The elephant in the room: the role of failed invasions in understanding invasion biology

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Most species introductions are not expected to result in invasion, and species that are invasive in one area are frequently not invasive in others. However, cases of introduced organisms that failed to invade are reported in many instances as anecdotes or are simply ignored. In this analysis, we aimed to find common characteristics between non-invasive populations of known invasive species and evaluated how the study of failed invasions can contribute to research on biological invasions. We found intraspecific variation in invasion success and several recurring explanations for why non-native species fail to invade; these included low propagule pressure, abiotic resistance, biotic resistance, genetic constraints and mutualist release. Furthermore, we identified key research topics where ignoring failed invasions could produce misleading results; these include studies on historical factors associated with invasions, distribution models of invasive species, the effect of species traits on invasiveness, genetic effects, biotic resistance and habitat invasibility. In conclusion, we found failed invasions can provide fundamental information on the relative importance of factors determining invasions and might be a key component of several research topics. Therefore, our analysis suggests that more specific and detailed studies on invasion failures are necessary.

Historically the field of invasion biology has focused on the study of species that successfully invaded (i.e. invasive alien species) after introduction to a new range, and during the past decades invasion biologists have collected numerous case studies of successful invasions (Richardson and Pyšek 2008, MacIsaac et al. 2011). This focus on successful invaders helps us understand their overall importance as a threat to global biodiversity and why certain introduced species become invasive. However, most species introductions are not expected to result in invasion (Kowarik 1995, Williamson and Fitter 1996a) and species that are invasive in one area can be non-invasive elsewhere (Simberloff et al. 2002). Even though the fact that most introductions do not result in invasions is generally accepted (Lockwood et al. 2005, Blackburn et al. 2011), we still lack a comprehensive understanding of failed invasions. It is clear that failures are not part of the mainstream research on invasive species, as can be observed in many of the most important books in the discipline (Sax et al. 2005, Lockwood et al. 2007, Davis 2009, Richardson 2011, Simberloff and Rejmánek 2011).

After individuals of a species are released within a new range, invasion failure can occur during any stage of the invasion continuum (Blackburn et al. 2011). Populations can be incapable of surviving, reproducing, or maintaining a sustainable population, and therefore they cannot invade (failure to naturalize). In other instances, populations may naturalize and not spread, also failing to invade (failure to invade after naturalization). Different mechanisms can operate at each stage; populations can either stagnate in a stage previous to invasion or recede to earlier stages, up to the point of local or regional extinction (Simberloff and Gibbons 2004). Often, failure to naturalize is unknown and difficult to detect (especially for unintentional introductions), while failure to invade after naturalization is more commonly observed (Phillips et al. 2010).

For this study, we reviewed the literature and searched for cases where a non-native species that is a known invader in one habitat or region has failed to invade a differing region or habitat or at a different time. We only considered cases of intraspecific variation in invasion success. Even though studies of species that never invaded can produce informative results, comparisons of invasive and non-invasive populations of a given species may be more likely to determine the cause of current failure (Blackburn et al. 2011). If a species has never been documented as invasive there may be many non-exclusive causes.

Assessment of the published reports on failed invasions

We conducted different searches to collect cases of failed invasions. Given that this is not a research topic, it cannot

be expected that summaries, titles, or key words would adequately sample and locate many cases of failed invasions. Therefore, we conducted extensive searches by querying academic search engines (ISI Web of Science and Google Scholar) using combinations of the key words introduction, naturalization, invasion, invasive, fail, and failure. We also searched the reference lists and citations received by the papers identified in the search. Complementary, we searched mentions for failures in global catalogues of naturalized species (Lever 1987, 1996, 2003, Long 2003). Experts in the field also helped identify cases of failed invasions. We included 76 cases where there was intraspecific variation in invasion success across continents, local habitats, or time frames (Table 1). We did not aim for a complete list of cases, but instead we hoped to provide examples that illustrate the extent of invasive species failures. We grouped the examples based on hypotheses that were proposed to explain these failures and compared the number of times where a hypothesis for the failed invasion was only suggested, the number of times a proposed hypothesis was suggested and tested, and the number of times where no factor was suggested (Fig. 1).

Factors associated with invasion failure

From the 76 reported species with invasive and non-invasive populations (Table 1), we found five distinct factors suggested as reasons for invasion failures: propagule pressure, abiotic resistance, biotic resistance, genetic constraints and mutualist release (Fig. 1). We found taxonomic and geographic biases in reports of invasion failures and these biases are also present in Table 1. Reports of failed invasions for trees and terrestrial vertebrates abound, while cases of failure for herbaceous plants and arthropods (except biocontrol insects) are scarce. Also, there are many more reports for failures in Europe, Oceania and USA. We found very few cases for Africa and Asia. We lack formal explanations for these biases; although they can be partially explained by unequal introduction effort and history of attention to species' introductions (Nuñez and Pauchard 2010). In most cases, only one mechanism for failures was suggested, and 11 studies tested the proposed factors. One striking result is that two-thirds of the cases presented (48), lack explanation for invasion failures. Abiotic and biotic resistances were found to be commonly associated with failures, but in very few cases these factors were experimentally or statistically tested. Below we present the evidence available for the factors we found are associated with failures to invade.

Failed invasions and propagule pressure

Current theory predicts that increased propagule pressure increases the likelihood of invasion, which has been proposed as the main determinant of invasion success (Lockwood et al. 2005, Colautti et al. 2006, Simberloff 2009). With few individuals, species can fail to naturalize because of demographic stochasticity (e.g. lack of mate encounters or pollen outcrossing). However, some small populations do naturalize and fail to invade after naturalization for various reasons that are unrelated to initial propagule pressure (Boyce 1992, Simberloff and Gibbons 2004). For example, on Isla Victoria (Argentina) propagule pressure did not explain the current invasion failure of 18 non-native tree species known to be invasive elsewhere (Simberloff et al. 2010, Nuñez et al. 2011). Also, invasive populations of *Pinus radiata* in Australia are scarce, despite being widely planted (Williams and Wardle 2007), while in South Africa and New Zealand, where *P. radiata* was extensively planted during the 19th and 20th centuries, invasive populations are common (Richardson 1998, Simberloff et al. 2010). In Argentina, *P. radiata* is well established in some regions but fails to establish in others, and in southern Brazil and Uruguay plantations of *P. radiata* exist but there is no record of naturalized populations outside plantations (Simberloff et al. 2010, Zenni and Simberloff 2013).

Failed invasions and abiotic resistance

The ability to cope with abiotic factors in the introduced range might determine the survival and reproductive capacities of non-native organisms, and the environmental suitability of the introduced range seems to be crucial for naturalization success (Moyle and Light 1996, Blackburn and Duncan 2001, Menke and Holway 2006). Abiotic factors act strongly at the naturalization stage, prior to invasion, because they affect the survival of introduced individuals prior to reproductive maturity (Moyle and Light 1996, Castro et al. 2002). Also, different factors can operate at different scales. While climatic variables such as mean annual temperature and precipitation are mostly macroclimatic factors, soil moisture and depth can vary locally. Abiotic resistance may be the strongest mechanism causing invasions to fail in some regions (Blackburn and Duncan 2001).

Abiotic factors are key determinants of invasion success or failure of non-native fish species in California streams and estuaries (Moyle and Light 1996). The rainbow trout *Oncorhynchus mykiss*, one of the most widely introduced and invasive fish species (Welcomme 1985), varies from highly successful to failed invader in the USA (Fausch et al. 2001). Similarly, the bluegill *Lepomis macrochirus* failed to invade freshwater systems in California (Meffe 1991) even though it successfully invaded streams in Japan (Nakao et al. 2006) and Korea (Kawamura et al. 2006). Invasion failures for these populations could be related to stream free-flow (Meffe 1991). Several studies with plants also have reported variation in invasion success of introduced populations. For example, *Prunus serotina* is unable to invade waterlogged and calcareous soils, whereas it successfully colonizes well-drained, nutrient-poor soils in northern France (Closset-Kopp et al. 2011). Also, the naturalization success of non-native plants in coastal dunes of California is related to exposure of the different sites to wind (Lortie and Cushman 2007). Nitrogen-fixing plants may fail to invade when phosphorus is limited since nitrogen fixation requires high availability of this nutrient (Vitousek 1999, González et al. 2010). As for invertebrates, cooler and wetter climate determined where dung beetles populations failed to naturalize in Australia (Duncan et al. 2009), and local soil moisture correlated with Argentine ants *Linepithema humile* local abundances in California (Menke and Holway 2006).

Table 1. List of 76 species with known invasive and non-invasive populations (sensu Blackburn et al. 2011). When available, the factor suggested for failure of the non-invasive populations was included. The level of detail provided for locations of invasive and non-invasive populations vary according to the data available in the literature. We added an "(?)" after some proposed factors when it was not explicitly suggested in the citation, but it was implied in the discussion. Species marked with * were introduced as biological control agents.

Group	Species (common name)	Examples of invasive populations	Examples of non-invasive populations	Reason for failure of non-invasive populations	References
Algae					
Seaweed	*Fucus serratus* (toothed wrack)	North America (east coast and/or estuarine)	North America (east coast and/or estuarine)		Ruiz et al. 2000
Animals					
Amphibian	*Alytes obstetricans* (common midwife toad)	Great Britain, Netherlands	Poland		Kraus 2009
	Bufo marinus (cane toad)	American Samoa, Antigua (second introduction attempt in the 1950s), Australia, Barbados, Bermuda, Japan (Ogasawara and Ryukyu Islands), Philippines, USA (Florida: after 1955, Hawaiian Islands, Louisiana)	Anguilla, Antigua (first introduction attempt in 1934), Barbados, Cook Islands, Cuba, Dominica, Egypt, Mascarene Islands, Taiwan, Thailand, USA (Florida: before 1955)	abiotic resistance (?)	Lever 2003, Kraus 2009
	Osteopilus septentrionalis (Cuban tree frog)	Anguilla, Antigua, Bahamas, Costa Rica, Puerto Rico, Saint Barts, USA (Florida), Virgin Islands (British and USA)	Canada (Ontario), Curaçao, Dominica, USA (Colorado, Maryland, Virginia)		Kraus 2009
	Rana catesbeiana (American bullfrog)	Brazil, Colombia, England, Italy, Peru, Puerto Rico, Spain, USA (Arizona, California, Colorado, Hawaii, Montana), Venezuela	Belgium, Italy, Netherlands, Portugal, USA (Massachusetts, North Dakota)	abiotic resistance	Lever 2003, Kraus 2009
	Xenopus laevis (African clawed frog)	Ascension Island, Chile, France, Great Britain, Italy (Sicily), Japan, Mexico, USA (Arizona, California)	USA (Colorado, Florida, Massachusetts, North Carolina, Texas, Virginia, Wisconsin)		Kraus 2009
Bird	*Acridotheres tristis* (common myna)	Australia, Hong Kong, Madagascar, Mauritius, New Zealand (North Island), South Africa	New Zealand (South Island), Tasmania (early 1900s)		Lever 1987
	Alauda arvensis (skylark)	Australia, New Zealand, USA (Hawaii)	USA (Continental)		Sol 2000
	Coturnix chinensis (king quail)	Australia	New Zealand, USA (continental, Hawaii)		Sol 2000
	Perdix perdix (grey partridge)	USA (west of Allegheny mountains)	Australia, New Zealand, USA (continental: east of Allegheny mountains, Hawaii)	abiotic resistance (?)	Lever 1987, Sol 2000
	Streptopelia decaocto (Eurasian collared dove)	Czech Republic, New Zealand, USA (continental)	Australia, USA (Hawaii)		Sol 2000, Šefrová and Laštůvka 2005
	Sturnus vulgaris (European starling)	Australia, Canada (after 1917), Jamaica, New Zealand, South Africa, USA (after 1920)	Canada (earlier introductions in 1875 and 1889), Russia (Buryat Republic), USA (earlier introductions in 1872 and 1897)		Lever 1987
	Zenaida macroura (mourning dove)	Bermuda, USA (Florida)	South Africa		Lever 1987
Freshwater fish	*Carassius auratus* (goldfish)	England	Belgium		Copp et al. 2005, 2007
	Lepomis macrochirus (bluegill)	Japan and Korea	USA (west)	abiotic resistance (?)	Meffe 1991, Kawamura et al. 2006, Nakao et al. 2006
	Micropterus dolomieui (smallmouth bass)	South Africa, Sweden (south), Vietnam	Austria, Finland, Germany, Japan, Mariana Islands, Uganda	abiotic resistance (?)	Lever 1996

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Table 1. (Continued).

Group	Species (common name)	Examples of invasive populations	Examples of non-invasive populations	Reason for failure of non-invasive populations	References
	Micropterus salmoides (largemouth bass)	Europe (south and center), South Africa	Brazil, England		Schulz and Leal 2005, Copp et al. 2007, Olds et al. 2011
	Oncorhynchus mykiss (rainbow trout)	USA	USA	abiotic resistance (?)	Welcomme 1985, Fausch et al. 2001
	Oreochromis mossambicus (Mozambique tilapia)	China (south), Hong Kong, India, Nicaragua	Bangladesh, Ecuador, Egypt, South Korea	abiotic resistance (?)	Lever 1996
	Pseudorasbora parva (stone moroko)	Many regions in Europe	Belgium, Lithuania, United Kingdom (ponds and lakes)		Copp et al. 2005, 2007, Witkowski 2009
Insect	*Anoplolepis gracilipes* (yellow crazy ant)	Australia, Christmas Island, Indonesia, Malaysia, Papua New Guinea, Seychelles, Solomon Islands, USA (Hawaii)	New Zealand	abiotic resistance (?)	Holway et al. 2002, Gerlach 2004, Lester 2005, Hoffmann and Saul 2010
	Bombus terrestris sassaricus (Sardinian bumblebee)	Argentina, Chile, Japan, New Zealand	France (south)	biotic resistance (?)	Morales 2007, Ings et al. 2010
	*Ceutorhynchus litura**	Canada, USA	New Zealand	propagule pressure	Julien and Griffiths 1998
	*Procecidochares utilis**	Australia, China, India, New Zealand, South Africa, USA (Hawaii)	Thailand		Julien and Griffiths 1998
	*Rhinocyllus conicus**	Canada	Australia, South Africa		Julien and Griffiths 1998
	*Rhopalomyia californica** (coyote bush)	Australia (after second introduction in 1982)	Australia (first introduction in 1969)	propagule pressure	Julien and Griffiths 1998
	Solenopsis invicta (red fire ant)	Puerto Rico, USA (southeast), Virgin Islands	New Zealand		McGlynn 1999, Holway et al. 2002, Lester 2005
	Solenopsis papuana (Papuan thief ant)	USA (Hawaii)	New Zealand		LaPolla et al. 2000, Holway et al. 2002, Lester 2005
	*Trichosirocalus horridus**	Canada (British Columbia, Ontario), USA	Argentina		Julien and Griffiths 1998
	*Tyria jacobaeae**	Canada, New Zealand, USA (west coast)	Australia (six release attempts were made)	biotic resistance	Julien and Griffiths 1998
	Wasmannia auropunctata (electric ant)	Galápagos, New Caledonia, USA (Hawaii)	New Zealand	abiotic resistance (?)	Clark et al. 1982, Le Breton et al. 2003, Lester 2005

	Species	Distribution	Distribution	Mechanism	References
Mammal	*Capra hircus* (goat)	Australia (all States and territories except the northern territory), Ascension Island, Canary Islands, Desertas, Galápagos, Saint Helena, USA (Channel Islands)	Australia (Northern Territory), Costa Rica, Crozet Archipelago, Falkland Islands	biotic resistance (?)	Letts 1964, Long 2003
	Castor canadensis (North American beaver)	Argentina (Tierra del Fuego), Chile, Russia	Europe (central)		Lizarralde et al. 2004, Nummi 2006, Pastur et al. 2006, Novillo and Ojeda 2008
	Cervus axis (axis deer)	Argentina, Australia, Yugoslavia (Istria)	Australia (Tasmania), Brazil, France, Java		de Vos et al. 1956, Long 2003
	Macropus rufogriseus (red-necked wallaby)	New Zealand, Tasmania (Maria Island)	Czech Republic (Poděbrady), Germany	biotic resistance (?)	Long 2003
	Mustela vison (mink)	Denmark, Finland, Iceland, Norway, Scandinavia, Sweden	Chile (lake Todos los Santos), Europe (central), Netherlands		Long 2003
	Oryctolagus cuniculus (European rabbit)	Argentina and Chile (Beagle Channel, Tierra del Fuego)	Argentina and Chile (Beagle Channel, Tierra del Fuego)	biotic resistance (?) and abiotic resistance (?)	de Vos et al. 1956, Long 2003
	Ovis ammon (mouflon)	USA (Hawaiian Islands: Lanai)	USA (Hawaiian Islands: Hawaii, Kauai)		Long 2003
	Sus scrofa (wild boar)	Argentina, Falkland Islands (Malvinas), New Zealand (Ruapuke), South Africa (Cape Peninsula), USA (Hawaii)	Argentina, Australia, Puerto Rico, USA		Long 2003, Novillo and Ojeda 2008
Mollusc	*Crassostrea gigas* (Pacific oyster)	North America (west coast and/or estuarine)	North America (west coast and/or estuarine)		Ruiz et al. 2000
	Crassostrea virginica (Atlantic oyster)	North America (west coast and/or estuarine)	North America (west coast and/or estuarine)		Ruiz et al. 2000
	Ilyanassa obsoleta (eastern mudsnail)	North America (west coast and/or estuarine)	North America (west coast and/or estuarine)		Ruiz et al. 2000
	Laternula marilina (littoral spoon clam)	North America (west coast and/or estuarine)	North America (west coast and/or estuarine)		Ruiz et al. 2000
	Littorina littorea (common periwinkle)	North America (east coast)	North America (southwest coast)	abiotic resistance (?)	Chang et al. 2011
	Mercenaria mercenaria (hard clam)	North America (west coast and/or estuarine)	North America (west coast and/or estuarine)		Ruiz et al. 2000
	Neotrapezium liratum (quadrate trapezium)	North America (west coast and/or estuarine)	North America (west coast and/or estuarine)		Ruiz et al. 2000
	Ostrea edulis (european flat oyster)	North America (west coast and/or estuarine)	North America (west coast and/or estuarine)		Ruiz et al. 2000
	Venerupis philippinarum (Japanese littleneck)	North America (west coast and/or estuarine)	North America (west coast and/or estuarine)		Ruiz et al. 2000
Reptile	*Agama agama* (common agama)	Comoros, USA (Florida)	Malta, Spain		Kraus 2009
	Anolis sagrei (brown anole)	Cayman Islands, Grenada, Jamaica, Mexico, Taiwan, USA (Alabama, Florida, Georgia, Hawaii, Louisiana, Texas)	Canary Islands, USA (Ohio, South Dakota, Tennessee, Virginia)		Kraus 2009
	Bradypodion pumilum (Cape dwarf chameleon)	Namibia	Greece		Kraus 2009
	Gallotia galloti (Tenerife lizard)	Canary Islands	Madeira		Kraus 2009

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Table 1. (Continued).

Group	Species (common name)	Examples of invasive populations	Examples of non-invasive populations	Reason for failure of non-invasive populations	References
	Gekko gecko (tokay gecko)	Martinique, USA (Florida, Hawaii)	Australia, Guam, New Zealand		Kraus 2009
	Trachemys scripta (red-eared slider)	Brazil, France, Spain	Sweden	abiotic resistance (?)	Lever 2003, Cadi et al. 2004, Perez-Santigosa et al. 2008
Plants					
Fern	*Asparagus scandens* (climbing asparagus)	New Zealand (disturbed forest)	New Zealand (other habitats)	biotic resistance (?)	Timmins and Reid 2000
Grass	*Eragrostis plana* (South African lovegrass)	Brazil (degraded and overgrazed steppes)	Brazil (steppes)	biotic resistance (?)	Zenni and Ziller 2011
	Phalaris arundinacea (reed canarygrass)	North America	North America	genetic effects	Chambers et al. 1999
	Phragmites australis (common reed)	North America (past 100 years)	North America (>100 years)	genetic effects	Chambers et al. 1999
Herb	*Echium vulgare* (blueweed)	Australia, Chile, South Africa	USA (California)		Marcel Rejmánek pers. comm.
Tree	*Abies grandis* (grand fir)	Great Britain	Ireland, Sweden		Richardson and Rejmánek 2004
	Afrocarpus falcatus (sickle-leaved yellowwood)	South Africa	Australia (north and southwest)		Richardson and Rejmánek 2004
	Cryptomeria japonica (Japanese cedar)	Azores	Argentina (Patagonia: Isla Victoria), Brazil, Germany, Hawaii, New Zealand		Simberloff et al. 2002, Richardson and Rejmánek 2004, Zenni and Simberloff 2013
	Larix decidua (European larch)	Czech Republic, Great Britain, New Zealand	Argentina (Patagonia: Isla Victoria), Canada (Newfoundland), Ireland, Lithuania, USA (New England, New York)		Simberloff et al. 2002, Richardson and Rejmánek 2004
	Melia azedarach (Chinaberry)	Argentina, Brazil (deciduous forests, mostly on basaltic soils), South Africa	Africa (east), Brazil (other soils and habitats), USA (California)		Marcel Rejmánek pers. comm.
	Myrica faya (fayatree)	USA (Hawaii: nitrogen limited, phosphorous rich ecosystems)	USA (Hawaii: phosphorous limited ecosystems)	abiotic resistance	Vitousek 1999, González et al. 2010
	Pinus caribaea (Caribbean pine)	Australia (northeast), Brazil (central), New Caledonia	Brazil (south), Puerto Rico, USA (Hawaii), Venezuela		Richardson and Rejmánek 2004, Simberloff et al. 2010
	Pinus contorta (lodgepole pine)	Australia (north and southwest), Chile, Great Britain, Ireland, New Zealand, Sweden	Argentina (Patagonia: Isla Victoria), Russia, Sweden	mutualist release	Richardson and Rejmánek 2004, Langdon et al. 2010, Simberloff et al. 2010

Species				References
Pinus elliottii (slash pine)	Argentina, Australia (north and southwest), Brazil, USA (Hawaii), South Africa	New Zealand		Richardson and Rejmánek 2004, Simberloff et al. 2010, Zenni and Simberloff 2013
Pinus halepensis (Aleppo pine)	Argentina (eastern), Australia (south, Victoria), Israel, New Zealand, South Africa	Argentina (Patagonia: Isla Victoria), Brazil, USA (California)		Richardson and Rejmánek 2004, Simberloff et al. 2010
Pinus nigra (Austrian pine)	Czech Republic, New Zealand	Argentina (Patagonia: Isla Victoria)		Simberloff et al. 2002, Bellingham et al. 2004, Křivánek et al. 2006
Pinus radiata (Monterey pine)	Australia, Chile (forest edges), New Zealand, South Africa	Brazil, Chile (forest interiors)	biotic resistance (Chile)	Williams and Wardle 2007, Simberloff et al. 2010, Zenni and Simberloff 2013
Pinus taeda (loblolly pine)	Argentina, Australia (north, southwest and Queensland), Brazil, South Africa, USA (Hawaii)	Brazil (interior of dense forests), New Zealand, Zimbabwe	biotic resistance (Brazil)	Richardson and Rejmánek 2004, Emer and Fonseca 2010, Simberloff et al. 2010, Zenni and Simberloff 2013
Prunus serotina (black cherry)	France (well-drained, nutrient-poor soils)	France (waterlogged and calcareous soils)	abiotic resistance	Closset-Kopp et al. 2011
Pseudotsuga menziesii (Douglas fir)	Argentina, Austria, Bulgaria, Chile, Czech Republic, Great Britain, New Zealand (open habitats)	Germany, Ireland, New Zealand (forests), USA (New York)		Von Holle et al. 2003, Richardson and Rejmánek 2004
Thuja plicata (western redcedar)	Great Britain	Argentina (Patagonia: Isla Victoria), New Zealand, Poland		Richardson and Rejmánek 2004
Shrub *Acacia paradoxa* (kangaroo thorn)	Australia (Victoria), South Africa (Western Cape), USA (California)	Chile, Israel		Zenni et al. 2009
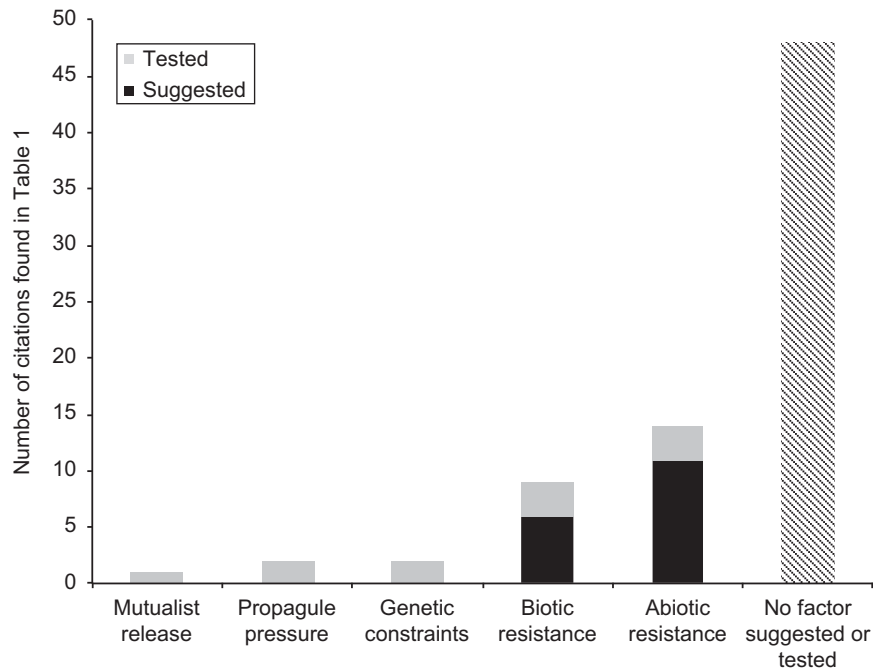
Figure 1. We summarized from Table 1 the factors proposed to explain failed invasions, and counted the number of times each factor was suggested or tested. Black bars represent instances where the factor was proposed, but not tested, and grey bars represent instances where the factor was experimentally or statistically tested. The dashed bar indicates mentions to failed invasions from Table 1 where a possible driver of failure was not suggested.

Failed invasions and biotic resistance

Community factors can locally prevent populations of non-native species from invading. Resident species cover (Levine 2000), competition (Crawley et al. 1999), or predation (Nuñez et al. 2008) can play key roles in determining a community's resistance to invasion. For example, thousands of colonies of the Sardinian bumblebee *Bombus terrestris sassaricus* were introduced in southern France for crop pollination between 1989 and 1996, but after 1998 no feral workers or hybrids between the introduced subspecies and the native subspecies were observed. The failure is probably due to competition with the three native subspecies existing in the region (Ings et al. 2010). By contrast, in Argentina, Chile, Japan and New Zealand, *B. terrestris* has become an invasive species of increasing concern (Morales 2007). The success of the nonnative *B. terrestris* in Japan is related to its greater reproductive capacity and greater competitive ability in comparison with native bumblebees (Matsumura et al. 2004). Biotic resistance also seems to play an important role in invasion failure of populations of several *Pinus* species across a number of ecosystems predicted to be climatically suitable for these species (Bustamante and Simonetti 2005, Nuñez et al. 2011). Plant communities dominated by woody species, like forests and shrublands, seem to be more resistant to invasion by pine trees than other communities, like grasslands and dunes (Richardson et al. 1994). Also, many non-native populations thrive only in constantly disturbed sites (e.g. roadsides and pastures) and fail to invade undisturbed habitats. For example, the South African lovegrass *Eragrostis plana* currently invades more than two million hectares in Brazil but only in degraded or overgrazed steppes (Zenni and Ziller 2011). Another example is the climbing

asparagus *Asparagus scandens*, which has a patchy distribution in New Zealand, mainly in disturbed forest remnants near urban areas (Timmins and Reid 2000). Probably these non-native species are not able to thrive under competition in the native communities where they were introduced. However, it remains unclear if biotic resistance can deter invasions completely or if it only slows the invasion process.

Failed invasion and genetic constraints

Genetic factors could affect invasion success and different genetic lineages can exhibit different levels of invasiveness. The grasses *Phragmites australis* and *Phalaris arundinacea* in North America are good examples. The former is a macrophyte native to North America that over the last century has expanded into tidal and non-tidal wetlands, displacing native vegetation (Chambers et al. 1999). The expansion is due to the introduction of a non-native genetic lineage that exhibits greater rates of photosynthesis and greater rates of stomatal conductance, which allows the exotic lineage to outcompete native lineages of *P. australis* and native vegetation (Saltonstall 2002, Mozdzer and Zieman 2010). *Phalaris arundinacea* is also a native wetland grass in North America that became invasive after previously isolated non-native genotypes combined to create a novel genotype (Lavergne and Molofsky 2007). Likewise, population genetic diversity influences colonization success of the weedy herb *Arabidopsis thaliana* more than population density (Crawford and Whitney 2010). However, we could find no study exploring the role of genetics in invasion failures or comparing genetic characteristics between successful and unsuccessful populations. Although a genetic bottleneck is commonly argued

to be one of the main reasons why introductions fail (Simberloff 2009), empirical evidence is missing or too biased towards cases of successful invasions, a fact that impedes the understanding of this factor as a limit to invasion.

Failed invasions and the lack of mutualists

Many species rely on mutualisms to grow or reproduce and will not successfully naturalize and invade until their mutualistic partner arrives (Richardson et al. 2000). For example, a lack of mycorrhizal fungi limited invasion by non-native trees in Patagonia (Nuñez et al. 2009), and non-native fig species were not invasive in Florida until their specific wasp pollinators arrived (Ramírez and Montero 1988, McKey and Kaufmann 1991, Nadel et al. 1992). Leguminous plants, which depend on mutualisms with root-nodule bacteria (rhizobia), may also fail to naturalize if the introduced population is small and if rhizobia density is low (Parker 2001), or if the co-evolved rhizobia strains from the native range are not co-introduced (Rodríguez-Echeverría et al. 2012). Given that many plant species rely on facilitation for their survival (e.g. for pollination, dispersal and growth), and that sometimes mutualisms can be highly specialized, it is possible that numerous failed invasions are caused by the lack of a mutualist in the new habitat (Richardson et al. 2000). Contrary to the 'enemy release' mechanism of invasion success (Keane and Crawley 2002), 'mutualist release' can be one key mechanism of failure for populations of invasive species with obligatory mutualists. On the other hand, co-invasions seem to be common and many mutualists are generalists (Dickie et al. 2010, Rodríguez-Echeverría et al. 2012).

When is it important to know about failure and when is it not?

In this study, we report many species that successfully invaded somewhere and also failed to invade somewhere else, and this intraspecific variation in invasion success occurs across habitats as well as continents (Table 1). Yet, most studies of invasions rely on invasion successes only. For instance, the most common approach to study the determinants of invasiveness is to compare invasive vs non-invasive species in a given, usually fairly large and heterogeneous, region (Diez et al. 2009, Van Kleunen et al. 2010). Also, studies on species potential invasive ranges mostly use invasion data only (Elith et al. 2006). The assumption that species can only be assigned to the invasive or non-invasive categories pose serious limitations to the interpretation of results in broader contexts, especially if spatial scale and heterogeneity are not clearly taken into account. Some research questions might require information about failed invasions more than others, and sometimes very different results can be obtained if failures are considered or are ignored. We have identified six research topics for which incorporating intraspecific variation in invasion success can help improve current understanding. Below, we describe these areas and suggest ways to incorporate failed invasions.

Historical factors associated with invasions

Several authors have pointed out historical factors (i.e. factors associated with human decision or activities and not with the biology of the species) such as dispersal pathways, reason for introduction, and propagule pressure, play important roles in invasion success (Harris et al. 2007, Wilson et al. 2009). For example, cultivation is generally agreed to be one of the most important dispersal pathways for invasive plants because the propagation of species increases propagule pressure and the cultivated species benefits from human-assisted long distance dispersal (Von Der Lippe and Kowarik 2007, Huang et al. 2010). However, it is also known that the numbers of species introduced through different dispersal pathways vary greatly (Richardson and Rejmánek 2011), and most studies on the topic include only records of naturalization and invasion (Harris et al. 2007, Huang et al. 2010). Omission of the failures can inflate the relative importance of historical factors responsible for many failed invasions. For example, forestry is considered an important pathway for tree invasions because many species introduced for forestry became invasive (Essl et al. 2010, Simberloff et al. 2010), even though in several cases plantations of the same species repeatedly fail to naturalize (Mortenson and Mack 2006, Nuñez et al. 2008, Carrillo-Gavilán and Vilà 2010). To improve our understanding of the relative importance of historical factors in invasion success, the next step is to explicitly include records of failed invasions in the analyses (Gravuer et al. 2008).

Small numbers of individuals might fail to invade owing to chance or idiosyncratic factors. However, high propagule pressure by itself cannot guarantee invasion success, although it certainly can increase the likelihood. Propagule pressure should be considered a null hypothesis in studies of invasions, and if it does not explain patterns of successes and failures, other mechanisms should be considered (Lockwood et al. 2005, Colautti et al. 2006, Simberloff 2009). Learning why introductions with abundant propagules (i.e. unlikely to go extinct because of demographic stochasticity) fail to naturalize and invade can further our understanding of invasions because they would not only demonstrate which historical factors contribute to invasions but also their relative strengths. It is not clear yet if certain dispersal pathways are more important because they truly promote invasion more often than others, or if they simply were more often used and had more opportunities to transport and release a successful invader.

Species distribution models

Studies of the potential distributions of invasive populations, or species distribution models (SDM), often use known presence records of the invasive species, both in the native and introduced ranges. Most SDMs generate pseudo-absences, in place of true absences, to predict the areas species could potentially occupy (Elith et al. 2006, Phillips et al. 2006). Pseudo-absences are points in the environmental layers of the model where the species is not known to be present and are used to simulate areas where the species is absent (Zaniewski et al. 2002). The lack of

records of true absences is an important caveat in model accuracy because of several uncertainties generated by pseudo-absences (Elith et al. 2006); SDMs do not verify the species does not occur at 'absence' locations, or that a species could not potentially thrive if introduced or dispersed to the 'absence' point. For potential distribution models of invasive species, records of failed invasions represent true absences that might significantly improve model calibration and validation and decrease the uncertainties surrounding the predictions (Duncan et al. 2009, Václavík and Meentemeyer 2009). If a species was introduced to a place and did not thrive there, and local extinction is not attributable to demographic stochasticity, this is key evidence for poor fit to the site, which can potentially cause important changes in model outcomes. Since many widely used species distribution models require presence and absence data (e.g. GAM, GLM and MAXENT), replacing pseudo-absences with true absences will clearly improve the predictive model (Fig. 2).

Species traits and invasiveness

Comparisons of invaders and non-invaders help elucidate the role of species traits in invasions (Hayes and Barry 2008). However, to learn if a trait increases the chances for a species to invade, it is key to test if the lack of this trait is involved in failed invasions. Herbert G. Baker, in his 1965 seminal paper (Baker 1965), did not systematically include failures, which was a source of later criticism of the 'ideal weed' hypothesis. Many species possessing traits considered unfavorable invade and many other species with traits

considered favorable fail to invade (Williamson and Fitter 1996b). Moreover, traits often exhibit considerable intra-specific variation and the optimal trait value is context-dependent. It is possible that a better approach would include quantitative analysis of mean trait values between invasive and non-invasive populations. Stoichiometry-based mechanisms have been also suggested as possible reasons for invasion failures, but these hypotheses remain largely untested. Under this mechanism, only individuals meeting their nitrogen and phosphorous demands would thrive, and invasion would happen when the non-natives are able to acquire these nutrients more efficiently than the natives (González et al. 2010). Without a detailed account of failed invasions, studies can overestimate the importance of traits in invasions and hide potential differences among traits that might be intrinsically related to invasiveness (e.g. length of juvenile period) (Rejmánek and Richardson 1996) and traits that might be important only in specific circumstances (e.g. shade tolerance) (Emer and Fonseca 2010).

Biotic resistance

From the examples drawn from the literature, we found biotic resistance may prevent naturalized populations from invading. Even though some evidence suggests that high levels of predation are sometimes unable to prevent spread and encroachment of populations of non-native species (Maron and Vilà 2001), competition and predation can strongly affect offspring survival and population growth of non-natives (Levine et al. 2004, Pearson et al. 2011). The existing literature on the importance of biotic resistance
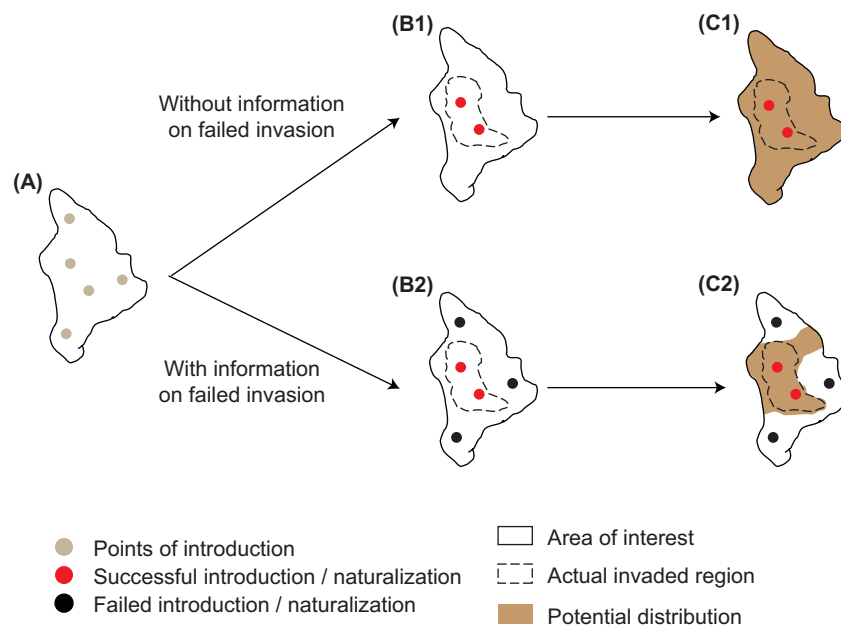

Figure 2. Information on failed invasions is important for predicting potential distributions of invasive species within an area of interest (e.g. bioclimatic, biogeographical or geopolitical regions). Given (A), several introduction events, it is expected that (B) some introductions will not thrive (black dots) while others may invade (red dots), forming an invaded area (dashed area). If the data on the failed naturalizations/invasions are lacking (B1), it would be easy to misestimate the invasive species potential distribution (C1), and it would be impossible to distinguish from a more accurate model (C2). However, if data on failed naturalizations/invasions exist (B2) and failures are because of deterministic causes, it becomes feasible to subtract unsuitable regions from the potential area based on the failures and obtain a more accurate prediction (C2).

in invasion failures is limited. Currently, we do not know when biotic resistance causes invasion of introduced populations to fail because most experiments use species that have already overcome the naturalization barrier in the studied system (Maron and Vilà 2001, Levine et al. 2004). For example, many studies on biotic resistance focus on comparisons between 'weak' and 'strong' invaders (Pearson et al. 2011) or between invasive and native species (Blaney and Kotanen 2001). More powerful tests of the role of biotic resistance would include known invaders that are failing to invade in the studied system (Nuñez et al. 2008).

Genetic effects

To understand if genetic factors determine invasion outcomes, it can be important to consider failed invasions. For example, failure may be important for understanding the role of genetic diversity, hybridization, and other factors associated with the genetic structure of non-native populations that affect invasions (Hardesty et al. 2012). Incorporating failures in studies of genetic processes related to invasions might be especially important when populations undergo sudden changes in behavior (e.g. from innocuous to aggressive colonizer), since these changes can be associated with admixture, novel genotypes, or adaptation and help explain variation in invasiveness and evolution of increased competitive ability (EICA). Also, invasion failures can certainly be valuable in studies of genotype-by-environment interactions in introduced ranges, because intraspecific comparisons between successes and failures could help elucidate mechanisms producing fitness variations in different environments using empirical studies (Lee 2002). Finally, genetic data for failures can improve our understanding of factors typically associated with invasion failures but with little direct evidence supporting their importance, such as bottlenecks (Fridley et al. 2007, Roman and Darling 2007).

Studies on invasibility and invasiveness

Ignoring failed naturalizations can also result in erroneous predictions about invasibility of habitats or about the invasiveness of certain taxa. For example, previous studies based only on successful naturalizations show islands as inherently more invasible than continents (Lonsdale 1999). However, when successful and failed naturalizations are taken into account, overall rates of naturalization between islands and continents did not differ (Diez et al. 2009). If failures were ignored, the probability of success would have been overestimated for most species (Diez et al. 2009). Even well-established patterns, such as the tens rule (Williamson 1996), are impossible to test given the lack of reports on failed invasions and the bias to report only successful invasions (Rodriguez-Cabal et al. 2013). Without solid data on failed invasions, it is hard to detect if some taxa are intrinsically more invasive than others or if some habitats are more invasible than others.

When it may not be important to consider failed invasions

The absence of studies of failed invasions may not be problematic for several areas of research. For example, studying the impact of invasive species is a key question in conservation biology, and understanding failed invasions may be of little significance. Also, it may not be relevant to know about failed invasions when comparing attributes in the native vs introduced ranges of species (Hierro et al. 2005).

Discussion

After reviewing many cases of species that exhibit invasive and non-invasive populations, it is clear that failed invasions are a common outcome of species introductions and that species show intraspecific variation in invasion success (Table 1). We found five mechanisms associated with failures: low propagule pressure, abiotic resistance, biotic resistance, limited or inappropriate gene pool and lack of mutualists (Fig. 1). If studies do not take into account the number of introduction attempts and intraspecific differences between invasive and non-invasive populations, the estimates of intrinsic invasiveness of a species may be biased. Moreover, failed invasions may be one key component for understanding and controlling invasive populations, because understanding what makes a species that is highly invasive elsewhere fail to invade can be crucial to improve its effective control. Understanding when and why populations of invasive species fail to invade is as important as understanding when and why they invade.

Despite the importance of understanding invasion failures, there are key aspects to consider when determining if an exotic species truly failed to invade. For instance, a long residence time is sometimes necessary for the species to overcome a lag phase (Caley et al. 2007, Crooks 2011), and, in fact, many non-native populations do experience a delay between introduction and the first instance of invasion (Kowarik 1995, Daehler 2009, Simberloff et al. 2010). Some cases indicated in the literature as failed invasions could be of a species undergoing a lag phase. However, in many cases the populations are established for several decades and still have not invaded. With increased residence time, it is possible that site conditions may change, that other genotypes able to trigger invasion will arrive, or that populations may evolve, allowing the species to invade. Some examples of niche evolution suggest that this can be the case (Fitzpatrick et al. 2007, Medley 2010). Even if a population's invasive status changes because of ecosystem changes or evolutionary dynamics, it is still important to understand why under the current circumstances the population is not invading.

After reviewing the current literature, we identified two main gaps. First, the data on failed invasions are circumstantial and not easily accessible; and second, comprehensive comparisons of successful and failed invasions, especially comparisons at the same stage of invasion (e.g. before or after naturalization) are still rare. Long-term monitoring and early detection programs are probably good sources of information for identifying and tracking species introductions and variations in population size that could lead to local extinction or invasion. Also, the literature has many anecdotal notes of regions where populations of invasive species are not invading and comparative studies between these introduced ranges could be made.

For instance, the biological control literature has kept excellent records of successful and failed introductions (Julien and Griffiths 1998). In many cases, the type of data needed to be collected to address questions on failed invasion can be the same as data collected to answer questions on successful or potential invasions. Each question and hypothesis will demand different types of data, but information on date of arrival, number of individuals initially present, number and origin of source populations, type and reason for introduction, and genetic variation can be fundamental for studies of failures. With these data available, researchers would be able to draw strong inferences about the importance and strength of the mechanisms proposed to predict and explain the outcome of species introductions. Ideally, researchers would start collecting data on introduced populations just after the introduction or first detection, especially for populations of species invasive elsewhere.

Invasion biology is a science with many biases and constraints because species are never introduced from a random sample and they are not introduced to random places. The taxonomic and geographic biases of introduced species, donor regions, and recipient habitats complicate many analyses. Ignoring failed invasions may hinder our understanding of the process of invasion, especially for some research topics such as species distribution modeling and analyses of historical factors associated with invasions. The limited number of studies on failed invasions has already provided some important insights to invasion biology, and more studies on failed invasion can only promote a deeper understanding of the invasion process.

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