. These home-grown non-natives (Cox 1999) can cause substantial harm to ecosystems they enter (e.g., rainbow trout dropped from planes into the high mountain lakes of the Sierra Nevada; Moyle 2002), yet there is occasional reluctance to label them as invasive because they are native to the larger regional species pool (i.e., the continent/biogeographic region). Our definition of non-native includes species that have clearly been introduced outside of their native range via human actions even if they are still within their native continent (e.g., house finches introduced within North America). We see no difference in the ecological patterns and mechanisms behind the expansion of these species as compared to those that were introduced further

afield. Indeed, several species that may be considered home-grown non-natives in their local region also have introduced populations outside of their native continent or island.

But what of species that are native but have expanded their ranges, or increased in abundance, for reasons that were only somewhat related to human actions (e.g., urbanization or global climate change)? Sometimes these native species go on to cause economic and ecological harm, often earning them the label invasive, and as a consequence they are heavily managed for restoration and conservation purposes (Baiser *et al.* 2008; Simberloff *et al.* 2012). These native species may even have expanded their ranges via hitchhiking on humans or their vehicles, albeit usually just taking a ride to the next town and not necessarily across an ocean, mountain, or ice sheet. Are these species non-native, and should they be considered under the same research structure as those species that have intentionally been moved much further afield? Clearly the definition of non-native inherently involves a judgment of spatial scale, but the spatial scale at which to draw that line is open to debate (Colautti & MacIsaac 2004; Preston 2009; Valery *et al.* 2009; Wilson *et al.* 2009).

In a series of articles Mark Davis and colleagues have argued that biological invasions are an extension of normal colonization processes such as succession and range expansion, and thus the terminology used should reflect this fact and not be based on the species' geographic origins (Davis & Thompson 2000; Davis *et al.* 2001; Davis 2009). Given this evidence, Davis *et al.* (2011) suggest that labels like "native" and "non-native" do more harm than good as they inflame non-scientists' ire and evoke unwarranted militancy towards non-native species. They suggest ecologists should instead assess the environmental impact of *all* species rather than using pejorative labels *a priori*. Davis and others suggest that the impact of native and non-native species that are increasing and spreading aggressively is often equivalent and that the number of "native invaders" may increase with continued climate and land-use change (Davis *et al.* 2011). Interestingly, both of these suggestions are under-studied (van Kleunen *et al.* 2011).

Nonetheless, there is some evidence that the effects of natives and non-natives are somewhat different, and these effects again come back to the axes of space and time. A compelling recent investigation found that non-native plants in the USA were 40 times more likely than native plants to have strong negative impacts and be designated invasive (Simberloff *et al.* 2012). Simberloff and colleagues propose that the shared long evolutionary history between native species and the physical environment helps to explain the reduced effects of natives that expand their range. Non-native species do not share this evolutionary history and thus may be more likely to disrupt the native systems they enter. But what sort of spatial region allows a shared evolutionary history? Clearly the answer depends on dispersal distances for the natives, and potentially also for the species with which they interact closely in the community. Does it also depend on weather and regional effects? More similar studies are clearly warranted.

The evolutionary history argument of Simberloff *et al.* (2012) also points to the time axis that we said was critical to the definition of native versus non-native. How long does a species need to reside in one area before it is considered native? For the vast majority of species we consider in this book, the time frame

of residence in the non-native range is quite short, usually far less than 100 years. As we will discuss further in Chapters 2 and 3, the overwhelming majority of non-native species were transported after the start of the Industrial Revolution (about 1750), with the rate of introduction rising exponentially since then. The length of residence, therefore, is unlikely to be long enough to constitute a shared evolutionary history (Preston 2009).

Nonetheless, time can be important. Some ecologists have argued that time contributes to the destructiveness of non-native species while others have argued that time makes the distinction between natives and non-natives less important. There are clearly examples of species that have been resident in their non-native range for well over 100 years (Preston *et al.* 2004), and more of these long-established non-native species are becoming apparent through the use of molecular tools (e.g., Storey *et al.* 2007; Ricklefs & Bermingham 2008; Xavier *et al.* 2009). These long-established non-native species have perhaps undergone evolutionary shifts in morphology or life history in response to the biotic and physical properties of their new ecosystem (Preston *et al.* 2004), which raises the possibility that their impact may also have altered over time (see Chapter 13). Some of these species only began having noticeable effects after long periods of innocuous residency (Chapters 7, 8, 9, 10, and 11). Most human communities associated with these long-established species are not aware of their non-native status, and people often have very positive associations with such long-term residents (Preston *et al.* 2004). Davis and Thompson (2000) suggest that these positive associations are yet another reason that it makes little sense to refer to such long-established non-natives as “alien invaders.”

We (the authors) generally think that there are some ways in which natives and non-natives can behave similarly but that there are numerous things that ecologists and conservation biologists can learn from maintaining the distinction and observing the altered dynamics and effects that come with introducing novel species into established systems (Lockwood *et al.* 2011). Along with many other ecologists, we worry that following the advice of Davis *et al.* (2011) and disregarding non-native status would do more harm than good to applied and basic ecological and evolutionary biology (Alyokhin 2011; Lerdau & Wickham 2011; Lockwood *et al.* 2011; Simberloff 2011b). With this stance we echo arguments made by Daehler (2001a) that many questions in invasion ecology, and more broadly in biology, rely on knowing the origins of the species under study. This is certainly the situation for understanding the impacts of non-native species (Chapters 9 and 10). We do think it would be useful to directly investigate the influence of residency time on declarations of invasiveness in a way analogous to Simberloff *et al.* (2012), but retaining the native/non-native distinction is also helpful in a wide range of newly opening fields. Understanding and predicting the effects of global climate change may depend on comparatively different effects on native versus non-native species, as outlined by van Kluenen *et al.* (2011) and Colautti and MacIsaac (2004). Even from a basic science standpoint, it is highly pertinent to know the colonization/invasion history of a species under investigation because a species’ source offers considerable insight into subsequent ecological and evolutionary dynamics (Sax *et al.* 2005; Cadotte *et al.* 2006a). Despite the nuances associated with the definitions of native and non-native

(and perhaps because of them), we should not disregard the considerable insight we gain from the distinction between these two categories of species.

### Definition of “invasive”

Many in the field have adopted the term “invasive” to describe species that have a demonstrable ecological or economic impact. This definition is in use by about half of all invasion ecologists according to the survey work of Young and Larson (2011) and is in keeping with how the term is used by governmental and non-governmental agencies. The problem with this definition is that it relies on human valuation or investigation into damage. This means that the species included in this category will change based on who is doing the looking (Chapter 10). Plus, this definition ignores the possibility that non-native populations can have positive impacts on the ecosystem in which they have become members (Davis *et al.* 2011). About one-third of Young and Larson’s (2011) surveyed invasion ecologists feel strongly that impact is not an important part of the definition of invasive and define a species as invasive if its populations are self-sustaining and spreading in its new environment, regardless of impacts (Richardson *et al.* 2000a; Daehler 2001b). This definition requires no human judgment of damage but instead relies on empirical evidence that a population is spreading beyond its initial location of establishment (Richardson *et al.* 2000a; Daehler 2001b; Colautti & MacIsaac 2004). This usage ties the term to a more easily recognizable biological phenomenon, geographic range expansion, as opposed to the subjective and sometimes nebulous notion of impact. Daehler (2001b) suggests that this latter definition serves to “minimize subjectivity and maximize consistency,” although he does recognize that creating definitive criteria for what counts as spreading (appearing a certain number of “body” lengths from the original establishment site? Moving a particular multiple of the usual lifetime travel distance? Crossing disjunct habitat patches?) is also a subjective determination made by interested parties. An added difficulty with using spread criteria to define invasive is that it is hard to escape the fact that some non-native species do cause serious ecological and economic damage (Simberloff 2003a; Cassey *et al.* 2005), and it is helpful to label such species with a unique term. In fact, for many ecologists and conservation biologists, this impact is a driving reason for studying invasion dynamics.

Daehler (2001a) suggests that these two definitions, one based on damage/impact and the other on spread criteria, in practice tend to designate the same populations as invasive. The work of Richardson *et al.* (2000a) indicated that 50–80% of the species they evaluated would be labeled as invasive using *either* definition. Daehler (2001a) suggests that if the impact formulas of Parker *et al.* (1999) are widely adopted (see Chapter 10), this overlap in categorization may be much higher, perhaps nearing 100%. This high degree of overlap in the definitions is likely a consequence of the positive relationship between the level of damage a non-native population inflicts and the abundance or geographical range size of the non-native population (Chapter 10). However, the correlation between spread and damage is not a perfect one, and invasion ecologists should attempt to evaluate empirically the mechanistic links between the two definitions (e.g., Ricciardi & Cohen 2007).

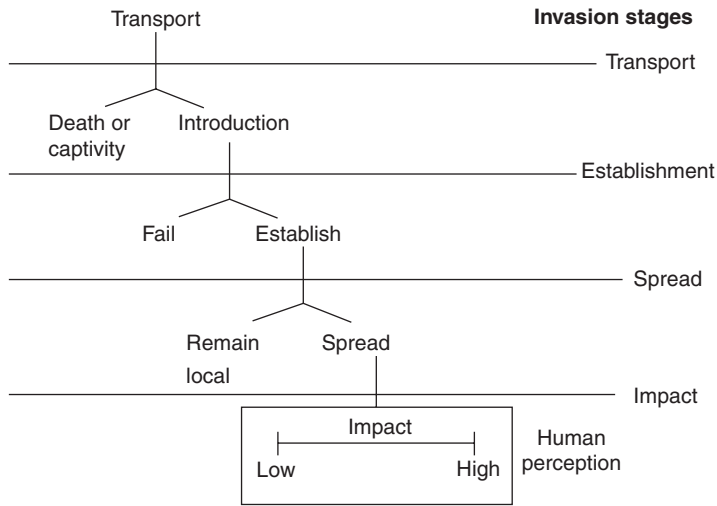
For the reader of this book, it is perhaps most important to realize that the term “invasive” should refer only to those species that either clearly have an ecological or economic impact or spread aggressively. Here we lean toward the impact definition, as is clear from our chapters on impact, because we are interested in these end effects. We also suggest, though, that readers who prefer the spread definition will find that all the chapters of the book work for them and that the impact sections offer insight into the effects of species many readers will have already labeled as invasive.

An overriding aspect of either definition is that an invasion is really the end product of a series of stages, where factors in each stage may serve as barriers to the next stage. By explicitly recognizing biological invasion as a process instead of a dichotomous classification (i.e., invasive or not), it becomes clear where and when standard ecological principles alter invasion dynamics and how society can most effectively manage invaders (see also Colautti & MacIsaac 2004). A related criticism of both terms is that they tend to be applied to an entire taxonomic group rather than to the members of that group that cause an ecological phenomenon (impact or spread); thus entire species will be labeled as invasive when only some of the non-native populations of the species cause harm (Colautti & MacIsaac 2004). An explicit recognition of the invasion process also goes a long way to alleviating this problem. Thus, for a variety of reasons, we recommend that “invasive” should not be used as an all-purpose label for newly arriving non-native populations or be broadly affixed to all populations of a non-native species, even if one of those populations could legitimately be labeled as invasive.

## The invasion process

In studying invasive species, as we have mentioned, it is important to start with the idea that invasion is a process not an event and therefore has various stages. If we start at the beginning and work our way forward, we can readily see that non-native species must pass through at least three stages before they are able to inflict ecological or economic harm (Fig. 1.3 and Box 1.2). All non-native species originally begin as individuals that are picked up in their native range, transported to a new area, and released into the wild (Transport in Fig. 1.3). These individuals must then establish a self-sustaining population within their new non-native range (Establishment in Fig. 1.3), or else the population becomes extinct. An established non-native population may then grow in abundance and expand its geographic range (Spread in Fig. 1.3), otherwise it remains small in numbers and local in distribution. Typically it is only when the non-native population is widespread and abundant that it will cause some sort of ecological or economic harm, and thus earn the name “invasive.” Acknowledging the stages of the invasion process allows the explicit recognition of the actions of humans as either facilitators or inhibitors in transitioning a stage (e.g., Kolar & Lodge 2001). For these reasons we adopt this simple model as the general organizing framework for the rest of the book.

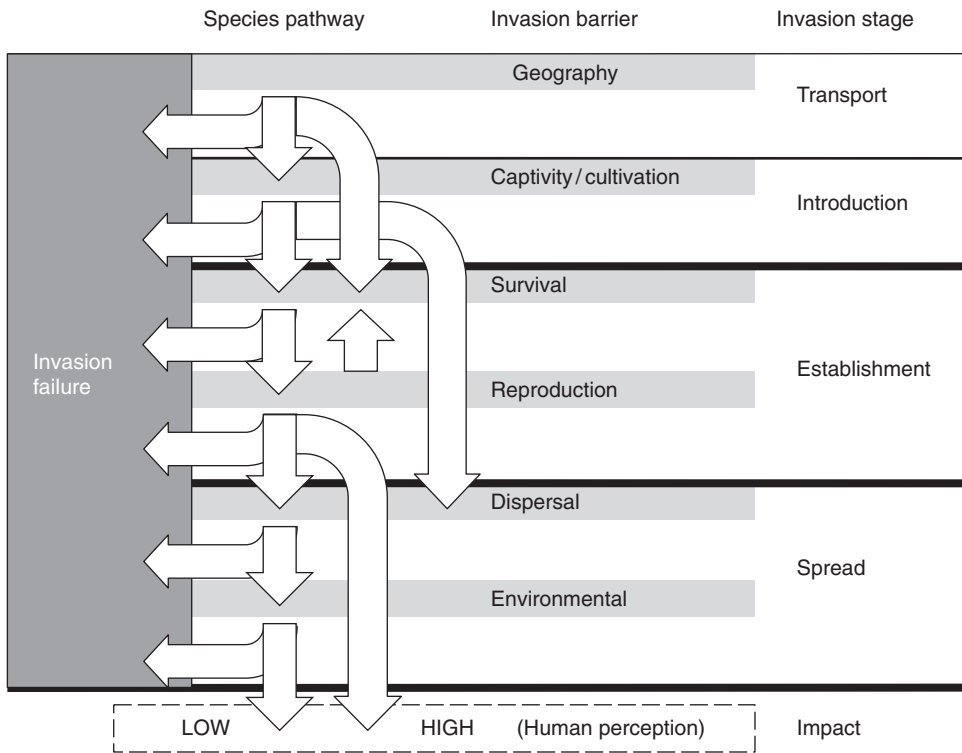
While the simple model presented in Fig. 1.3 is a good starting point, it is clear that progress in the field of invasion ecology has been stymied at times due to



**Figure 1.3** Simple invasion process model depicting the discrete stages an invasive species passes through, as well as alternative outcomes at each stage.

individual scientists or schools of thought assembling the invasion process in different ways (Blackburn *et al.* 2011). Tim Blackburn and seven other invasion ecologists attempted to bring clarity to this issue by proposing a standardized terminology for the process of invasion (Blackburn *et al.* 2011). They created what they call a “unified framework” for studying the invasion process. They found they had to combine the two most commonly employed invasion constructions, one typically used by plant ecologists (e.g., Richardson *et al.* 2000a; Theoharides & Dukes 2007) and one often adopted by animal ecologists (i.e., Williamson 1996 and our simple model in Fig. 1.3). The main difference between the two is that the plant model focuses on barriers to progress between and among stages, while the animal model largely focuses on the stages or status that a species attains. We agree with both the spirit and result from Blackburn *et al.* (2011) and have therefore included a slightly edited version of their invasion process model for this book (Fig. 1.4). Our version of the unified framework model combines stages, barriers, and species pathways and differs from Blackburn *et al.* (2011) in that we explicitly include an impact stage in the invasion process. We include this element partially because of our definition of the invasion process and partially because understanding impact is an essential element of understanding invasion dynamics. This extra stage complicates the figure somewhat because the level of impact can be influenced by many of the invasion stages. In addition, as we make clear in Figs 1.3 and 1.4, the level of impact is integrally tied to human perception and valuation. We will discuss these cross-stage effects and the human element of impact at length in Chapter 10, but suffice to say here that we feel the impacts from non-native species are intrinsic pieces of the complex invasion puzzle.

Blackburn *et al.* (2011) suggest that prior to, and associated with, passage through any of the invasion stages we described in Fig. 1.3, a potential invasive



**Figure 1.4** Edited version of unified framework model by Blackburn *et al.* (2011), which combines stages, barriers, and species pathways. Our version of the unified framework model differs from Blackburn *et al.* (2011) in that we explicitly include an impact stage in the invasion process. Reproduced with permission of Elsevier, from Blackburn *et al.* (2011), A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26, 333–339.

species must also overcome a series of inherent barriers (Fig. 1.4). The first of these barriers is simply the obstacle posed by geography; namely that species have an inherent geographical range that imposes physical barriers to movement beyond their natural boundaries. Human-assisted entrainment and transport around these barriers or boundaries is clearly the first step toward transport and introduction (Fig. 1.4). The model also identifies a captivity/cultivation barrier to acknowledge that entrained species may never actually make it out of a captive or cultivated state. Despite being moved to a novel location, many species remain within human-imposed confines in the new environment. Nonetheless, it is also possible for a species within this unified framework to essentially skip over the captivity barrier and become established (Fig. 1.4 pathway arrow), especially when the species is transported unintentionally, as we will see in Chapter 2. In addition, we also added a pathway to the Blackburn *et al.* (2011) model that allows for captive/cultivated individuals to essentially act as established populations and move directly to the spread stage (Fig. 1.4 pathway arrow) because some captive populations may be self-sustaining but restrained; escaping the barriers of captivity would

then lead directly to spread. Finally, it is possible for a transported introduced species to have an impact even if it never passes through any of the subsequent stages. A rare example would be a single, long-lived top predator on an island killing large numbers of prey before it dies. A more common and ecologically interesting example could be a species (such as a beaver or dominant wetland plant) that survives for a few generations and alters ecosystem function before dying out. Given that either of these examples would lead to an arrow straight from introduction to impact, we have not cluttered the figure with every arrow that leads to impact, but please add these arrows mentally as you look at Fig. 1.4.

During the establishment stage, a non-native species faces two additional and significant ecological/environmental barriers, namely survival and reproduction. If the population fails at one of these tasks, it either will not establish, or the established population will eventually go extinct. Factors that can influence these two barriers can arise from the populations themselves (e.g., intrinsic reproductive rate), from the particular location (e.g., habitat quality and interactions with local species), from stochastic or random features of the introduction event (e.g., propagule pressure), or from interactions among these factors (Blackburn *et al.* 2011). It is also possible for a species to get caught in population cycles at this stage (Fig. 1.4; see Chapter 8). This pair of barriers helps clarify why some species fail to establish at a given time and location but can succeed in proximate locations or even in the same location at a later time (Blackburn *et al.* 2011).

If a non-native population spreads beyond its place of initial establishment, it must have some ability to disperse, and thus dispersal (particularly poor dispersal) itself can be a potential barrier (Fig. 1.4). If it manages to disperse, each subsequent novel location can pose additional barriers to establishment and further spread similar to those that it passed through previously. However, as the species moves further from the original locus of introduction, the barriers are likely to become increasingly dissimilar from those it first encountered (Blackburn *et al.* 2011). In some sense, therefore, a spreading population faces multiple, sequential, and potentially increasingly difficult barriers, which in this unified framework are labeled as generalized “environmental” barriers. It is also during transit through the spread stage barriers that a population can experience boom and bust cycles (see Chapter 8; Blackburn *et al.* 2011). Changes in the barriers encountered during spread may lead to surprising switches from increased success to decreased success and may result in reduced population size, invasion failure, or both. Impacts may also vary with these cycles, which may lead to changing or mismatched management. Finally, note that although impacts may happen at earlier stages, impacts that occur after the spread stage are fundamentally different from impacts at earlier stages because these impacts do not occur in just a single location. It is this pervasive threat that makes the difference between widespread impacts from invasive species and local impacts from non-native species. These local impacts may be critical to identifying non-native species to control, but the enormous impacts attributed to invasive species are the ones that come from species that spread.



Both process models depicted in Figs 1.3 and 1.4 imply biologically identifiable steps along the path to becoming an invader, although these steps may not be as distinct as our cartoon versions portray. One of the key insights from Williamson's 1996 book was his recognition that most species that have the opportunity to transit between invasion stages do not successfully do so. He and his colleagues examined many examples of this phenomenon and generally found that between 5 and 20% of species successfully transit any of the individual invasion stages, with the average being 10%. Williamson (1996) dubbed this pattern the Tens Rule, and it suggests two insights. First, the barriers we have discussed are formidable, and thus there is a lot to learn about why some species successfully negotiate these barriers and others do not. Second, the nested structure of the invasion process ensures that only a small fraction of all the species introduced outside their native range will eventually cause the ecological or economic harm associated with invasive species. Thus, one of the tasks set before invasion ecologists is to find a way to sift through all the non-natives that will not survive, spread, or cause harm to find the few that will. As we will see, these two insights simultaneously make the study of invasion ecology rewarding and frustrating.

Beyond these insights, using a model to examine the invasion process, as we do, has a couple of key advantages. First is the recognition that it is something of a misnomer to label an entire species as invasive or not (as mentioned above). Individuals of particular species are transported and introduced into new environments, and it is this set of individuals that must survive and reproduce if the non-native population is to persist (Chapters 2 and 3). In cases where individuals of one species have been transported to a variety of different places, it is possible that some of these incipient populations established, became widespread, and affected native biota (i.e., became invaders), while other populations did not. Thus, a species may be considered invasive in one location but not in another. Of course, the individuals of a species share a set of common traits that may allow all non-native populations of this species, on average, to become invasive. However, a shift in focus from species to populations opens doors to our understanding of invasions that would otherwise be closed (Colautti & MacIsaac 2004; Lockwood *et al.* 2005).

Second, using the unified framework in Fig. 1.4 allows us to pull away from simplifying dichotomies such as "Do species traits or community properties determine the success of an invader?" There is no simple answer to that question, as we will see. Non-native populations confront a host of extrinsic forces that determine whether they will persist into the future (Chapters 4, 5, and 6). These forces include competition, predation, parasitism, and other interactions between individuals of two (or more) species. They also include stochastic physical forces such as flooding, freezing, and fire. How non-native populations respond to these forces depends on their life history. One set of extrinsic forces modifies the effect of others, and the species themselves can modify the magnitude and extent of the extrinsic forces. These interactions make it nearly impossible to gain a clear picture of what determines success and failure of a non-native population by focusing on one side of the dichotomy or the other. Furthermore,

properties of the community, environment, and species often play a role in the successful transition of non-native populations through the barriers and across all invasion stages although they may take different forms and perhaps vary in their importance (Kolar & Lodge 2001; Cassey *et al.* 2004a). The waxing and waning in importance of various ecological mechanisms across invasion stages adds yet more confusion when trying to answer simple dichotomous questions (Lockwood *et al.* 2005).

Third, our models allow us to see more clearly where the actions of humans interact with the fate of non-native populations. By our definitions, humans begin the invasion process by purposefully or inadvertently transporting individuals beyond their natural range limits and then releasing them into the wild (Chapters 2, 3, and 4). This aspect of the invasion process has often been divorced from the rest of the process, despite the growth in our knowledge of this stage (Puth & Post 2005). Humans also enter the picture through their effects on the ecosystem in which the non-native population is attempting to establish (e.g., causing disturbance; Chapter 5). They can facilitate the geographic range expansion of an established non-native population via their commerce or travel, although this is not necessary for a non-native population to spread (Chapters 7 and 8), or to cause some type of harm (Chapters 9, 10, and 14). Finally, human actions serve to strengthen the barriers between invasion stages through the use of direct eradication techniques or through sociopolitical actions that slow the transportation of non-native individuals (Chapters 12 and 13).

One disadvantage to using the simple model as an organizing structure for this book is that we end up separating discussions of key ecological processes such as facilitation and competition between chapters. There are certainly insights to be gained from concentrating on one ecological force at a time, such as competition, and considering its overall effects throughout the invasion process (Shea & Chesson 2002), but, ultimately, we found it more compelling to follow the invasion stages in order to look at how several forces might interact at any one stage. There are many papers that examine the role of single forces in the success of an invasive species, and we reference some of these papers in the hope that readers will benefit from both approaches.

## Summary

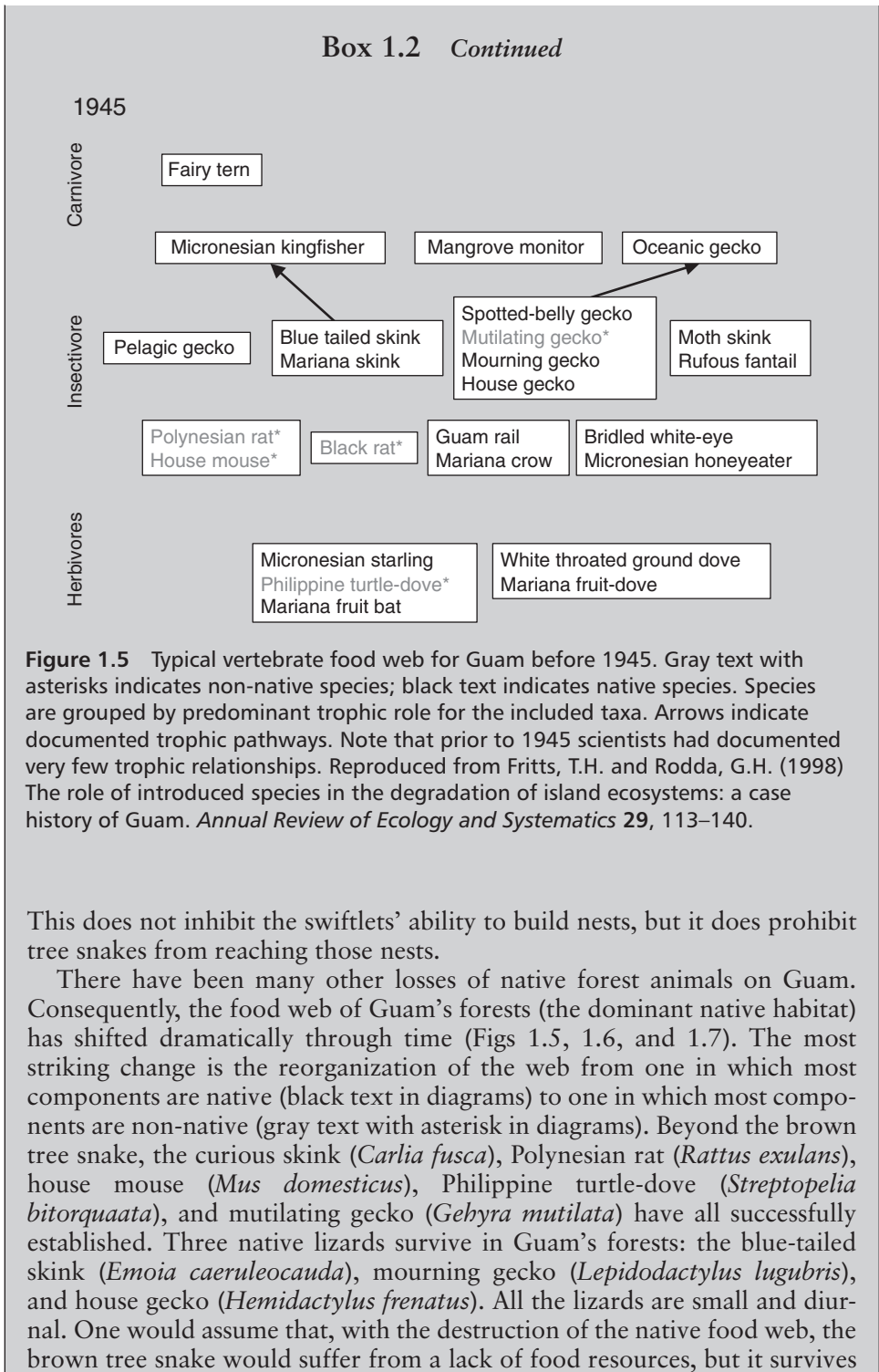
Clearly, invasion ecology is a field that is growing and changing rapidly. This introduction is like an appetizer sampler platter with a quick taste of many of the flavors or topics to come. The figures for the process model should be useful as you move through the chapters of the book, and we hope that the quick coverage of terminology and some of the recent debates can clear the way for more substantive treatment of the ecological issues in the coming chapters. One advantage to touching on these debates early is that it helps both to clear the air but also to remind readers to keep an open mind. Invasion ecology is a science, which moves forward best when we build on past results, remain open to new information, and ask critical questions.

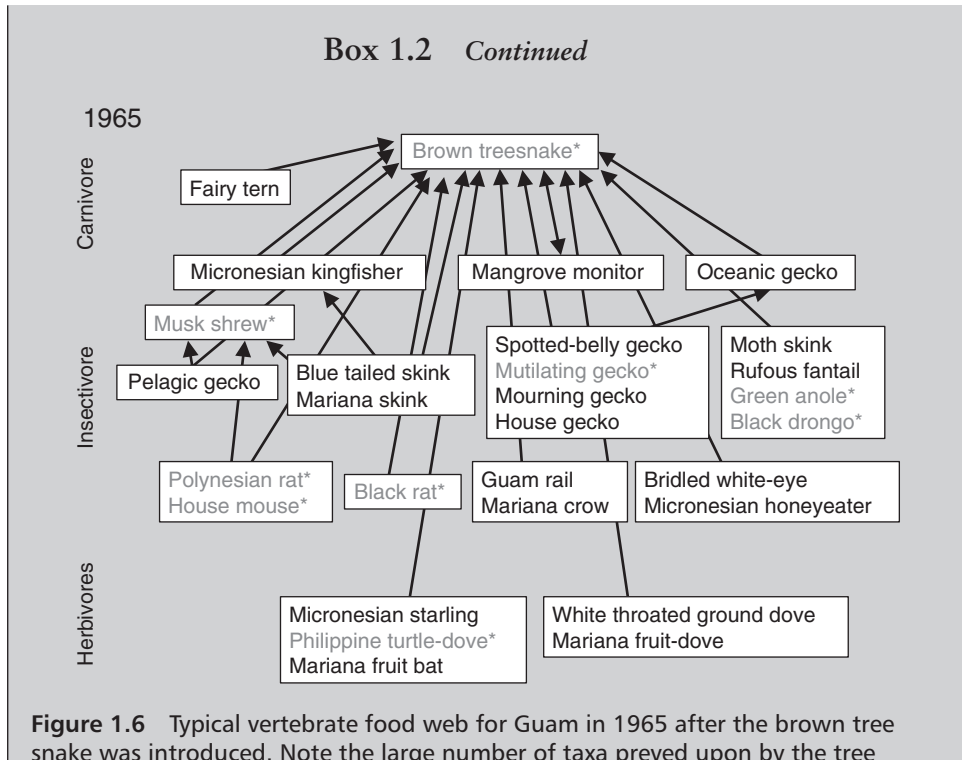
### Box 1.2 Union of the snake

Guam is the largest island of Micronesia (54,000 ha) and, like many islands, once harbored a fantastic assemblage of native endemic birds, reptiles, and mammals. The vast majority of these species are now considered extinct, and the remaining ones are threatened with extinction. Although the colonization of the islands by Polynesians contributed to the loss of species, as did massive habitat conversion and pesticide use following World War II, the principal culprit in this extinction drama is the invasive brown tree snake (*Boiga irregularis*). The following account of the brown tree snake in Guam is based heavily on the excellent summary of Fritts and Rodda (1998).

The modern era for Guam began with the US Navy's use of the island as a staging ground for a planned invasion of Japan during World War II. Guam's human population grew more than 10-fold between 1944 and 1945. With the end of World War II in 1945, such a large naval base proved useful for salvaging derelict war materials from the region. In particular, the US Navy transported vehicles, aircraft, and other supplies from New Guinea where these items may have sat unused for some time. The brown tree snake is native to New Guinea and other regions of Australasia. It is typically nocturnal and, during the day, rests within crevices and holes that provide good cover. It is commonly found in wheel-wells on airplanes, under the hoods of cars, and in boxes of cargo. For this reason, most biologists think the brown tree snake was a hitchhiker within surplus Navy equipment brought to Guam from New Guinea in the post-war years of 1945–1950.

The brown tree snake was first noticed along Guam's southern shore near Apra Harbor. It then spread, somewhat slowly, until it occupied the entire island by 1970. Guam has no native snakes and no native predators that could have controlled tree snake numbers. Instead, the native vertebrates were all small species vulnerable to predation by the generalist tree snake. Because the native animals were evolutionarily naïve to such predators, they were easy targets. The decline of most native forest animals was immediate and dramatic. Guam's Division of Aquatic and Wildlife Resources discontinued surveys of native birds and bats in the 1970s, as there were no more individuals of these species to count. The three native birds and mammals that persisted the longest were the Mariana fruit bat (*Pteropus mariannus mariannus*), Guam rail (*Rallus owstoni*), and island swiftlet (*Aerodramus vanikorensis bartschi*). The fruit bat and rail were relatively long-lived species that likely persisted simply because some individuals escaped predation and lived out the remainder of their lives; however neither species had any reproductive success in the presence of the tree snake. The island swiftlet persists to this day but is confined to one cave on Guam. The swiftlet builds nests on the walls of caves using its own saliva and mud to adhere the nest to the cave wall. Despite this unusual habit, swiftlets are still vulnerable to tree snake predation as tree snakes can easily capture prey in total darkness and climb most surfaces. The one cave where swiftlets persist is unique in that the cave walls are not textured enough for snakes to support themselves.



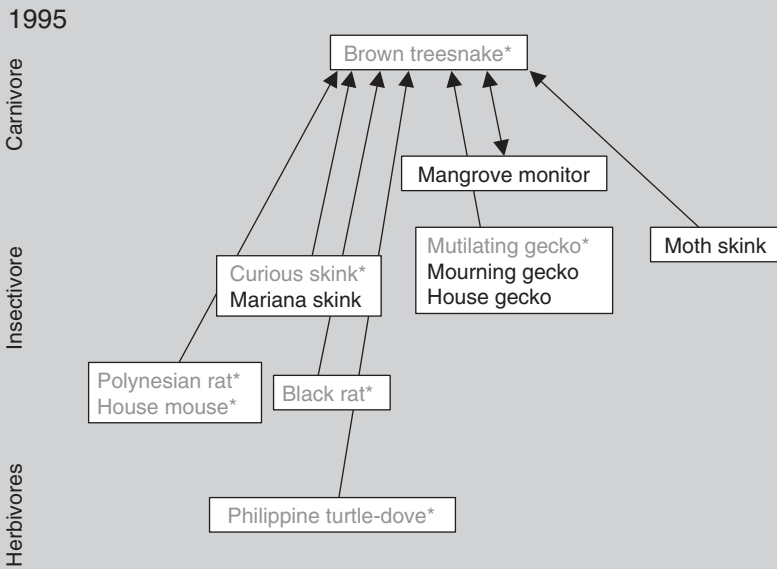


**Figure 1.6** Typical vertebrate food web for Guam in 1965 after the brown tree snake was introduced. Note the large number of taxa preyed upon by the tree snake. Gray text with asterisks indicates non-native species; black text indicates native species. Species are grouped by predominant trophic role for the included taxa. Arrows indicate documented trophic pathways. Reproduced from Fritts, T.H. and Rodda, G.H. (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annual Review of Ecology and Systematics* 29, 113–140.

because the available pool of invasive prey and native lizards maintains tree snake densities and keeps predation pressure high on the susceptible natives. Consequently native species quickly went extinct with no corresponding negative effect on the tree snake. The tree snake even seems to be adapting to the diurnal habits of the remaining native lizards. Biologists have documented a shift in the tree snake's activity patterns from one of solely nocturnal movements to one that increasingly includes activity during daylight hours.

The reduction in the complexity of the Guam food web has had consequences beyond the loss of the native animals. The loss of mammalian and avian insectivores presumably increased insect abundances at some cost to agricultural crops and to crop production. Newly introduced non-native species may find it easy to invade Guam given the many "open niches" left by the loss of native species. However, these newly arriving species must have some evolutionary experience with generalist predators to survive. Since the tree snake invasion, Guam seems to have much higher densities of web-building spiders than nearby islands free of tree snakes. Spiders that place

## Box 1.2 Continued



**Figure 1.7** Typical vertebrate food web for northern Guam in 1995. Note the large reduction in both species numbers and trophic functional roles among the remaining taxa. Gray text with asterisks indicates non-native species; black text indicates native species. Species are grouped by predominant trophic role for the included taxa. Arrows indicate documented trophic pathways. Reproduced from Fritts, T.H. and Rodda, G.H. (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annual Review of Ecology and Systematics* 29, 113–140.

obvious filaments in their webs to avoid bird damage to the web do so less often on Guam than on nearby islands that still have native birds. Like many oceanic islands, Guam has several bird-pollinated trees and, with the near total loss of native birds on the island, there is evidence that these trees are suffering substantial reproductive failure (Mortensen *et al.* 2008). Similarly, we should expect to see reduced frugivory and herbivory of native (and invasive) plants on Guam in the absence of most avian and mammalian herbivores. Such indirect effects of the brown tree snake invasion still require full documentation and exploration.

There are now massive efforts to control or eradicate the brown tree snake from Guam. Ships and airplanes from Guam require careful scrutiny to guard against introduction of the brown tree snake into other susceptible ports-of-call. Perry and Vice (2009) report about 10 airlines servicing Guam with over 230 flights stopping on the island per week. Using a simple but elegant mathematical model, these authors estimated the risk to other islands and countries for introduction of the brown tree snake via commerce or trade with Guam.

**Box 1.2** *Continued*

The most susceptible locations were those as-yet uninvaded islands nearby (e.g., Saipan) and locations with the suitable tropical habitat and strong transportation connections (e.g., Hawai'i, New Caledonia, and Fiji; Rödder and Lötters 2010). The establishment of brown tree snakes on any of these others islands could precipitate yet another catastrophic loss of biodiversity. At least for Hawai'i, the presence of the tree snake could also inflict between \$600 million and \$2 billion in economic damage via medical costs associated with snakebites, power-outages, and loss of tourism (Shwiff *et al.* 2010).

**Foundational papers**

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- Davis, M.A., Thompson, K. and Grime, J.P. (2001) Charles S. Elton and the dissociation of invasion ecology from the rest of ecology. *Diversity and Distributions* **7**, 97–102.
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**Further reading**

- Colautti, R.I. and MacIsaac, H.J. (2004) A neutral terminology to define “invasive” species. *Diversity and Distributions* **10**, 135–141.
- Shea, K. and Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* **17**, 170–176.
- Simberloff, D. (2003a) Confronting introduced species: a form of xenophobia? *Biological Invasions* **5**, 179–192.
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