Chapter 8
Differentiating Successful and Failed Invaders: Species Pools and the Importance of Defining Vector, Source and Recipient Regions

A. Whitman Miller and Gregory M. Ruiz

8.1 Introduction

Attempts to understand the dynamics of biological invasions continue to abound in aquatic and terrestrial ecosystems. Identifying the biological attributes of successful invaders, or what makes a good invader, are among the most tantalizing questions still to be answered, especially in marine ecosystems. Numerous studies across a range of taxonomic groups have examined species' characteristics to determine whether certain species level factors strongly differentiate successful from failed invaders (see Rejmánek and Richardson 1996; Williamson and Fitter 1996; Reichard and Hamilton 1997; Miller 2000; Kolar and Lodge 2002; Prinzing et al. 2002; Cassey et al. 2004a,b; Miller et al. 2007). At the heart of these analyses is the comparison of successful and failed species pools, which are defined in various ways with specific consequences for the inferences that can result.

When trying to understand the effects of species characteristics on invasion outcome, most studies compare physiological tolerances, life history characteristics, and behavior of successful and failed invaders. Although it is certainly valid to compare any two groups to understand differences in their respective attributes, only a subset of such comparisons can answer questions about the invasion process. More specifically, invasions have a specific context and result from interactions among source regions, recipient regions, and transfer mechanisms (vectors). Thus, comparing invaders from one source region to non-invaders from a different source region may tell us little about attributes of successful invaders, because the latter group may not share the same opportunities for transfer and invasion, thereby introducing additional variables and confounding interpretation.

In this chapter we examine the role of source region, vector, and recipient region in evaluating successful vs unsuccessful invasions. First, we provide a general framework for identifying introduced species assemblages according to their vectors and sources. Second, we provide a conceptual model to illustrate explicitly the effects of controlling for vector, source region, and recipient region when comparing successful and failed invaders. Third, we review approaches used in some previous analyses to identify biological characteristics of successful invaders,

G. Rilov, J.A. Crooks (eds.) *Biological Invasions in Marine Ecosystems.*
Ecological Studies 204,

including multiple taxonomic groups and ecosystems. Throughout, our intention is to highlight the potential effects of specific types of comparisons on conclusions about invaders' attributes.

In this chapter, we consider a successful invasion to be the establishment of a self-sustaining population in a non-native region, regardless of abundance, geographic range, or impact. Thus, species are considered successful invaders, independent of any degree or classification of invasiveness (Prinzing et al. 2002, but see Richardson et al. 2000).

8.2 Identifying the Roles of Source Region, Recipient Region and Vector

Biological invasions result from multiple vectors and geographic sources. In addition to natural range extensions, recipient regions receive species from one or more regions via multiple human-mediated mechanisms, operating either simultaneously or at different times. For any given recipient region, the diversity of species transfers (i.e., the species richness of inoculants) and genetic diversity can be increased by drawing from (1) more than one source region, (2) more than one vector, and (3) more than one time period. For simplicity, we exclude the temporal dimension from further discussion in this paper and examine the implications of different sources and vectors on the analysis of invasion patterns.

For a single recipient region, inoculant diversity clearly results from the combined (summed) contributions across multiple source regions and vectors. In a simple framework, Fig. 8.1a illustrates how source regions and vectors yield unique, component species assemblages (pools) for delivery to a single recipient region. Thus, the species pool delivered from the first vector (V_1) and source region (S_1) will differ from that delivered by either V_1 operating from other source regions ($S_{2,3,n}$) or another vector ($V_{2,3,n}$) in the same source region (S_1). For example, species that were transferred to San Francisco Bay in ships' ballast water from Japan differ from those that arrived in ballast from China, and both differ from species that arrived on outer hulls of vessels or with live seafood (e.g., oysters) from Japan. Certainly there may be some overlap in species composition among cells in Fig. 8.1a, but each compartment represents a different pool of species.

In theory, understanding the full species pool delivered to a recipient region requires an accounting of all species inoculations according to vector and source (vector × source) combinations. In reality, such complete assessments are impossible. However, the additive but distinctive nature of inoculation across different compartments underscores several important aspects of propagule supply. First, the taxa transferred to one recipient region will differ by both vector and source region. Second, the importance (and even existence) of specific vectors and source regions will differ strongly among recipient regions ($R_{1,2,n}$). This latter aspect is portrayed by adding a third axis (Fig. 8.1b), whereby some component cells may be completely inactive in one source region but operational in others.

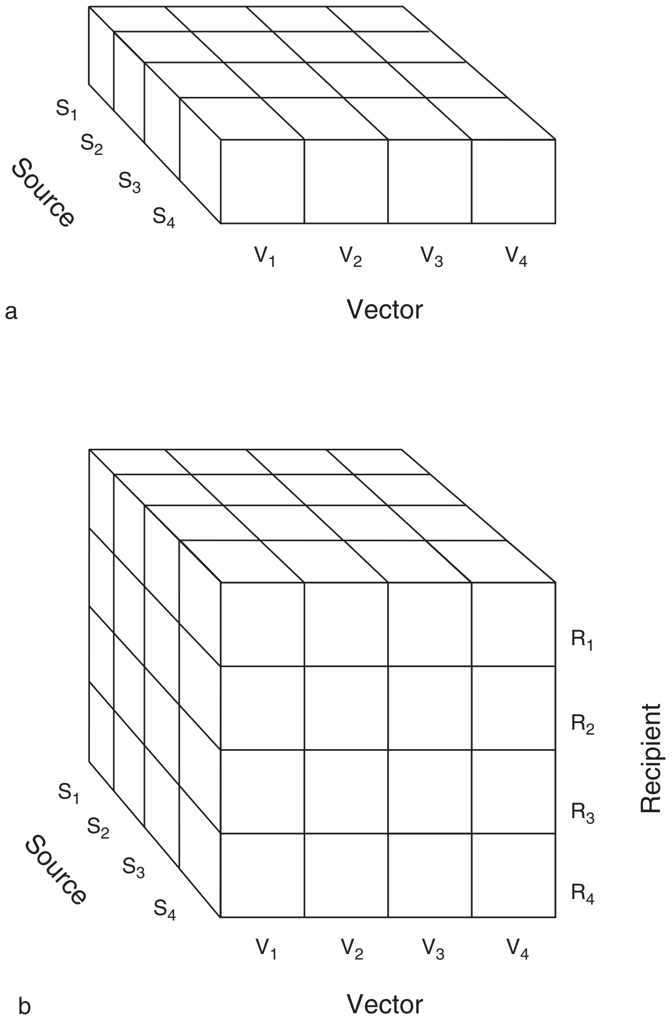

Fig. 8.1 Potential species assemblages entrained by vector (V) from source region (S) and introduced to recipient region (R). **a** Sixteen theoretical assemblages arising from four source regions and four vectors and introduced to a single recipient region. **b** How the same (source × vector) combinations can be introduced to more than one recipient region. For any given (source × vector) combination, time, distance, and degree of ecosystem matching will vary across recipient region, resulting in different patterns of invasion success and failure

Although this is perhaps an obvious accounting framework, it has some important implications for defining relevant species pools for analyses of invasion processes and patterns. For example, whereas one species entrained by a ballast water vector may survive transit only to die of salinity exposure after introduction, another species dies in transport. Each case ends in invasion failure, but the latter is an effect of the vector and the former a consequence of the recipient region. Still other species are never moved in ships' ballast water, so fail to colonize for yet another reason. Recognizing and disentangling the effects of sources, vectors, and recipient ecosystems is crucial for making informed comparisons among groups of species, especially when trying to identify biological attributes that lead to invasion success and failure. The remainder of this chapter is devoted to exploration and discussion of this issue.

8.3 Modeling Invasion State Space – Defining and Comparing Species Pools

When investigating biological attributes that correspond to invasion success and failure, it is vital to focus on the context and elements of the invasion process. Carlton (1979), Kolar and Lodge (2001) and others have described the invasion process as a series of sequential steps or filters whereby a species incrementally succeeds or fails. The generic invasion sequence includes: (1) vector entrainment, (2) transportation and survival, (3) introduction, (4) establishment and (5) subsequent spread. Several authors have specified the importance of treating the various stages of the invasion sequence separately (e.g., Kolar and Lodge 2001; Marchetti et al. 2004), since the attributes that enable a species to prevail at one stage may be quite different from those at another stage (e.g., establishment vs spread).

In their analyses of the biological attributes that lead to invasion success among parrots of the world, Cassey et al. (2004b) apply similar logic, arguing that invasion stages should be invoked to help define the discrete species pools used for comparison. For parrots, the putative biological and biogeographic factors correlated with invasion success differ, depending on whether the pool of successful parrot invaders (i.e., those that have successfully established self-sustaining populations beyond their native range) is compared with (1) those species released but which failed to establish, (2) species that were transported (with or without release) but which failed to establish, or (3) all parrot species of the world. By specifically modeling different species pool comparisons (i.e., comparison with (1) vs (2) or (3)) the authors demonstrate the genuine potential for drawing unsupported conclusions about invader attributes. Furthermore, Cassey et al. (2004a,b) explicitly constrained their analyses taxonomically by choosing all members of the parrot order. Additionally, they constrained the vector under consideration to intentional entrainment and transport beyond native ranges (i.e., the commercial pet trade), and the subsequent accidental release of parrots into the environment. Using a global-scale approach that includes all parrot species, regardless of source region (e.g., old world and new world parrots have equal weight in analyses), Cassey et al. (2004a) show that successful invaders tend to have broader diets and are more sedentary than failed invaders.

We agree with the type of explicit approach outlined above and suggest that invasion stages must always be considered in analyses that test for biological attributes of invaders. In general, studies investigating the contribution of biological attributes to invasion success should, when possible, constrain source and recipient regions and vector, ensuring appropriate comparisons that remove confounding (uncontrolled) variables. To understand more fully how biological attributes affect invasion success we must consider how a species, by dint of its biological attributes, interacts with: (1) its native environment – both the physical and biological aspects, (2) the vector by which the would-be invader is entrained, transported, and released into the receiving environment, and (3) the physical and biological aspects of the receiving environment.

To illustrate the consequence of selecting or constraining particular pathway parameters (source region, vector, and recipient region) for invasion analyses, we provide a conceptual model. Specifically, we identify theoretical pools of species for comparison and describe how different comparisons address different aspects of the invasion process. In practice, the exact membership of some species pools will often not be readily identifiable, and this is especially true for accidental introductions vs intentional introductions. Nevertheless, we believe the model has utility in that it highlights some of the limitations and pitfalls of incomplete knowledge, informing both the design and inference of analyses.

8.3.1 Species Pool Designations

The domain of potential introduced species to a recipient region was described above as the sum of species assemblages across all vectors and source regions (Fig. 8.1). Such a representation describes which species are theoretically associated with each compartment (vector × source), but it does not address the fate of these species at different stages of the invasion sequence (e.g., survival during transport or upon delivery). Disentangling the effects of source region, vector, and invasion stage is crucial to understanding both the invasion process and identifying key biological attributes that affect invasion success. Here we describe a conceptual model to identify specific successful and unsuccessful species pools at different stages of the invasion sequence, examining effects of source region, vector, recipient region.

Since individual invasions occur generally by inoculation from one discrete geographic region to another via some vector(s), we use Venn diagrams to define explicitly various sets of species that require consideration, or the potential invasion state space. These sets represent theoretical species pools whose intersections connote their relationship within the modeled invasion state space. Using this general approach, Fig. 8.2 graphically defines the complete domain of species (i.e., Total Source Diversity or SD) available in a single source region. SD_1 is the full set of species present in one source region, and its domain can be subdivided into the following: a set of species with biological attributes and capabilities of establishing self-sustaining populations (E_1) in a specific recipient region if introduced (R_1); the set of species that can be entrained by a particular vector (V_1); and the set of species with the potential to tolerate the rigors of transit in a particular vector (T_1).

SD_1 is not equal to S_1 of Fig. 8.1, as the latter represents those species that arrive by a particular vector to a particular recipient region, regardless of their survival in transit or following introduction. The sets or subdomains E_1, R_1, V_1, and T_1 are equivalent in Figs. 8.1–8.3.

Thus, potentially successful invaders that actually arrive to a recipient region are described by the intersection of sets V_1, T_1, and E_1 (i.e., $V_1 \cap T_1 \cap E_1$; Fig. 8.2, black). It is important to note that each of the subdomains V_1, T_1, and E_1 will overlap to a greater or lesser degree. For purposes of this and future discussion of this model, the following set notation will be used: a rectangle indicates the available universe of species in the source region (SD), the intersection of two sets is indicated with

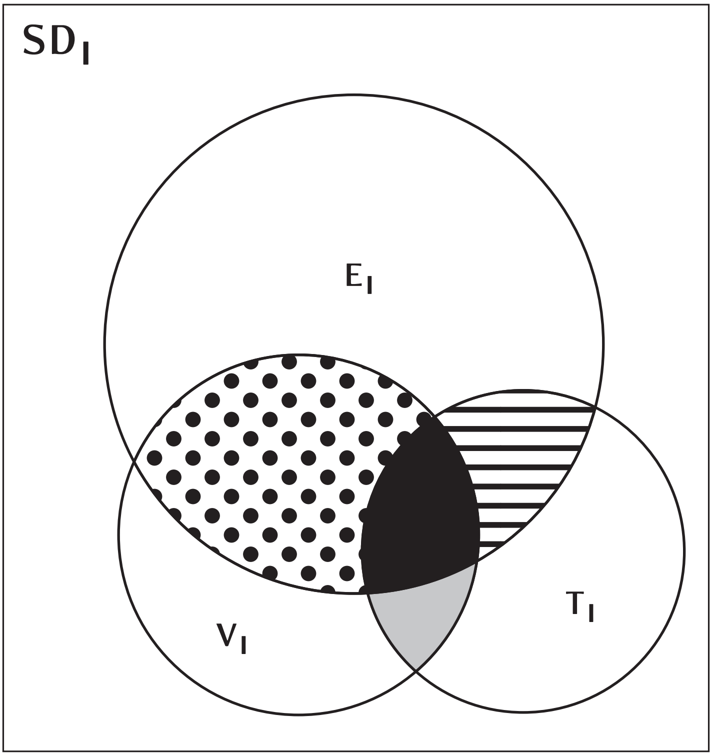

Fig. 8.2 Venn diagram describing the theoretical invasion state space for species that are introduced from one particular source region (SD_1, denoted by rectangle) to a discrete recipient region (R_1, not shown). *Circles* represent various species pools as they relate to the invasion process. E_1 refers to the theoretical pool of species residing in SD_1 that have the biological attributes and capacity to establish self sustaining populations in R_1, if introduced. V_1 represents the pool of species in SD_1 that are actually entrained by a particular vector. $E_1 \cap V_1$ is the subset of V_1 that could establish self-sustaining populations if introduced alive to a recipient region. The pool of species that could survive the rigors of a vector is denoted by T_1; however, only members of $V_1 \cap T_1$ are both entrained and can survive transit. The intersection all three species sets, $V_1 \cap T_1 \cap E_1$ (*black*), represent the theoretical pool of successful invaders that arrive to the recipient region

the symbol $\cap$, and a minus sign (–) denotes the complement of a set or intersection, i.e., the species excluded.

Table 8.1 provides a summary for how these variables combine and how these combinations are related to transfer opportunity and invasion outcome. For example, some species are entrained by a vector, tolerate transit, but fail to establish self-sustaining populations, $(V_1 \cap T1)–E_1$; Fig. 8.2, grey). Other species die in transit, $(V_1 \cap E_1)–T_1$ (Fig. 8.2, stippled). Another group of species has the capacity to survive transit and establish but is not ever entrained by V_1, $(T_1 \cap E_1)–V_1$ (Fig. 8.2, horizontal lines).

As noted by others (Prinzing et al. 2002; Cassey et al. 2004b; Pyšek et al. 2004), a crucial question is how "failed species" pools are designated for comparison with successful invaders (modeled here as $V \cap T \cap E$). Below, we explore various types of comparisons among species pools with our general conceptual model, adding increasing complexity from single to multiple source regions, vectors, and recipient regions. Throughout, our primary goal is to clarify the potential for confounding factors, and the inferences that can be drawn, when making specific comparisons among species assemblages.

8.3.2 Species Pool Designations and Comparisons (Fixed Recipient, Source, and Vector)

In this simple version of our model, which employs single subdomains, there are a variety of specific comparisons that seem most relevant. First, a comparison of successful invaders with the pool of species that are both entrained and introduced by the vector but which fail to establish self-sustaining populations, i.e., $V_1 \cap T_1 \cap E_1$ with $(V_1 \cap T_1)–E_1$ (Fig. 8.2, black vs grey, respectively). Because this analysis specifically constrains vector, source, and recipient region, it should yield biological differences associated with success and failure after introduction to the recipient region (R_1). A second comparison relates potentially successful invaders with species that were entrained, but which perished in transit before introduction (Fig. 8.2, black versus stippled). This comparison informs us of the effects of the vector (i.e., how species tolerate V_1). It should be noted that some members of $(V_1 \cap E_1)–T_1$ (Fig. 8.2, stippled) could be introduced via a different, non-lethal vector and go on

Table 8.1 Some expressions describing various states of entrainment (V_1), toleration of vector (T_1), and establishment (E_1), when species are taken from a source region (SD_1) and introduced to a recipient region (R_1)

Entrained, vector tolerated, established	Entrained, vector tolerated, not established	Entrained, vector not tolerated, not established	Not entrained, potential to tolerate vector, potential to establish	Invasion subdomains (V_1)	(T_1)	(E_1)
$V_1 \cap T_1 \cap E_1$				y	y	y
	$(V_1 \cap T_1)$-E_1			y	y	n
		$(V_1 \cap E_1)$-T_1		y	n	n
			$(T_1 \cap E_1)$-V_1	n	y	y

to establish self-sustaining populations in R_1. A third comparison, $V_1 \cap T_1 \cap E_1$ vs $(T_1 \cap E_1) - V_1$ (Fig. 2, black vs horizontal lines) contrasts successful invaders with a group of species that can establish self-sustaining populations in R_1 and survive transportation, but which are never entrained by the vector V_1. Importantly, members of $(T_1 \cap E_1) - V_1$ could also be successfully introduced to R_1 by a separate vector.

A somewhat coarser approach compares successful and failed invaders entrained by a particular vector, without regard to their ability to tolerate transport in the vector. In this comparison, the entire vector subdomain is compared with successful invaders $V_1 \cap T_1 \cap E_1$ (Fig. 8.2, black). This comparison does not distinguish whether failure to invade results from mortality in transit or upon arrival, but simply examines the joint outcome across both stages in the invasion sequence. In reality, detailed information may rarely exist for many vectors to measure such stage-specific effects, making this the best available approach.

For intentional introductions (e.g., fish stocking, aquaculture, horticulture, biocontrol) the selective actions of the vector on survivorship are largely neutralized, at least for the target species of interest. In these cases, the intersection of vector and survivorship is essentially complete ($V = T$), and a comparison of successful invaders ($V \cap T \cap E$ or $T \cap E$) vs introduced but failed species ($(V \cap T) - E$ or $T - E$) is a contrast for biological attributes that correlate with invasion success. This approach has been used with California fishes (Marchetti et al. 2004), although fish were derived from multiple source regions. While effective for examining traits associated with successful intentional introductions, there may still be differences by source region. A fully controlled comparison would explicitly contrast $E \cap T$ and $T - E$ separately for each source region (see below), to minimize any effect (weighting) by region, but this may present significant real-world challenges with respect to sample sizes needed for such analyses.

8.3.3 Fixed Recipient and Source Regions, Multiple Vectors

Depending on the number and types of vectors (V_1 to V_k) connecting SD_1 and R_1, the subset of potentially successful invaders will vary; however, the pool of species with the biological attributes and capabilities to succeed once introduced will remain constant for a given point in time E_1 (Fig. 8.3, black areas). Here we denote such species $E_{i,j}$, or the set of species from the *j*-th source region that could become established in the *i*-th recipient region, where $E_{1,1}$ represents the pool of species occurring in SD_1 with the biological capacity to establish in R_1. As the number of vectors connecting SD_1 with R_1 increases, a greater proportion of species with capacity to survive in R_1 will be sampled (Fig. 8.3). The species pool is described by the expression: $\sum_{k=1}^{k} E_{1,1} \cap V_k \cap T_k$, where K types of vectors are possible.

Since the vector is selective at two levels, both by the number and types of species it entrains and the rates of mortality it imposes on those species, vector type has direct influence on species introductions. Therefore, for each subset of successful

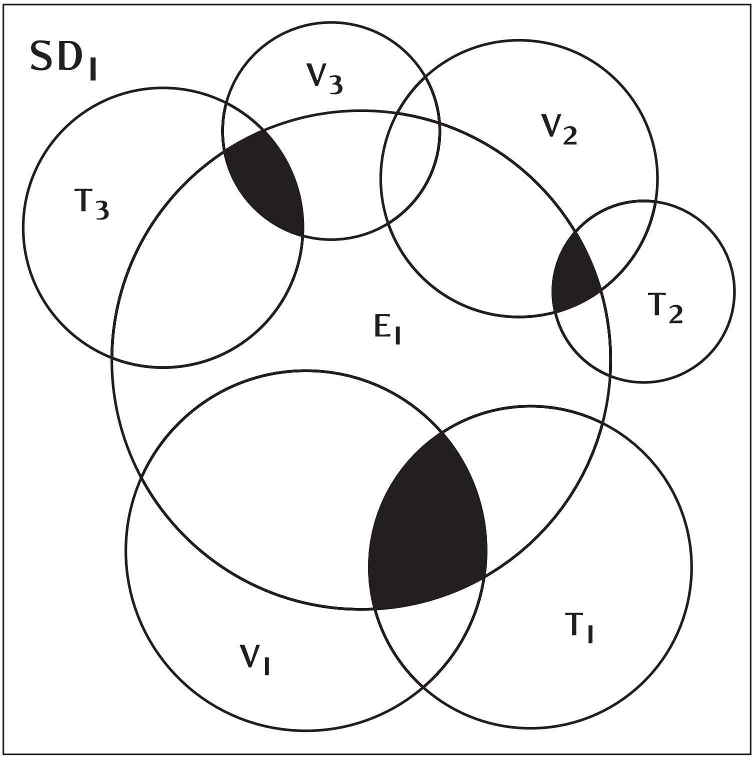

Fig. 8.3 Subsets of successful invaders (*black*) that emanate from a single source region (SD_1) and that are introduced via multiple vectors (V_1 to V_n) to a single recipient region (R_1). Associated abilities to tolerate vector-specific transits are depicted as (T_1 to T_n). The sum of successful invaders across vectors is described by the following expression: $\sum_{i=1}^{n} E_{1,1} \bigcap V_i \bigcap T_i$

invaders, individual comparisons should be constrained to subsets of "failed species" that correspond to like vectors, cumulatively denoted as $\sum_{k=1}^{k} (V_k \bigcap T_k) - E_{1,1}$, otherwise comparisons become confounded due to differential effects of multiple vectors on the delivery of viable organisms.

An uncontrolled approach is simply to identify those species that have invaded a particular region (R_1) from a specified source region, regardless of vector or time. In our model, successful invaders are defined as the intersection $V \cap T \cap E$ (Fig. 8.2, black); however, across multiple vectors invaders are illustrated by more than one such intersection (Fig. 8.3, black). When vector is not specified, successful invaders of R_1 are compared with the total species diversity of the source region, SD_1. On its own, this comparison may not reliably identify characteristics of successful invaders, because many species may simply never interface with a vector. Nevertheless, this approach may advance our understanding of invasion biogeography. For example, it may help identify (1) vector operation (historical and contemporary) and (2) those aspects of environmental matching that are crucial for invasion success.

8.3.4 Fixed Recipient Region, Multiple Source Regions, Multiple Vectors

For a single recipient region (R_1), alien species may arrive from numerous source regions (SD_1 to SD_k) and by numerous vectors (V_1 to V_k). Species with biological attributes and capabilities of establishing self-sustaining populations in R_1 are denoted as $E_{1,j}$. The sum of all such sets is limited by the number of vectors connecting R_1 and SD_j and is denoted $\sum_{j=1}^{j}\sum_{k=1}^{k} E_{1,j} \cap V_k \cap T_k$. Likewise, the complete collection of "failed invader" pools for comparison containing species that are both entrained and introduced by vectors but which fail to establish self-sustaining populations in R_1 are denoted $\sum_{j=1}^{j}\sum_{k=1}^{k} (V_k \cap T_k) - E_{1,j}$. Since comparisons seeking differences between successful and failed invaders are dependent on vector and source, corresponding pools must be parsed from the previous expressions and then compared individually to be meaningful.

In the Great Lakes, Kolar and Lodge (2002) compared successful fish invaders and failed introductions resulting from multiple source regions and multiple vectors. Biological attributes unique to the pool of successful invaders were used to parameterize a predictive model. The model was then applied to a group of 66 Ponto Caspian fish species to predict each species' likelihood to (1) establish, (2) spread, or (3) become a nuisance. This approach assumes the biological characteristics that conferred invasion success to the Great Lakes are similar across source regions (i.e., $E_{1,1}$ through $E_{1,j}$ are similar biologically). As in the analysis of California fish introductions by Marchetti et al. (2004), the effect of source region was not evaluated.

Perhaps more critically, the Great Lakes analysis appears confounded when considering vector. Here, attributes of failed and successful species pools were derived from multiple vectors and multiple source regions, being compared to characterize attributes of successful fish invaders. Nonetheless, these attributes were then applied in a predictive manner to a single vector, ballast water from a single region. This assumes there are no vector-effects, source region effects, or interaction between the two. The biological attributes of species that are capable of establishing when intentionally introduced may differ from those of species that can withstand the physiological rigors of a transatlantic voyage in a ballast tank. To our knowledge, no studies have yet quantitatively examined the simultaneous action of multiple vectors and/or source regions to a fixed recipient region.

8.3.5 Multiple Recipient Regions, Fixed Source Region, Multiple Vectors

A similar approach can be taken to describe potential species pools that hail from a single region (SD_1) but which are entrained and moved by one or more vectors to one or more recipient regions. Addressing the issue from this perspective allows one to consider comparisons of all the species being exported from a specific source to those species that actually have the biological capacity to succeed (i.e., E_1 to E_i) and establish self-sustaining populations in other locations. In this case, the theoretical sets of successful invaders of multiple recipient regions that arrive by multiple vectors are described by $\sum_{i=1}^{I}\sum_{k=1}^{K} E_{i,1} \cap V_k \cap T_k$. Again, to be instructive, each pool of successful species arriving by a particular vector must be treated individually for each vector and recipient region of interest. To illustrate, one could imagine focusing on the plankton assemblage available from SD_1 (e.g., port A) and then quantifying the entrainment and survivorship of such species in ballast tanks bound for ports B and C (i.e., R_1 and R_2) via onboard measurements. Theoretically, one could compare the collection of species successfully inoculated to ports B and C with those that (1) consistently perished in transit and (2) those species that have successfully established populations in ports B and C. Because of the polyvectic nature of invasion pathways (i.e., simultaneous operation of multiple vectors – see Carlton and Ruiz 2005), similar comparisons for other vectors linking ports A, B, and C would be necessary to understand the effects of the individual vectors that link a single source to one or more recipient regions.

To complicate the picture further, the following expression denotes the theoretical cumulative sum of species with the capacity to establish self-sustaining populations in multiple recipients regions, from multiple sources, and via multiple vectors: $\sum_{i=1}^{I}\sum_{j=1}^{J}\sum_{k=1}^{K} E_{i,j} \cap V_k \cap T_k$. Ironically, if not regrettably, this expression may be reflective of the world's increasingly connected network. One need only look to the complicated picture of commercial shipping to realize that ships link the ports of the world together to varying degrees and by a variety of simultaneously operating vectors ranging from ballast water, hull fouling, the biological content of sea chests, as well as organisms associated with cargo itself.

8.4 Some Recent Analyses of Invader Attributes Using Species Pool Comparisons

Species pool comparisons have been used extensively in studies of terrestrial faunal and floral invasions and more recently, in aquatic systems. Although source region, vector, and recipient region are broadly viewed as important to invasion success, they are rarely considered simultaneously or formally in analyses. In the literature, studies addressing invasion success versus failure typically focus on biological attributes associated with (1) recipient region, (2) vectors and pathways of transmission, or less commonly (3) source regions. Rarely have all three factors been considered in conjunction.

Table 8.2 summarizes some selected recent comparisons of successful and failed invaders' attributes, indicating which of the three pathway parameters, (source region, vector, and recipient region) were considered explicitly and controlled in analyses. This list is by no means exhaustive but is only meant to include some illustrative examples of terrestrial and aquatic studies across a broad taxonomic range. Each approach has merit, depending on the question being investigated, but it is also important to recognize the possible limitations and ramifications of excluding one or more of these invasion parameters when evaluating attributes of successful invaders. Among the studies reviewed here, six constrain a single invasion pathway parameter (three vector, three recipient region); seven constrain two parameters (five vector × recipient region, two vector × source); and two constrain all three parameters (source region × vector × recipient region – Table 8.2). Below, we discuss several of these examples in more detail, expanding on some references already presented.

A common approach constrains the species taxonomically and then compares successful with failed invaders generally, across many regions. In some instances vector is held constant and others not. For example, Rejmánek and Richardson (1996) employed this method in their study of pines, whereby they compared the biological attributes of cultivated (i.e., intentionally introduced) pine species.

Table 8.2 Invasion parameters constrained (indicated by "x") in selected recent analyses that attempt to differentiate successful and failed invaders according to their biological attributes

Source	Vector	Recipient	Taxa	Author
-	-	x	Fishes	Kolar and Lodge (2002)
-	x	x	Freshwater fishes	Marchetti et al. (2004)
-	x	-	Freshwater fishes	Ruesink (2005)
-	-	x	Marine bivalves	Roy et al. (2001)
x	x	x	Marine bivalves	Miller et al. (2002)
x	x	x	Marine gastropods/bivalves	Miller et al. (2007)
x	-	x	Plants	Goodwin et al. (1999)
-	-	-	Conifers	Richardson and Rejmánek (2004)
-	x	-	Pines	Rejmánek and Richardson (1996)
-	x	x	Woody plants	Reichard and Hamilton (1997)
-	-	x	Gymnosperms/angiosperms	Williamson and Fitter (1996)
x	-	x	Plants	Prinzing et al. (2002)
-	x	-	Parrots	Cassey et al. (2004a,b)
-	x	x	Birds	Duncan et al. (2001)
-	x	x	Birds	Duncan et al. (1999)
-	x	x	Birds	Veltman et al. (1996)

Using discriminant analyses they compared successful and failed pine species for a suite of biological characteristics and found that mean seed mass, minimum juvenile period and mean intervals between large seed crops differentiated the groups. No effort was made to control source or recipient region. Likewise, in their global survey of conifers, Richardson and Rejmánek (2004) compared the biological characteristics of invading conifers to those of other, non-invading, gymnosperms. Among freshwater fishes, Ruesink (2005) examined global introductions of freshwater fishes by humans, both with intention to establish non-native populations and for cultivation or use without intention to naturalize. Source and recipient regions were widespread and thus not controlled. Establishment was shown to increase in families with small body size, fish wish omnivorous diets, high endemism in recipient regions, and strength of introduction effort by humans. Such approaches can uncover much about the biology of invaders and non-invaders, but they may be limited in their ability to explain and predict invasion since they do not compare pools of successful and failed invaders that have followed similar invasion pathways.

A number of investigators have controlled vector by studying well documented, intentional introductions. Veltman et al. (1996) found that among 79 bird species intentionally introduced to New Zealand across 496 introduction events, 27 species succeeded and 52 failed. Invasion success was positively correlated with initial population size and negatively associated with native migratory behavior. This study held recipient region and vector constant, but drew from bird species hailing from more than one source. Duncan et al. (1999) correlated the life history characteristics of invading bird species of New Zealand with their invasion range size. Of 34 species, 17 were introduced intentionally from Britain and the remaining 17 were introduced from other source regions. In a separate study, Duncan et al. (2001) showed that of 52 bird species intentionally introduced to mainland Australia, introduction effort, habitat matching, invasion success elsewhere, and climate matching predicted invasion outcome. Again, however, vector and recipient region were constant, but source regions varied.

Among freshwater fishes, Marchetti et al. (2004) investigated the biological attributes of fish that were intentionally introduced to California watersheds, and thus constrained vector and recipient region, but not source region, since they compared fish species from numerous source areas. The biological attributes associated with success at each stage along the invasion pathway varied widely: establishment (parental care, size of native range, physiological tolerance, propagule pressure), spread (long-lived, regional origin, non-herbivores), and integration (a measure of abundance used as a proxy for degree of invasiveness – small, regional origin, non-invertebrate predators).

A pattern of divergent characters associated with invasion stages is also evident among introduced freshwater fishes in the Great Lakes, but the stage-specific characters are somewhat different from California invaders. According to Kolar and Lodge (2002) the hallmarks for establishment among the Great Lakes invaders were fast growth, broad temperature and salinity tolerance, and history of invasion elsewhere. In contrast, slow growth, low survivorship in high water temperatures, but an otherwise wide temperature tolerance, appear to be associated with the ability to spread within the recipient region.

The analyses by Kolar and Lodge (2002) constrained recipient region, but not source region or vector. To generate and parameterize a predictive model, Kolar and Lodge compared species characteristics from 24 species which failed to establish self-sustaining populations and 21 species that successfully established populations in the Great Lakes. As discussed earlier (see Sect. 8.3.4), the members of these species pools hailed from multiple source regions throughout the world, including regions in United States, East Asia, Northern Europe, the Ponto Caspian, Eurasia, South and Central America, and elsewhere. Furthermore, these species were introduced separately "via a variety of pathways including, but not limited to, intentional stocking, canals, natural waterways, release of baitfish and pets, escapes from aquaculture, and ballast water" (Kolar and Lodge 2002), which may have confounded their results.

Results from the California and Great Lakes studies, as well as the global freshwater fish analysis of Ruesink (2005), are difficult to compare, as the methods of analysis were not similar. Differential contributions of biological attributes could be reflections of (1) differences in recipient regions (e.g., California vs Great Lakes), (2) mixed vector effects (e.g., the ballast water vector may impose very different pressures on entrainment and en route survivorship than does intentional introduction), or (3) increased variability stemming from species pools drawn from diverse biogeographic origins, and distances.

In their study of European plant invaders of New Brunswick, Canada, Goodwin et al. (1999) controlled source and recipient regions, but not vector since invaders were introduced both intentionally and accidentally. Biological and distributional characteristics of successful invaders were compared with randomly chosen, non-invading congeners native to Europe. Successful invaders were shown to have significantly larger native geographic distributions than non-invaders, but the groups did not differ with respect to other life history characteristics. They concluded that larger native range size may reflect greater environmental tolerance and/or greater opportunity for accidental transport with humans. While both may be true, the conclusions are complicated because the invader and non-invaders species pools do not share the same introduction histories. Successful invaders comprise species that were introduced (1) intentionally or (2) accidentally, whereas non-invaders might be either failed invaders (i.e., entrained and/or introduced, but failed) or species that were never introduced by any means and thus never challenged by either vector or New Brunswick's physical and biological environment.

In an effort to control such uncertainties, Miller et al. (2002, 2007) held vector, source and recipient regions constant as a means for identifying pools of successful and failed species for comparison. The invasion pathway examined was the intentional introduction of live oysters *(Crassostrea virginica)* from the East coast of North America to San Francisco Bay. This pathway is viewed as responsible for the accidental introduction of scores of Western Atlantic invertebrates, including a selection of shelled mollusks (Cohen and Carlton 1995). By choosing a single vector, i.e., dredging and subsequent live shipment of eastern oysters by railroad, from a single source region (New York City and environs, the primary source of historical live oysters shipped to San Francisco Bay; see Carlton 1979 and references therein), and a single recipient region (San Francisco Bay), Miller et al. (2002, 2007) compiled a list of mollusk species that occurred with oysters and which would have been collected as by-catch in oyster dredges over the ~80-year period of vector operation. Statistical comparisons of successful San Francisco Bay invaders and failed invaders differentiated these groups according to tolerance of low salinity, reproductive mode, and abundance of species in the source region (Miller et al. 2002, 2007). It should be noted that, even in this case, mortality en route vs failure after inoculation into San Francisco Bay could not be evaluated. Although live oyster transport strived to maximize survivorship through the use of ice and refrigeration, measures that surely conferred success to some members of the entrained species pool, some species may have failed in transit, perhaps due to desiccation. In this case, without direct measures, it remains impossible to determine the exact cause of failure.

8.5 Discussion

Elucidating the interactions of species with their biotic and abiotic environments is of fundamental importance to ecologists. As non-native species are introduced beyond their historical ranges and cause environmental, economic, and human health impacts, these interactions become relevant to a much broader audience. From this perspective, there has been long-standing interest in understanding the biological profile of invasive species and predicting invasion success (Elton 1958; Baker 1965; Daehler and Strong 1993; Williamson and Fitter 1996). Species profiling, as an element of invasive species risk assessment, continues to be of great interest for the prediction and management of such species (Kolar and Lodge 2002; Ruesink 2005).

When trying to understand effects of species characteristics on invasion outcome, past research has often focused on biological attributes related to the invader's physiological tolerances, life history characteristics, and behavior. Beyond these, population level variability and biogeographic attributes are likely important to a species' ability to successfully establish self-sustaining populations beyond its native range. For example, the abundance of a species may have major implications for the number of propagules entrained, transported, and released in a recipient region. From a biogeographical standpoint, the size of a species' native range can influence the probability of a species' invasion success. This influence may be purely probabilistic, representing the level of human activity and thus the opportunity and likelihood of species entrainment, transport, and introduction (Simberloff 1989; Pyšek et al. 2004; Jeschke and Strayer 2005). Conversely, larger native ranges are sometimes interpreted as correlations of a species' ability to tolerate wider spectra of environmental/physiological conditions (Williamson and Fitter 1996; Goodwin et al. 1999). In both cases, knowledge of the physiological variability of the species across its native range (i.e., existence of specialized locally adapted biotypes) and the location of the donor population within a species' native range may also be crucial.

As already indicated, previous studies highlight the importance of species pool selections when attempting to accurately identify correlates of invasion success (Cassey 2004b; Pyšek et al. 2004). Prinzing et al. (2002) promoted the use of the so-called "source-area" approach as a means for identifying proper species pools to compare successful and failed invaders of particular source and recipient regions. They identified the need to constrain comparisons to species that originate in the same native region and which are introduced to a common recipient region. They used this approach to investigate plant species that occurred in Central Europe and subsequently succeeded or failed to establish populations in two provinces of Argentina. Although Pyšek et al. (2004) agree with the source-area approach in theory, they point to the importance of controlling for the size of invader's native range, and caution that such analyses should restrict source region species pools to native species rather than mixes of natives and non-natives, regardless of non-native residence time prior to re-introduction elsewhere. We agree with these assessments, but contend that analytical requirements should be even more stringent, and include explicit identification and treatment of vector when possible.

Finally, the distance of a source region from the recipient region may correlate with transit time, the degree of stress imposed by a vector, and ultimately the condition of the biota upon arrival to the recipient region (Pyšek et al. 2004; Carlton and Ruiz 2005). The interaction of vector and source region can affect survivorship during transportation and after introduction, depending on the duration and particular stresses of transit. Verling et al. (2005) have demonstrated differential zooplankton survivorship in ballast tanks based on voyage length. One limitation of our present treatment is that it does not explicitly capture the effects of time and distance during transport. For example, a species that can survive transit from source region A to recipient region B may experience much higher mortality during transit to a more distant recipient region C. In such cases, the physiological tolerance of organisms may limit their ability to survive transit.

Temporal aspects of invasion and species pool choice and comparison are not incorporated in our model; however, they are no doubt integral to invasions success. Time likely influences the invasibility of recipient regions as well as the supply of propagules from source regions. Seasonal variation and environmental shifts act to open and close windows of invasion opportunity (see Carlton 1996). Thus, analyses should strive to control or explicitly define the time period of study to counter temporal bias.

Despite numerous studies aimed at understanding the biological aspects of invasion success and failure, this remains a challenge, especially given the expanding diversity of source regions and vectors in play. Few studies have adequately controlled the effects of vector, or the interactions of vectors with source and recipient regions to enable robust comparisons of the biological attributes of successful and failed species. This is not an easy undertaking, and selection of appropriate species pools for comparison is essential if we are to understand the influence of biological attributes on invasion success.

Our goal in this chapter was to present a general framework for comparing traits among species pools to evaluate issues of invasion success. Clearly, this represents an ideal, where individual effects at each stage in the invasion sequence are measured. While the experimental effort required for unraveling all the interactions posed by multiple vectors that connect multiple regional species pools is surely beyond reach, our aim is to highlight, define, and parse such complexity in order to identify those parts that are most tractable to invasion scientists, either through comparative observations or by manipulative experiments.

Acknowledgements We would like to thank Richard Ambrose, Gail Ashton, Jeff Crooks, Richard Everett, Melissa Hagan, Steve Lonhart, Mark Minton, Gil Rilov, and Ray Wakeland, for their contributions to this chapter. We also wish to thank the Smithsonian Institution, National Sea Grant Program, and the United States Coast Guard for their assistance in funding this work.

References

Baker HG (1965) Characteristics and modes of origin of weeds. In: Baker HG, Stebbins GL (eds) The genetics of colonizing species. Academic Press, New York, New York, USA

Carlton JT (1979) History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. PhD dissertation. University of California, Davis. 904 pp

Carlton JT (1996) Pattern, process, and prediction in marine invasion ecology. Biol Conserv 78:97–106

Carlton JT, Ruiz GM (2005) Vector science and vector management in bioinvasion ecology: conceptual frameworks. In: Mooney HA, Mack RN, McNeely JA et al. (eds) Invasive alien species, a new synthesis. Island Press, Covelo, California, USA, pp 36–58

Cassey P, Blackburn TM, Russell GJ, Jones KE, Lockwood JL (2004a) Influence on transport and the establishment of exotic bird species: an analysis of the parrots (Psittaciformes) of the world. Global Change Biol 10:417–426

Cassey P, Blackburn TM, Jones KE, Lockwood JL (2004b) Mistakes in the analysis of exotic species establishment: source pool designation and correlates of introduction success among parrots (Aves: Psittaciformes) of the world. J Biogeogr 31:277–284

Cohen AN, Carlton JT (1995) Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and Delta. A report for the U.S. Fish and Wildlife Service, Washington, D.C. and the National Sea Grant College Program Connecticut Sea Grant. 272 pp

Daehler CT, Strong DR (1993) Prediction and biological invasion. Trends Ecol Evol 10:380

Duncan RP, Blackburn TM, Veltman CJ (1999) Determinants of geographical range sizes: a test using introduced New Zealand Birds. J Anim Ecol 68:963–975

Duncan RP, Bomford M, Forsyth DM, Conibear L (2001) High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. J Anim Ecol 70:621–632

Elton CS (1958) The ecology of invasions of animals and plants. Methuen, London, UK

Goodwin BJ, McAllister AJ, Fahrig L (1999) Predicting invasiveness of plant species based on biological information. Conserv Biol 13:422–426

Jeschke JM, Strayer DL (2005) Invasion success of vertebrates in Europe and North America. Proc Natl Acad Sci USA 102:7198–7202.

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends Ecol Evol 16:199–204

Kolar CS, Lodge DM (2002) Ecological predictions and risk assessment for alien fishes in North America. Science 298:1233–1236

Marchetti MP, Moyle PB, Levine R (2004) Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. Freshwater Biol 49:646–661

Miller AW (2000) Assessing the importance of biological attributes for invasion success: Eastern oyster *(Crassostrea virginica)* introductions and associated molluscan invasions of Pacific and Atlantic coastal systems. D.Env. dissertation. University of California, Los Angeles 209 pp

Miller AW, Hewitt CL, Ruiz GM (2002) Invasion success: does size really matter? Ecol Lett 5:159–162

Miller AW, Ruiz GM, Minton MS, Ambrose RF (2007) Differentiating successful and failed molluscan invaders in estuarine ecosystems. Mar Ecol Prog Ser 332:41–51

Prinzing A, Durka W, Klotz S, Brandl R (2002) Which species become aliens? Evol Ecol Res 4:385–405

Pyšek P, Richardson DM, Williamson M (2004) Predicting and explaining plant invasions through analysis of source area floras: some critical considerations. Divers Distrib 10:179–187

Reichard SH, Hamilton CW (1997) Predicting invasions of woody plants introduced to North America. Conserv Biol 11:193–203

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77:1655–1661

Richardson DM, Rejmánek M (2004) Conifers as invasive aliens: a global survey and predictive framework. Divers Distrib 10:321–331

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib 6:93–107

Roy K, Jablonski D, Valentine JW (2001) Climate change, species range limits and body size in marine bivalves. Ecol Lett 4:366–370

Ruesink JL (2005) Global analysis of factors affecting the outcome of freshwater fish introductions. Conserv Biol 19:1883–1893

Simberloff D (1989) Which insect introductions succeed and which fail? In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmánek M, Williamson M (eds) Biological invasions: a global perspective. . Wiley, New York, pp 61–75

Veltman CJ, Nee S, Crawley MJ (1996) Correlates of introduction success in exotic New Zealand birds. Am Nat 147:542–557

Verling E, Ruiz GM, Smith LD, Galil B, Miller AW, Murphy KR (2005) Supply-side invasion ecology: characterizing propagule pressure in coastal ecosystems. Proc R S 272:1249–1257

Williamson MH, Fitter A (1996) The characters of successful invaders. Biol Conserv 78:163–170