## Chapter fourteen

# Exploring the relationship between niche breadth and invasion success

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## INTRODUCTION

The ultimate goal of invasions biology should be to generate a body of general, predictive theory. Ideally, such theory would help determine whether a species with a particular set of traits will be able to invade a given system. In its almost fifty years, the discipline has seen many attempts to provide such predictability through a focus on the traits of the potential invaders and those of the invaded community. Regrettably, most attempts have been so far unsuccessful.

One attempt at generalization that has been often discussed in the literature is the idea that niche breadth is positively correlated with invasion success, so that species with broad niches (“generalists”) are more likely to invade than species with narrower niches (“specialists”), because they are more likely to find the necessary resources or environmental conditions; throughout this paper, I will refer to this notion as the “niche breadth–invasion success hypothesis.” As with many other ideas in ecology, it is difficult to track the historical development of this hypothesis. Probably one of the first to include some measure of niche breadth in thinking about invasion success was H. G. Baker. Baker (1965, 1974) defined the traits of what he called the “ideal weed” — species prone to become

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weedy and invade disturbed habitats. Among these traits, three were related to niche breadth, namely (i) that the species can produce seeds in a wide range of environmental circumstances and has high tolerance of (and often plasticity in face of) climatic and environmental variation; (ii) that the species has no special environmental requirements for germination (i.e., wide environmental niche); and (iii) that, when cross pollinated, pollination can be achieved by a nonspecialized flower visitor or by wind (i.e., wide pollination niche; note, however, that it is assuming wide niche breadth of pollinators, not of the plant, which brings up the issue of asymmetric specialization discussed below).

More recently, Rejmánek (2000) proposed ideas similar to those of Baker's in the broader context of plant invasions in general. He described what he thinks are ten major predictors of plant invasiveness, three of which are related to niche breadth: (i) "fitness homeostasis," the ability of an individual or population to maintain relatively constant fitness over a range of environments; fitness homeostasis will depend on phenotypic plasticity (homeostasis at the individual level) and population genetic polymorphism (homeostasis at the population level); (ii) size of "primary" (native) geographical ranges (see also Daehler and Strong 1993), which ultimately depends on population fitness homeostasis; and (iii) specificity of mutualisms, so that species that depend on non-specific mutualisms (root symbionts, pollinators, and seed dispersers) are more likely to overcome many abiotic and biotic barriers in new environments (see also Richardson *et al.* 2000).

Many others have discussed the idea that broader niches confer higher invasion success. For example, in a review on biotic homogenization McKinney and Lockwood (1999) concluded that extinction–resistant species and successful invaders are characterized by omnivory, rapid growth and dispersal or breeding in ephemeral habitats, whereas extinction-prone groups have a predominance of traits associated with specialization, slow reproduction and other traits not associated with opportunism. Similarly, Richardson *et al.* (2000) stated that "It is logical to predict that plants with specialized pollination syndromes are less likely to be pollinated in foreign environments than plants without specialized requirements" (p. 70). Likewise, Ricciardi and Rasmussen (1998) regard broad geographic, environmental and dietary ranges as general attributes of invasive aquatic species. Although these ideas are interesting and appealing, their evaluation is complicated by several conceptual and methodological problems. I will argue that progress towards a predictive theory of invasions will be difficult unless these issues are resolved.

Below I present a review of the literature, summarizing several studies that have evaluated the relationship between different aspects of niche breadth and invasion success. I then provide a critical examination of the mechanisms potentially involved in generating these results, stressing several conceptual issues that have been overlooked in previous discussions. My review is not exhaustive, and is taxonomically biased, focusing on plants, birds, and heterotrophic mutualists of plants. This bias reflects the fact that most studies evaluating this hypothesis have dealt with these groups. In summarizing the available literature I use a vote-counting approach, because the number of studies available per taxon and measure of niche breadth was too small to allow the application of more quantitative meta-analytical techniques (see Arnqvist and Wooster 1995, Gurevitch *et al.* 2001).

The studies reviewed here are based on three different kinds of comparisons: some measure of niche breadth in native region of successful vs. failed invaders (SI vs. FI); niche breadth of invaders in their native vs. their introduced regions (NR vs. IR); and niche breadth of native vs. introduced species in the introduced region (NS vs. IS). It is important to note several similarities and differences about the three approaches. The first comparison (SI vs. FI) uses a binary measure of invasion success, asking whether success is explained by the niche breadth in the native range. In contrast, the second approach (NR vs. IR) uses a quantitative measure of success, such as the size of the introduced range, to determine whether invasion success is explained by niche breadth in the native range. The third approach (NS vs. IS) compares niche breadth of introduced species with native species in the introduced range (i.e., species native to the recipient community); here the question is whether the success of invaders (i.e., the fact that they established in a new environment) is explained by their broader niche compared to that of native species, in sharp contrast with the question asked in the previous two approaches. Thus, although the three types of comparisons are intended to address the question of whether niche breadth of potential invaders is related to their invasion success, they are not equivalent and are likely to provide different answers.

My review consists of three main parts: (i) the role of geographic, habitat and climatic range on plant and bird invasions; (ii) the role of mutualisms on plant and pollinator invasions; and (iii) the role of trophic breadth on bird invasions. I end with a section summarizing the results of the review and offering concluding remarks.

## THE ROLE OF GEOGRAPHIC, CLIMATIC AND HABITAT RANGE

### Patterns: studies on plants and birds

Studies that have evaluated the invasion success of plants and its relationship to geographic, climatic or habitat range are based on the three types of comparisons outlined above. Studies based on the first two kinds of comparisons (SI vs. FI and NR vs. IR) have found that invasion success is positively related to native geographic, climatic or habitat range, so that more successful invaders tend to have broader native ranges than less successful invaders (Table 1). In general, these results support the notion that the native range of plant species is a predictor of their success as invaders in new regions where they did not occur naturally (Daehler and Strong 1993, Rejmánek 2000).

**Table 1** Studies evaluating the relationship between breadth of geographic, climatic or habitat range of plant species and invasion success.

| Type of comparison* | Major taxon | Native region | Introduced region | Measure of success | Measure of niche breadth | Relat. with niche breadth§ | Ref. |
|---|---|---|---|---|---|---|---|
| SI vs. FI | Higher plants | Central Europe | Mendoza and Buenos Aires provinces, Argentina | Establishment in new region | No. native habitat types | Positive | 1 |
| | Angiosperms | Europe | New Brunswick, Canada | Establishment in new region | Size of native range | Positive | 4 |
| NR vs. IR | Compositae, Gramineae | Eurasia | North America | Size of introduced range | No. native habitat types | Positive | 2 |
| | Angiosperms | South Africa | Australia | Weed status | No. native habitat types | Positive | 3 |
| | Angiosperms | South Africa | Australia | Weed status | No. climatic zones | Positive | 3 |
| | Bromus | Mediterranean regions | Mediterranean regions | No. climatic zones in native range | No. Mediterranean regions occupied | Positive | 5 |
| NS vs. IS | Higher plants | World/Hawaii | Hawaii | No. of habitat types occupied | No. habitat types | Negative | 6 |

References: 1, Prinzing *et al.* (2002); 2, Rejmánek (1995); 3, Scott and Panetta (1993); 4, Goodwin *et al.* (1999); 5, Roy *et al.* (1991); 6, Kitayama and Mueller-Dombois (1995).

* Comparisons included: S vs. F: native range of successfully established species vs. unsuccessfully established species; NR vs. IR: native range vs. introduced range of introduced species; NS vs. IS: range of native vs. introduced species in the introduced region.

§ Indicates statistical significance of test and direction of effect: Positive, significant effect in the direction expected by the specialization–niche breadth hypothesis; Negative, significant effect in the direction opposite to the expected by the specialization–niche breadth hypothesis.

In contrast, the one study comparing breadth of habitat use by native and introduced species (NS vs. IS; Table 1) found a pattern opposite to the prediction of the niche breadth–invasion success hypothesis: introduced species were found in fewer habitat types than native species. This result is difficult to interpret, however, mainly because the number of habitats in which a species is found will depend on its dispersal ability and the time elapsed after its arrival to the environment, which may obviously bias the results towards native species, given their longer presence in the study area.

Studies evaluating the relationship between geographic, climatic or habitat range and invasion success in birds (Table 2) all used the first approach outlined above; that is, they compare the size of the native range between successful and unsuccessful invaders (SI vs. FI). These studies have used either size of native geographic range, number of native habitat types, or climatic zones occupied in the native region as measures of niche breadth.

In agreement with studies on plants discussed above, studies of bird invasions in Hawaii, Australia and worldwide found a positive relationship between invasion success and size of native geographic range used in the native range (Table 2). However, two studies, one in four oceanic islands and the other in New Zealand, failed to find evidence for such an effect (Table 2). The two studies using the number of habitat types occupied in the native range found that successfully invading species or families had significantly greater native habitat ranges than species or families that failed to invade (Table 2).

In summary, it appears that breadth of native geographic, climatic and habitat range are related to the invasion success of plant and bird species. Although there are exceptions to these patterns, they appear to have some degree of generality.

## Mechanisms

Why does breadth of native geographic, habitat or climate range affect invasion success? Species with broad ranges may be more successful invaders than species with narrower ranges for several reasons. As discussed in the introduction, species' niches may determine their distribution, so that species with broader niches tend to have broader distributions and are so more likely to invade new environments (see also Brown 1984).

However, other factors not related to niche breadth may also affect species distributions. Under these scenarios, widespread species would have higher invasion success regardless of their niche breadth. First, species specialized on widespread resources, or species that are able to live under environmental characteristics that span large areas, may have wide distributions in spite of having a narrow tolerance to environmental conditions or of being able to use a narrow range of resources (Hanski *et al.* 1993, Gaston *et al.* 1997). This mechanism is particularly important for species that are able to exploit human-dominated ecosystems, which are themselves very widespread (Sol *et al.* 2002). Second, high dispersal ability can also lead to wide geographic ranges, at least in some

**Table 2** Studies evaluating the relationship between breadth of geographic, habitat range, trophic or behavioral breadth of bird species and invasion success.

| Measure of niche breadth | Taxonomic level of analysis | Introduced region | Relationship with niche breadth[§] | Ref. |
|---|---|---|---|---|
| Size of native range | Species | Hawaii | Positive | 1 |
| | | Australia | Positive | 2 |
| | | New Zealand | NS | 3 |
| | | Four oceanic islands | NS | 4 |
| | | World | Positive | 5 |
| | Families[†] | World | Positive | 6 |
| No. native habitat types | Species | World | Positive | 7 |
| | Families[†] | World | Positive | 6 |
| Diet breadth | Species | New Zealand | NS[a] | 3 |
| | | Nine oceanic islands | Positive[b] | 8 |
| | Families[†] | World | Positive[c] | 6 |
| Behavioral flexibility | Species | World | Positive | 9, 10 |

References: 1, Moulton and Pimm (1986); 2, Duncan *et al.* (2001); 3, Veltman *et al.* (1996); 4, Lockwood *et al.* (1999); 5, Blackburn and Duncan (2001); 6, Cassey (2002); 7, Brooks (2001); 8, McLain *et al.* (1999); 9, Sol and Lefebvre (2000); 10, Sol *et al.* (2002).

Measures of diet breadth used in studies: [a]Diet breadth measured as carnivore or herbivore (specialist) and omnivore (generalist). [b]Diet breadth measured as frugivore or granivore (specialist) and omnivore (eating fruits and seeds; generalist); a fourth category was included for species that fed on neither fruits or nectar. [c]Diet breadth measured as number of seven major food types consumed.

[§] Indicates statistical significance of test and direction of effect: Positive, significant effect in the direction expected by the specialization–niche breadth hypothesis; NS, statistically nonsignificant result.

[†] Cassey (2002) also did analyses at species level. However, his species-level multivariate analyses are mostly descriptive, and are difficult to compare with other studies listed in the table and were therefore not included.

groups, whereas limited dispersal can result in geographic ranges much narrower than would be predicted based on a species' niche (Gaston 2003). Thus, species with high dispersal abilities may tend to have both wide native ranges and high chances of colonizing and spreading in new environments. Third, species with wider native ranges may be more likely to be transported to new areas by humans through passive sampling (Prinzing *et al.* 2002), particularly considering that widespread species also tend to be locally abundant (Gaston *et al.* 1997). Cassey *et al.* (2004) have recently shown that propagule pressure of introduced birds explains invasion success worldwide; these authors also found that propagule pressure is positively related to geographic and trophic breadth, and so these measures of niche breadth are not independent of propagule pressure and could be confounded with it. Understanding the role of the habitat and climatic components of niche breadth in determining invasion success will require teasing apart these factors.

## THE ROLE OF SPECIALIZATION IN MUTUALISTIC INTERACTIONS

### Patterns

Several studies have evaluated the relationship between specialization in mutualistic interactions and invasion success of plants and/or animal mutualists. Richardson *et al.* (2000) have reviewed the role of mutualisms in facilitating plant invasions. Their review suggests that plants with extremely specialized mutualistic interactions (including interactions with pollinators, seed dispersers, mycorrhizal fungi and nitrogen-fixing bacteria) may be prevented from establishing and spreading in a new environment. However, the rarity of extreme specialization in mutualistic interactions may greatly minimize the potential role of mutualisms in limiting plant invasion success.

One of the examples of how extremely specialized mutualistic interactions may prevent the establishment and spread of introduced plant populations discussed by Richardson *et al.* (2000) is the invasion ecology of figs (*Ficus*, Moraceae). Of the sixty species of *Ficus* introduced to Florida, USA, only three have become invasive, and they have done so only after the accidental introduction of their specific wasp (see Richardson *et al.* 2000 and references therein). However, Richardson *et al.* also discuss the case of *F. lutea* in South Africa, where one isolated female individual of this nonindigenous species has been pollinated by wasps that were not its normal pollinator. Although in this case the absence of male individuals prevented reproduction (hybrids with native *Ficus* did not produce viable seedlings), spread might have been possible if male individuals of *F. lutea* had also been introduced. As a side note, Richardson *et al.* (2000) point out that several pine species (*Pinus* spp.) native to North America and the Mediterranean Basin that are wind-dispersed in their native ranges are dispersed by cockatoos in Australia. Although birds destroy most of the seeds, some survive to establish isolated foci in habitats (eucalypt forests) that they would otherwise not have been able to invade. Thus, even apparent extreme specialization on a particular pollen vector (fig wasp) or seed dispersal agent (wind) may not preclude survival and successful reproduction in a new environment.

Albeit intriguing, the extreme specialization observed for *Ficus* is not representative of the majority of pollination interactions (Waser *et al.* 1996), and most species within a community fall somewhere along a gradient that spans from extreme specialization to extreme generalization (Bascompte *et al.* 2003, Jordano *et al.* 2003, Vázquez and Aizen 2003, 2004a). A similar situation occurs in seed dispersal mutualisms (Bascompte *et al.* 2003). The question is whether species located towards the specialized extreme of the continuum are less likely to invade successfully than more generalized species.

In a recent review of introduced bees and their ecological impacts, Goulson (2003) points out that most introduced bee species appear quite generalized. Goulson argues that among bees, which depend on floral food resources throughout their entire life cycles, dietary generalization seems to be a precondition for becoming successful invaders. However, this interpretation should be taken with caution. All species of bees known to have been introduced outside their native ranges (the honey bee, five bumblebees, ten megachillids and one halictid) have been purposefully introduced by humans to enhance crop pollination, usually of several species. Given this goal, dietary generalization of introduced bees is probably a desirable trait, and it is therefore difficult to tease apart the effect of human selection from the effect of dietary specialization on invasion success.

Another way of evaluating the niche breadth–invasion success hypothesis as it applies to mutualistic interactions is by comparing the degree of specialization in mutualistic interactions between native and introduced species in a given area. The expectation under the niche breadth–invasion success hypothesis is that interactions are less specific for introduced than for native species (because exotic species with more specific interactions may have been "filtered out" during the establishment process). I have found studies in four systems attempting to answer this question by comparing the degree of specialization of plant and/or pollinators between native and introduced species (i.e., a NS vs. IS comparison; see above). In addition, I have found comparable data for a fifth system, for which I calculated degree of specialization in a way comparable to the other studies. These studies are summarized in Table 3. None of the studies support the niche breadth–invasion success hypothesis, and in some cases the observed pattern was contrary to the expectation (i.e., introduced species had more specific interactions). Thus, the few available studies tell us that interaction specificity of introduced plants and pollinators does not influence their invasion success.

### Mechanisms

From the studies reviewed above evaluating the role of mutualisms in invasions it appears that only extremely specialized mutualisms have the potential to influ-

**Table 3** Studies that have compared degree of specialization of plants or pollinators between native and introduced species.

| | | Mean number of mutualist species | | | |
|---|---|---|---|---|---|
| Introduced region | Major taxon | Native | Exotic | Result of statistical test§ | Ref. |
| Illinois, USA | Angiosperms | 34.0 | 24.0 | Negative | 1 |
| Nahuel Huapi, Argentina | Angiosperms | 14.8 | 17.6 | NS | 2 |
| Galápagos Islands | Angiosperms | 2.2 | 1.3 | Negative | 3 |
| Aigrettes | Angiosperms | 3.9 | 3.4 | NS | 4 |
| Flores (Azores) | Angiosperms | 3.3 | 2.3 | NS | 4 |
| Nahuel Huapi, Argentina | Hymenoptera (rare species excluded) | 6.3 | 11.3 | NS | 2 |
| Nahuel Huapi, Argentina | Hymenoptera (Apidae only) | 9.0 | 11.5 | NS | 2 |
| Flores (Azores) | Pollinators | 3.4 | 1.9 | NS | 4 |
| Aigrettes | Pollinators | 4.1 | 3.8 | NS | 4 |

References: 1, Memmott and Waser (2002); 2, Morales and Aizen (2002); 3, McMullen (1993); 4, Olesen *et al.* (2002).

§ Indicates statistical significance of test and direction of effect: Negative, significant effect in the direction opposite to the expected by the specialization–niche breadth hypothesis; NS, statistically nonsignificant result.

ence invasion success, and in general specificity of mutualistic interactions does not seem to influence invasion success significantly. These results contrast with those obtained in studies evaluating the relationship between geographic, habitat or climatic range and invasion success reviewed in the previous section. How can we explain these contrasting results? Why does narrow climatic or geographic range appear to translate into low likelihood of invasion, whereas narrow range of mutualistic interactions does not? The answer to this question may require some conceptual refinements in our thinking about the relationship between niche breadth and invasion success as it applies to mutualism.

First, we need to distinguish between the fundamental and realized niche (Hutchinson 1957). In the context of species interactions, fundamental specialization refers to the potential interactions that would lead to positive fitness for a given species, under any possible ecological circumstances (van Klinken and Edwards 2002, Vázquez and Aizen 2004b). Thus, fundamental specialization will ultimately depend on the genetic background of a species, whereas realized specialization refers to the actual specialization attained under a particular ecological context. For example, most fig species are fundamentally specialized on one or a few species of pollinating wasps; they fail to reproduce if they are moved to different environments, unless their specialized pollinators are introduced as well. Conversely, many other plant species that are pollinated by a single pollinator in a particular habitat are often pollinated by a different species in other habitats where they are introduced (Richardson *et al.* 2000). Regrettably, the best we can do in the field is to measure the realized niche, but if we want to predict invasions what we need to know is the fundamental niche. In other words, knowing the niche breadth of a species in a particular environment does not tell us what the realized niche will be in another environment. Although studying the climatic component of the fundamental niche may be possible by, for example, experimentally growing a species under a wide range of environmental conditions, doing so in the context of species interactions may be simply unfeasible, because it would require exposing the species to all possible combinations of interaction partners that it could encounter in any given environment. Even many species selected as biocontrol agents, which are usually selected to be specialists, exhibit unexpected host shifts in their introduced ranges (Simberloff and Stiling 1996, Henneman and Memmott 2001, van Klinken and Edwards 2002, Pearson and Callaway 2003), and these shifts are usually not the result of changes in the fundamental niche through rapid evolution, but an expression of a different realized niche under the new environment (van Klinken and Edwards 2002).

Second, as I pointed out above, species that use widespread resources, live under widespread environmental conditions or use widespread habitats are likely to be widespread themselves. This idea can be easily extended to species interactions to argue that species that specialize on widespread mutualists may themselves be widespread. An emerging pattern in plant-animal mutualistic interactions is the existence of highly asymmetric specialization, whereby specialists tend to specialize on generalists (Bascompte *et al.* 2003, Vázquez and Aizen 2004a). Given that abundant, frequently interacting species tend to be more generalized than rare species (Dupont *et al.* 2003, Vázquez and Aizen 2003, 2004a), and that locally abundant species tend to be geographically widespread (Gaston *et al.* 1997), species specialized on widespread mutualists will have a greater chance of finding their mutualists in their introduced region. These general features of mutualistic interactions may substantially increase the likelihood of successful invasion by species that are relatively specialized on their mutualists.

## THE ROLE OF TROPHIC BREADTH

### Patterns

Another aspect of the niche that can potentially affect invasion success is dietary breadth, and it is frequently listed as one potential characteristic of successful invaders (Ehrlich 1986, Ricciardi and Rasmussen 1998, McKinney and Lockwood 1999). I discuss here a few studies that have addressed this issue in the context of bird invasions.

To my knowledge, three studies have evaluated the relationship between invasion success and diet breadth (Table 2). These studies compared trophic breadth in the native region of successful vs. failed invaders (SI vs. FI). McLain *et al.* (1999) defined specialists as species feeding on either fruits or seeds, and generalists as species feeding on both; they found that trophic generalists were more likely to be successful invaders of oceanic islands than trophic specialists. Veltman *et al.* (1996) defined herbivorous or carnivorous species as dietary specialists, and omnivores (species feeding on both plant and animal material) as generalists; they failed to find a statistical effect of size of native trophic range on the success of birds introduced in New Zealand. Finally, Cassey (2002) defined dietary breadth as the number of food types consumed out of seven possible categories. He found a weak but significant effect of dietary breadth explaining the invasion success of bird families.

### Mechanisms

From this limited number studies and from their disparate results, it is difficult to make generalizations about the importance of trophic breadth for invasion success. Furthermore, a major limitation of the studies discussed above is that the measure of specialization used is probably too coarse and may therefore be a poor surrogate of true trophic specialization. For example, in the study by McLain *et al.* (1999), only fruits and seeds are considered to characterize diet breadth, although the authors state that “virtually all introduced species [in these islands] eat some insects and often other invertebrates” (p. 552). Thus, it is unclear whether what the authors measured actually represents diet breadth, or rather whether it represents something else related to eating fruits or seeds. In fact, the quantification of degree of specialization is probably one of the main conceptual and methodological hurdles in the study of species interactions (Martinez *et al.* 1999, Novotný *et al.* 2002, Vázquez and Aizen 2004b). Many ideas in ecology, evolution and biogeography depend on assumptions about the degree of specialization of species interactions. For example, because the bulk of the Earth's species are believed to be tropical herbivorous insects, estimates of the number of species on Earth depend critically on assumptions about their degree of specialization. The realization that tropical herbivorous insects were less specialized than previously thought led to revising the estimated number of global species from 30 million (Erwin 1982) to approximately 5 million (Ødegaard 2000, Novotný *et al.* 2002).

To circumvent the problem of the measurement of trophic specialization in birds, Sol and Lefebvre (2000) and Sol *et al.* (2002) proposed the use of "behavioral flexibility" as a surrogate of trophic breadth. These authors defined behavioral flexibility as "the frequency of new and unusual feeding behaviors reported in the short note section of ornithology journals" (Sol *et al.* 2002, p. 495). They argue that a taxonomic group in which large numbers of new feeding behaviors are observed is likely to change its foraging techniques or diet frequently, to eat a surprisingly large range of foods and to use handling behaviors and novel situations in a way that strikes ornithologists by its complexity and flexibility. They further found that behavioral flexibility of bird species in their native range is related to their success as invaders worldwide. This approach is a promising alternative to estimating trophic niche breadth from feeding records.

Regardless of the problems of estimation of trophic specialization, two issues discussed above in the context of geographic range and mutualisms also apply here. First, species specializing on widespread resources, particularly those that exploit human-dominated ecosystems, may be likely to invade in spite of being specialized. Second, even if accurate, estimates using feeding records provide a measure of the realized niche but not of the fundamental niche, which would be necessary predict invasion success in a new environment with a different set of food resources.

## CONCLUDING REMARKS

My review of the literature suggests several generalizations about the role of niche breadth as a determinant of invasion success. In particular, native habitat, geographic or climatic range of plants and birds appear to be good predictors invasion success, whereas specificity of mutualistic interactions and trophic breadth appear to have a much weaker predictive power. However, even when results do fit the predictions of the niche breadth–invasion success hypothesis, it is usually not possible to know whether niche breadth is involved in generating the observed pattern. Future studies aiming at predicting the success of invaders should tease apart the relative contributions of niche breadth from other confounding factors. More broadly, I hope my review can serve as an example of how conceptual elaboration may be useful to improve our understanding in invasions biology.

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