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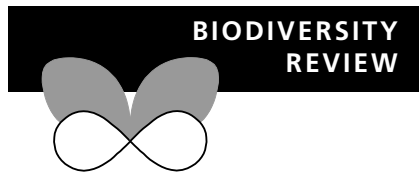


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Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential

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ABSTRACT

The damaging effects of invasive organisms have triggered the development of Invasive Species Predictive Schemes (ISPS). These schemes evaluate biological and historical characteristics of species and prioritize those that should be the focus of exclusion, quarantine, and/or control. However, it is not clear how commonly these schemes take microevolutionary considerations into account. We review the recent literature and find that rapid evolutionary changes are common during invasions. These evolutionary changes include rapid adaptation of invaders to new environments, effects of hybridization, and evolution in recipient communities. Strikingly, we document 38 species in which the specific traits commonly associated with invasive potential (e.g. growth rate, dispersal ability, generation time) have themselves undergone evolutionary change following introduction, in some cases over very short (≤ 10 year) timescales. In contrast, our review of 29 ISPS spanning plant, animal, and microbial taxa shows that the majority (76%) envision invading species and recipient communities as static entities. Those that incorporate evolutionary considerations do so in a limited way. Evolutionary change not only affects the predictive power of these schemes, but also complicates their evaluation. We argue that including the evolutionary potential of species and communities in ISPS is overdue, present several metrics related to evolutionary potential that could be incorporated in ISPS, and provide suggestions for further research on these metrics and their performance. Finally, we argue that the fact of evolutionary change during invasions begs for added caution during risk assessment.

Keywords

Climate matching, hybridization, invasion resistance, lag phase, microevolution, risk assessment.

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INTRODUCTION

Invasive species cause significant environmental damage, leading to changes in the structure and composition of communities (e.g. Fritts & Rodda, 1998; O'Dowd *et al.*, 2003) and the alteration of ecosystem-level processes and services (e.g. nitrogen cycling; Vitousek *et al.*, 1987). Globally, the annual costs of invasive species are in excess of \$US335 billion, the combined figure for just six large nations (Pimentel *et al.*, 2000). Furthermore, although proportions vary among taxa, many species introductions are deliberate rather than accidental (e.g. at least 72% of the 290 plants naturalized in Australia during 1971–95, Nairn *et al.*, 1996), suggesting that – given adequate resources and political will – we have the potential to limit future introductions of damaging species. Therefore, schemes that assess and rank the invasion potential of particular species are potentially of great utility.

Invasive species predictive schemes (hereafter ISPS; see Mack, 1996; Simberloff & Alexander, 1998; Kolar & Lodge, 2001; Panetta *et al.*, 2001; NRC, 2002; Keller, Lodge & Finnoff, 2007) are focused either prospectively or retrospectively. Some are designed to screen out high-risk species from those proposed for importation, while others aim to prioritize management efforts for accidental introductions or existing non-native species assemblages. Here, we define ISPS broadly, including not only risk assessment schemes (designed to assess future risk, and including assessment of environmental or economic consequences; NRC, 2002), but also schemes that associate species attributes with past establishment or invasive success, regardless of consequences (e.g. Marchetti *et al.*, 2004; Richardson & Rejmánek, 2004). A recent analysis (Keller, Lodge, & Finnoff, 2007) suggests that, at least in the case of an Australian ISPS for ornamental plant introductions, the economic benefits of screening out actual invasives have far

outweighed the costs of the 'false positives' (non-invasive, economically beneficial species that are misclassified and thus denied entry).

Criteria utilized in ISPS commonly fall into four categories: (1) biological attributes of the target organism, e.g. seed mass and generation time in plants, Richardson & Rejmánek (2004); (2) the distribution and historical pest status of the target organism in other regions (e.g. Scott & Panetta, 1993), sometimes also including consideration of the target's relatedness to other species that are invasive; (3) match of the target organism to the abiotic conditions of the area of concern, especially climate (e.g. Bomford, 2003); and (4) potential impacts of an invader, including biological and economic impacts (e.g. Randall *et al.*, 2001; Baker *et al.*, 2005). Information relevant to these criteria is then formalized, typically using decision-trees or invasiveness indices. In the former, attributes of the species guide the user through a series of binary choices, leading to a categorical assessment of risk, e.g. 'high', 'low', or 'further study needed'. In the latter, attributes of the species are scored numerically resulting in a continuous index of invasiveness.

We suggest that evolutionary change is common in invasive populations and in species comprising invaded ('recipient') communities, leading us to call into question the effectiveness of ISPS that treat species and recipient communities as static entities with fixed sets of traits. Although it has been briefly noted that evolution is a factor complicating predictions of invasive potential (Simberloff & Alexander, 1998; White & Schwarz, 1998), others have suggested that evolution may rarely be sufficient to change the fundamental niches of invaders (see Holt *et al.*, 2005) or that it is unimportant relative to plasticity (Rejmánek *et al.*, 2005). Thus, we believe the ramifications of evolutionary change for invasion predictions have been insufficiently explored.

In this paper, we review the accumulating evidence of rapid evolutionary change in invading plant and animal populations, particularly targeting examples in which the evolution affects traits thought to be causally associated with invasive behaviour. In addition, we highlight evolutionary change (also sometimes quite rapid) in recipient communities that could affect resistance to invasion. Our goal is not to provide a comprehensive review of evidence for evolutionary change during invasion (for recent excellent reviews, see Lee, 2002; Cox, 2004; Strauss *et al.*, 2006; Dlugosch & Parker, 2008), but to emphasize the types of evolutionary change that might influence the predictive power of ISPS. We then review 29 ISPS, focusing on the extent to which each explicitly or implicitly incorporates the potential for evolutionary change. We then provide suggestions for how revised schemes might function.

Rapid evolutionary change can occur in invading populations

Theoretical considerations suggest that invading populations should be prime candidates for both adaptive and non-adaptive evolutionary change. Introduced populations are often subject to founder effects and genetic bottlenecks (Brown & Marshall, 1981;

Dlugosch & Parker, 2008), opportunities for hybridization (Abbott, 1992; Ellstrand & Schierenbeck, 2000; Bleeker *et al.*, 2007), and a host of novel selective pressures (Mooney & Cleland, 2001; Sakai *et al.*, 2001). Furthermore, the rapid population growth characteristic of many invaders is expected to promote adaptive evolution, in that expanding populations should be better able to withstand (and respond to) strong directional selection that might drive non-expanding populations to extinction (Reznick & Ghalambor, 2001).

In keeping with these expectations, a large and rapidly growing body of literature has found widespread evidence of rapid evolutionary change in invading populations (reviewed in Mack *et al.*, 2000; Mooney & Cleland, 2001; Sakai *et al.*, 2001; Lee, 2002; Ashley *et al.*, 2003; Stockwell *et al.*, 2003; Cox, 2004; Lambrinos, 2004; Bossdorf *et al.*, 2005; Barrett *et al.*, 2008; Dlugosch & Parker, 2008; Suarez & Tsutsui, 2008). Here, we follow Hairston *et al.* (2005) in defining 'rapid' evolutionary change as 'genetic change occurring rapidly enough to have a measurable impact on simultaneous ecological change'. The types of traits and species that have undergone evolutionary change are diverse, and go far beyond the well-known evolution of resistance to anthropogenically applied pesticides, herbicides, and biocontrol agents, although admittedly those examples can be quite dramatic (Rosenheim *et al.*, 1996; Hufbauer & Roderick, 2005).

Evolution via natural selection

Exhaustive reviews are available elsewhere (see above); again, our aim is to use key examples to emphasize the types of evolutionary change relevant to the predictive power of ISPS. Two well-studied invasive plant species show evolutionary responses to broadly different selective pressures. Maron *et al.* (2004) demonstrated that *Hypericum perforatum* (St. John's wort), in response to the climatic conditions of its introduced range in North America, has rapidly evolved adaptive latitudinal clines in key morphological and life-history characteristics since its introduction about 150 years ago. Although introduced accessions did not uniformly outperform native accessions in the introduced range, locally adapted phenotypes were apparent in the replicated common gardens. In northern gardens, introduced plants collected from northern latitudes outperformed introduced plants collected from southern latitudes, while the reverse was true in southern gardens. Importantly, amplified fragment length polymorphism-based phylogenetic analyses strongly suggested that adaptation arose *in situ*, rather than reflecting multiple introductions of preadapted plant material from climatically matched areas of the native range. Whereas *Hypericum* has clearly evolved in response to the abiotic environment, *Silene latifolia* has apparently responded to biotic conditions, specifically natural enemies. The plant was introduced to North America from Europe c. 200 years ago, and experiences less herbivore attack in the introduced range (Wolfe, 2002). During this period, *Silene* has apparently evolved to allocate resources away from defence against herbivores and fungal pathogens and towards enhanced reproduction, as evidenced by 20 native and 20 introduced accessions planted in common gardens in the introduced and native ranges (Blair & Wolfe,

2004; Wolfe *et al.*, 2004). In both cases, evolution has produced phenotypes better adapted to the novel environments in which the invaders find themselves. While specific tests have not been done, these adaptations presumably have population-dynamic consequences, i.e. have increased the degree of invasiveness.

Interestingly, rapid adaptation in invasive species has apparently happened even when there are large losses of allelic diversity and heterozygosity due to bottlenecks (reviewed in Dlugosch & Parker, 2008). For example, the plant *Hypericum canariense* has lost 45% of its heterozygosity in its move from the Canary Islands to North America and the Pacific, yet has still evolved a (presumably adaptive) latitudinal cline in flowering time (Dlugosch & Parker, 2008).

Evolution in conjunction with hybridization

Introgressive hybridization, the exchange of genetic material between species through backcrossing, has long been suspected to be capable of providing novel genetic combinations which might precede adaptation and evolutionary diversification (Anderson, 1949; Stebbins, 1959), particularly in plants. These considerations mesh with more recent observations that many invasive plants (28 cases, Ellstrand & Schierenbeck, 2000) and some invasive animals (Facon *et al.*, 2005) have a history of hybridization and suggest that hybridization, followed by natural selection, may be a route to rapid evolution of invasive phenotypes. Cases include those in which a non-native species has hybridized with a native species, or in which two non-natives have hybridized to form a new lineage or taxon (e.g. *Raphanus raphanistrum* and *R. sativus*, see below). Such hybridization following species introductions may not be uncommon. Abbott (1992) calculated that, of the 1264 non-native plant taxa present in the British Isles in 1991, 70 (approximately 5.5%) had arisen by hybridization between native and introduced taxa, and an additional 21 (1.7%) were derived from hybridization between two introduced taxa. Similarly, 75 native-introduced hybrids have been detected in the German flora (Bleeker *et al.*, 2007).

While an analysis at the scale of plant families did not find a positive relationship between hybridization propensity and formation of invasive species (Whitney *et al.* in press), there are clear individual examples (Campbell *et al.*, 2006; Whitney *et al.*, 2006). A well-documented case is in radish, genus *Raphanus*. Two species of Eurasian origin were introduced to California by the 1800s, 'wild' radish *R. raphanistrum* and the crop radish *R. sativus*. The former became a serious weed. However, the identity of the invading populations have changed over time, as hybridization between the two species has produced a genetically and phenotypically novel taxon now known as 'feral' *R. sativus*. This taxon has displaced the pure populations of *R. raphanistrum* (Panetsos & Baker, 1967; Hegde *et al.*, 2006). Recent work (Campbell *et al.*, 2006) experimentally recreated early generation *R. raphanistrum* × *R. sativus* hybrids and demonstrated that, following just three generations of natural selection in the field, hybrids outperformed both parental species (nearly tripling seed production) in the novel environment of California. This experimental work corroborates the suggestion that a combination

of hybridization and natural selection was responsible for the evolution of increased invasiveness in radish.

Clearly, more work is needed to establish the general relationship between hybridization and the evolution of invasiveness in plants, animals, and other groups. A related issue is whether similar processes may be at work when different lineages come together in the introduced range. Given that multiple introductions and admixture of different source populations are not uncommon in species introductions (Novak & Mack, 2005), one might expect that novel genetic and phenotypic combinations might arise following even intraspecific sexual reproduction. This process has been postulated to underlie at least part of the invasive success of the lizard *Anolis sagrei*; secondarily invasive populations in Hawai'i, Taiwan, and other locales are likely intraspecific hybrids derived following multiple introductions into south Florida, USA (Kolbe *et al.*, 2004). However, a recent experimental test in a different system (the plant *Silene latifolia*; Wolfe *et al.*, 2007) found no evidence that intraspecific admixture is associated with invasive success.

Hybridization involving an exotic species can also have evolutionary consequences for native species via gene exchange. Novel fitness-related alleles may be transferred to wild populations with potential consequences for community composition and stability. These concerns are magnified when the invader is a genetically modified organism (GMO) carrying transgenes, which by their design have powerful effects on fitness (e.g. Snow *et al.*, 2003). In addition, under certain circumstances, native species can undergo 'extinction via hybridization' (Rhymer & Simberloff, 1996; Ellstrand & Schierenbeck, 2000; Bleeker *et al.*, 2007). This may occur if asymmetric introgression from the exotic dilutes the native gene pool, or if gamete wastage (due to hybrid infertility/sterility) consistently reduces a native's population growth rate below unity.

Rapid evolutionary change in traits associated with invasiveness is widespread

The idea that certain traits might drive colonization and/or invasion success has a long history, tracing back at least to Darwin (1859). A modern touchstone has been Baker's (1974) characterization of the 'ideal weed', which emphasized a capacity for sexual or asexual reproduction, rapid growth to maturity, phenotypic plasticity, and broad environmental tolerance. However, observations that these traits were present in some non-invasive species (and absent in some invasive species) suggested the Baker scheme may be of limited utility (Perrins *et al.*, 1992; Mack, 1996). More recently, the search for invasive traits has been improved by systematic analyses of regional floras and invasives lists (e.g. Pyšek *et al.*, 1995; Daehler, 1998) and multivariate statistical approaches (e.g. Perrins *et al.*, 1992; Richardson & Rejmánek, 2004).

Although no traits can universally predict invasiveness across all taxa and biomes, substantial progress has been made in identifying traits associated with invasiveness within specific taxa and specific habitats or regions (reviewed in Mack *et al.*, 2000; Kolar & Lodge, 2001; Sakai *et al.*, 2001; Rejmánek *et al.*, 2005;

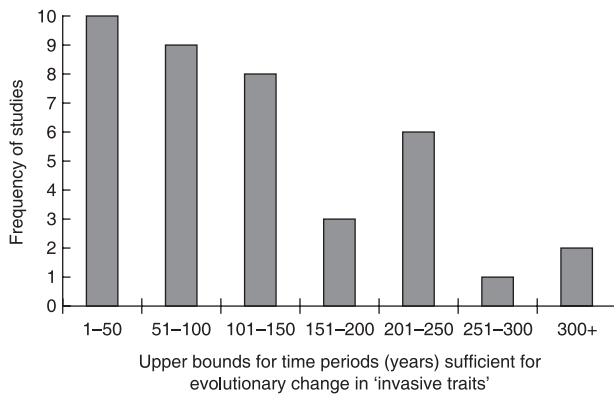


Figure 1 Distribution of upper bounds of the time periods (years) over which evolutionary change in important traits (see Appendix S1 in Supplementary Material) has been realized in invading species. The first bar includes four species with timeframes of ≤ 10 years, four with timeframes of ≤ 20 years, and one each with timeframes of ≤ 30 and ≤ 50 years. Each species in Appendix S1 has been counted once, except *Carpodacus mexicanus* and *Senecio vulgaris* (each counted twice because independent estimates of change in different traits were obtained from different populations) and *Poa bulbosa* (excluded as timeframe uncertain).

Pyšek & Richardson, 2007). Some of these key traits are: (1) high growth rate, (2) wide climatic or environmental tolerance, (3) short generation time, (4) prolific or consistent reproduction, (5) small seed or egg size, (6) good dispersal, (7) high capacity for uniparental reproduction, (8) absence of specialized germination or hatching requirements, (9) high competitive ability, and (10) ability to escape or survive natural enemies (for references, see Appendix S1 in Supplementary Material).

We found that evolutionary changes in these very traits are common, as evidenced by our compilation of 82 cases from 38 invading plant and animal species (Appendix S1). Each of the 10 traits examined shows evidence consistent with evolutionary change in multiple (four to 14) species. All the documented timeframes may be considered rapid on evolutionary and even ecological scales (Fig. 1). Significant change may occur over very short periods, highlighted by the eight species for which evolutionary trait change has occurred in 20 or fewer years (Fig. 1, Appendix S1). An important consideration is the amount of evidence supporting the genetic nature of the observed changes (see Appendix S1, rightmost column). Field observations, though informative, cannot rule out phenotypic plasticity or maternal effects as sources of observed variation. Common garden and reciprocal transplant experiments control for phenotypic plasticity by providing uniform environments in which individuals from different populations are reared. However, single-generation common gardens are still susceptible to maternal effects. Studies utilizing common gardens or reciprocal transplants that also include either tests capable of ruling out maternal effects or methodological steps sufficient to avoid maternal effects (such as rearing a pilot generation) furnish the strongest evidence for evolutionary change. All studies may produce erroneous results if the invasive populations are compared to inappropriate source

populations, highlighting the importance of using historical records and phylogenetic information to choose source populations during experimental design.

The direction of change in invasiveness-associated traits can provide particular insights into the invasion process. While most of the compiled examples (Appendix S1) demonstrate changes in expected directions (e.g. cane toads have evolved longer legs and correspondingly greater rates of spread during their invasion of Australia, Phillips *et al.*, 2006), potentially counterintuitive scenarios exist. For example, rather than observing the expected shift towards increased dispersal ability following introduction, reduced dispersal capabilities may be observed in certain types of invasions. Several wind-dispersed plants that recently colonized small islands in Canada have evolved smaller pappi and heavier achenes, which reduce their dispersal ranges but presumably have arisen by selection against individuals whose seeds land in the sea (Cody & Overton, 1996). In a second example, the 1609 introduction of wild parsnip to North America was followed initially by a reduction in chemically mediated herbivore resistance (Zangerl & Berenbaum, 2005), as predicted by the evolution of increased competitive ability (EICA) hypothesis (Blossey & Nötzold, 1995). However, this trend reversed around 1890; furanocoumarin levels in invading populations increased to match or exceed native-range levels, apparently in response to the accidental introduction of a specialist herbivore (Zangerl & Berenbaum, 2005). Other complex patterns of change in invasiveness-related traits may support the hypothesis that invasions are composed of multiple distinct stages (i.e. colonization, establishment, and spread), that particular traits are more or less important in different stages, and that the direction of selection on a given trait may change significantly over the full course of an invasion (Sakai *et al.*, 2001; Kolar & Lodge, 2002; Dietz & Edwards, 2006). In any case, this large number of examples clearly demonstrates that traits associated with invasive potential are anything but static, fixed characteristics of species.

An area of important future research is whether post-introduction evolutionary change can make the difference between successful and failed invasions, or whether such change mainly acts to increase invasiveness in taxa that would have been successful anyway. The former scenario has been suggested for Argentine ants invading North America. A genetic bottleneck has led to founding populations depauperate in recognition alleles, apparently resulting in an invasive phenotype with reduced intercolony aggression, increased cooperation, and the ability to form 'supercolonies' (Suarez & Tsutsui, 2008). However, whether this evolved phenotype explains all or just part of the invasive success of the ant is unresolved. Another suggestive case involves invasion of New Zealand by North American Chinook salmon. During colonization of a secondary drainage, evolution increased survival by 95% and a combined survival/fecundity measure by 164% relative to the population in the original drainage to which the fish were introduced (Kinnison *et al.*, 2008). These radical changes in population dynamic parameters during expansion of the invasion front occurred in less than 100 years (≈ 26 generations). While these data do not tell us whether evolutionary change was critical during the initial colonization of New Zealand, they do suggest

that evolution is capable of quite dramatic shifts in invasiveness. A general approach to this issue would be to compare source to evolved post-introduction populations in common environments in the introduced range, making the assumption, by necessity, that current native range source material is equivalent to the historical founding material. Demographic measurements and modelling could then be used estimate population growth rates. If λ were ≤ 1 for the source populations and > 1 for the post-introduction populations, evolutionary change would be supported as a key factor in the success of a given invasion.

Rapid evolutionary change can occur in recipient communities

Accumulating recent evidence (reviewed in Mooney & Cleland, 2001; Strauss *et al.*, 2006) demonstrates that invasive species can drive both natural selection and evolutionary response in the communities into which they integrate ('recipient communities'). Given that the most problematic invaders are recognized as such *because* they have large ecological impacts on recipient communities, it is perhaps unsurprising that strong selective pressures on native taxa are generated. However, the rapidity of the evolutionary responses is striking. In the examples detailed below, evolutionary change has been observed on timescales of 30–120 years, while other examples (e.g. Singer *et al.*, 1993; Cousyn *et al.*, 2001) suggest evolutionary change within a decade or less.

Evolution in competitive interactions in recipient communities

In grasslands of western North America, the Eurasian knapweed *Centaurea maculosa* is a superior competitor and has reached high levels of dominance. Its success has been attributed to an allelopathic root exudate (+/-)-catechin (Callaway *et al.*, 2005), although the toxicity of this chemical, its environmental abundance, and its importance relative to other *C. maculosa* allelochemicals have been questioned (Blair *et al.*, 2005). Regardless of the mechanism of competition, tests using native grasses from invaded and uninvaded sites have shown that populations of at least three species have apparently evolved increased resistance to *C. maculosa* in less than 30 years (Callaway *et al.*, 2005). While these resistant populations remain competitively inferior to *Centaurea* at present, over the long-term, further evolution of resistance may result in a resurgence of some native species and decreased dominance of the invasive (Callaway *et al.*, 2005). Similar evolution of competitive ability may be occurring in native grasses exposed to the invasive *Acroptilon repens* in Wyoming, USA (Mealor & Hild, 2007) and in native *Lotus* populations exposed to the invasive forb *Medicago polymorpha* in California, USA (Lau, 2006).

Evolution in predatory and herbivorous interactions in recipient communities

Phillips & Shine (2004, 2006) have demonstrated rapid evolution in native Australian black snakes (*Pseudechis porphyriacus*).

Invasive cane toads (*Bufo marinus*) pose a problem for the snakes because they contain bufodienolide cardiotoxins novel to Australia, which has no native species of bufonids. In less than 60 years (23 generations for *Pseudechis*), the snakes have evolved increased resistance to the toxin, decreased preference for the toad, and reduction in head size (which is correlated with reduced consumption of large prey items such as toads). These attributes show a predictable spatial pattern across snake populations, with a positive correlation between toxin resistance and years since the toad invasion front passed through. The toads are apparently evolving as well; both toad body size and toxicity have decreased since introduction (Phillips & Shine, 2005). Similar post-invasion evolutionary changes in predator/herbivore traits have been found in native insects confronted with novel host plants (Singer *et al.*, 1993; Carroll *et al.*, 2005), and are likely occurring in native parasitoids faced with novel host insects, given a pattern of increasing parasitoid richness with time since host introduction (Cornell & Hawkins, 1993).

Evolutionary changes in recipient communities may change our predictions about invasions in counterintuitive ways. For example, increased toxin resistance in the native snakes in *B. marinus*-invaded communities should logically decrease invasive potentials of novel species expressing the same or similar compounds. Given phylogenetic conservatism in chemical profiles of many organisms (and in ecological similarity generally; Webb *et al.*, 2002), the potential introductions most affected would likely be close relatives of the current invaders. Thus, a central criterion of many ISPS (having invasive relatives uniformly increases a taxon's invasive potential, e.g. Pheloung *et al.*, 1999; Weber & Gut, 2004) may be less valid in cases where the relatives have previously invaded the region under consideration. However, this idea requires much further testing before changes to ISPS are warranted.

Invasive species predictive schemes underestimate the potential for evolutionary change

We searched both published and grey literature for ISPS, focusing on those schemes with a clearly defined procedure resulting in an invasiveness score or classification (Table 1). We did not include guideline documents without such procedures (e.g. IPPC, 2004) or schemes that represented only minor modifications of an existing scheme (e.g. Daehler *et al.*, 2004). When several versions of a scheme were found, we excluded early versions and included only the most recent.

Of the 29 predictive schemes examined, the majority (76%) do not explicitly incorporate evolutionary considerations (Table 1). Importantly, no single ISPS recognizes all three of the areas of concern that we highlight (hybridization potential of invader, adaptive potential of invader, and evolutionary potential of the recipient community), and only two schemes (7%) recognize two of the three areas.

The most commonly cited evolutionary consideration is hybridization potential (six schemes or 21%; Table 1). In some cases, the justification for concern is that hybridization is associated with increased invasiveness in the target taxon itself (e.g. Randall

Table 1 Invasive Species Predictive Schemes (ISPS) for assessing invasion potential and the extent to which they incorporate the potential for evolutionary change.

Predictive scheme	Evolutionary criteria recognized:			Method type	Target taxa	Target region(s)
	Hybridization potential	Adaptive potential	Evolution in recipient community			
Perrins <i>et al.</i> (1992)*	–	–	–	Index†	Annual plants	Great Britain
Smallwood & Salmon (1992)	–	–	–	Index	Birds, mammals	California, USA
Hiebert & Stubbendieck (1993)*	–	Y	–	Index	Plants	National Parks, USA
Panetta (1993)	–	–	–	Decision Tree	Plants	Australia
Scott & Panetta (1993)	–	–	–	Index‡	Southern African plants	Australia
Tucker & Richardson (1995)	–	–	–	Decision Tree	'Canopy dominant weeds' (woody plants)	Fynbos biome, South Africa
Veltman <i>et al.</i> (1996)*	–	–	–	Index‡	Birds	New Zealand
Reichard & Hamilton (1997)§	–	–	–	Decision Tree	Woody plants	North America
Goodwin <i>et al.</i> (1999)	–	–	–	Index‡	European plants	New Brunswick, Canada
Pheloung <i>et al.</i> (1999)	Y	–	–	Index	Plants	Australia and New Zealand
Maillet & Lopez-Garcia (2000)	–	–	–	Index†	American agricultural weeds	France
USDA (2000)	–	–	–	Index	Plants and pests of plants	USA
CFIA (2001)	–	–	–	Index	Pests of plants	Canada
Champion & Clayton (2001)	–	–	–	Index	Aquatic plants	New Zealand
Randall <i>et al.</i> (2001)*	Y	–	–	Index	Plants	California, USA
Timmins & Owen (2001)*	–	–	–	Index	Plants	Natural Areas, New Zealand
Virtue <i>et al.</i> (2001)*	–	–	–	Index	Plants	Australia
Kolar & Lodge (2002)	–	–	–	Decision Tree, Index†	Fishes	Great Lakes, North America
Bomford (2003)	Y	–	–	Index	Vertebrate animals	Australia
Marchetti <i>et al.</i> (2004)*	–	–	–	Index‡	Fishes	California, USA
Richardson & Rejmánek (2004)	–	–	–	Index†	Conifers	Global
Weber & Gut (2004)	–	–	–	Index	Plants	Central Europe
Widrechner <i>et al.</i> (2004)	–	–	–	Decision Tree¶	Woody plants	Iowa, USA
Baker <i>et al.</i> (2005)	Y	Y	–	Index	All organisms	UK
Bomford <i>et al.</i> (2005)	–	–	–	Index	Reptiles and amphibians	Australia
Fox <i>et al.</i> (2005)*	Y	–	–	Decision Tree	Plants	Natural Areas, Florida, USA
Caley & Kuhnert (2006)	–	–	–	Decision Tree**	Plants	Australia
EPPO (2006)	Y	Y	–	Decision Tree + Expert Judgement	Plant, arthropod, and microbial pests of agricultural habitats	Europe and Mediterranean Region
Keller, Drake & Lodge (2007)	–	–	–	Decision Tree, Index‡	Molluscs	USA

*Scheme focuses on invasive potential of non-native taxa that are already present in target community, rather than on potential arrivals.

†Index based on discriminant function.

‡Index based on logistic regression.

§While *past* hybridization together with seed sterility is negatively correlated with invasiveness in this scheme, future hybridization potential is not considered.

¶We evaluate their 'regional model' (also called the 'new CART model'), not their application of the Reichard & Hamilton (1997) model.

**We evaluate their final 'optimal classification tree', not their application of the Pheloung *et al.* (1999) model.

Method type: 'Index' = a quantitative index or score is produced of the target taxon's risk of invasiveness or invasive impact; 'Decision Tree' = a categorical evaluation of the target taxon (e.g. low risk, high risk) is determined by a series of dichotomous choices.

et al., 2001), while in others it is the transfer of undesirable genes (particularly transgenes) to native species (Bomford, 2003; Baker *et al.*, 2005; EPPO, 2006) or genetic assimilation of native taxa or 'extinction via hybridization' (Fox *et al.*, 2005).

Only three schemes (10%) consider the adaptive potential of the target taxon (Table 1), recognizing that rapid evolutionary change may allow an invasive plant or plant pest, for example, 'to withstand environmental fluctuations, to adapt to a wider range of habitats or hosts, to develop resistance to [herbicides or pesticides] and to overcome host resistance' (EPPO, 2006; p. 13). To some extent, schemes that consider an 'invasive elsewhere' criterion may implicitly consider adaptive potential, in that they will flag taxa that regularly become invasive via this route. However, this is likely a poor surrogate for explicit consideration of adaptive potential; the 'invasive elsewhere' criterion will not catch taxa with high adaptive potential if they do not have a history of introductions elsewhere.

None of the schemes recognize that evolution in recipient communities can alter the impacts and probability of successful invasions (Table 1). However, as we discuss below, the only practical way to incorporate this information may be to acknowledge that risks of false negatives (dangerous species allowed entry) are greater than suggested by standard retrospective analyses. Evolutionary changes in recipient communities underscore the dynamism of the invasion process. Importantly, these changes can be expected to influence the outcomes of future introductions of new species. Alterations in competitive and predatory interactions (above) and presumably, in mutualistic interactions, should change the dimensions of niche space and alter 'matching' between potential invaders and a given community and ecosystem.

Evolutionary change impedes the evaluation of ISPS performance

A well-known characteristic of some invasions is the lag phase, a period of low population growth preceding the 'invasive' phase of rapid growth (Crooks & Soule, 1999; Groves, 2006). Documented lags range from a few years to several hundred years and affect both plants (Groves, 2006) and animals (Bomford *et al.*, 2005). Lag phases likely have diverse causes, and many may have purely ecological or demographic explanations, e.g. time needed for dispersal to more appropriate habitats within the novel range, or delays until favourable disturbance regimes are initiated. However, many have pointed out that lag phases could reflect time needed for evolutionary adaptation to the novel range (Ellstrand & Schierenbeck, 2000; Holt *et al.*, 2005). Holt *et al.* (2005) hypothesize that the length of lag phase should reflect the 'degree of difference between the novel and ancestral environments' as more evolutionary change will be required to bridge larger differences.

The presence of lag periods complicates the evaluation of ISPS performance. An ISPS is typically evaluated retrospectively, with reference to a set of exotic species already introduced to a location. Whether the scheme correctly separates known invasive from non-invasive species is then examined. Accuracy is typically defined as the percentage of correct classifications, and accuracies of 80–100% have been reported (e.g. Rejmánek & Richardson,

1996; Reichard & Hamilton, 1997; Kolar & Lodge, 2002; see Smith *et al.*, 1999 for a critical review of the utility of accuracy measurements). When these schemes are used prospectively, as their authors often recommend, the implicit assumption is that species that are currently non-invasive (and used to build the predictive algorithm) will remain so, and that the invasibility of recipient communities is static as well. Thus, ISPS will have lower-than-expected accuracy rates if species and communities undergo evolutionary changes that affect invasion dynamics. To our knowledge, the medium- or long-term stability of accuracies associated with particular ISPS have not been evaluated.

Recommendations

Our review demonstrates that rapid evolutionary change commonly occurs during species invasions, with numerous examples of change in the invaders themselves, in particular traits associated with invasiveness, and in communities of native species challenged by the invaders. It appears that exotic species are indeed 'moving targets' (Holt *et al.*, 2005), and that evolution in response to these invaders makes recipient communities 'shifting canvases' on which complex pictures of invasions and their consequences arise. Yet, the vast majority of predictive schemes treat species and recipient communities as static entities. Schemes that ignore evolution are at risk of overoptimistic claims about their accuracy, especially over the timescales (decades to centuries) over which we should be concerned about the effects of species introductions. We offer the following recommendations:

1 *The evolutionary potential of species should be incorporated into ISPS.* Hybridization potential can be incorporated as a historical attribute: does the species have a history of forming hybrids? In addition, more detailed metrics could be used. The number of closely related species already present in the recipient community (especially, the number of wild congeners of domesticates) should influence hybridization potential of an exotic. The number of rare species congeneric with an exotic could be informative, as they are potentially at risk of genetic assimilation. Finally, Simberloff & Alexander (1998) suggest that exotic species derived from groups with mainly pre-zygotic, behavioural means of reproductive isolation are a particular risk for hybridization, as there will not have been prior selection to avoid matings between the native and the introduced taxa, and hybrid offspring will often be fertile. Hybridization potential is most clearly indicated for ISPS focusing on plants, while more work is needed to understand the extent and consequences of hybridization during animal invasions and whether hybridization criteria are appropriate for animal-focused ISPS.

Several metrics could be indicative of the adaptive potential of an exotic species. The degree of sexual reproduction has been suggested as a metric (Hiebert & Stubbendieck, 1993) as it determines the rate at which beneficial combinations of alleles arise. For existing naturalized species potentially transitioning to invasive status, propagule size and number of sources (single versus multiple populations from the native range) should be influential: larger and/or admixed propagules should have more genetic variation and may be more adaptable than smaller

and/or single-source propagules (Holt *et al.*, 2005; Novak & Mack, 2005; Dlugosch & Parker, 2008). While genetic bottlenecks sometimes trigger the conversion of non-additive (epistatic or dominance) variance to additive variance, suggesting that adaptation in small founder populations may not always be constrained (Lee, 2002; Dlugosch & Parker, 2008), it remains to be seen how common this phenomenon is. Quantitative genetic variation can be directly assessed for an exotic species or propagule, although this could require substantial effort. Unfortunately, neutral genetic variation assessed via molecular markers usually is not highly correlated with patterns of adaptive genetic variation (Reed & Frankham, 2001) and therefore may be a poor metric; further evaluation is necessary. Overall, adaptive potential is a complex characteristic that will take different forms in species with different histories, life histories, and genetic architectures, and much work remains to be done (see no. 2, below).

Incorporating the fact of evolution in recipient communities into the screening component of ISPS would be very difficult. A scheme would have to first predict the attributes of the future community, and then assess how resistant or susceptible this altered community would be to potential invaders with various attributes. Instead, the risk quantification component of ISPS is the logical place to incorporate this information: awareness of the evolutionary potential of recipient communities should serve to instil greater caution in our assessment of the risks associated with species introductions (see no. 3, below).

2 More work should be done to develop better metrics for measuring evolutionary potential, and to establish the relationships between these metrics and invasive potential. The above suggestions for metrics associated with hybridization potential and adaptive potential are clearly preliminary, and much work remains to be done. Varied approaches are necessary, including compilations and meta-analyses to derive patterns as well as experimental manipulations. For plant hybridization potential, regional floras could be analysed to ask whether the incidence of invasive-native hybrids scales with the number of native congeneric species, as expected. If it does, then congeneric richness could be evaluated as a predictor of hybridization potential. For adaptive potential, existing data bases of outcrossing propensities (e.g. for plants, Goodwillie *et al.*'s (2005) data base of the outcrossing coefficient t) could be used to determine whether groups tending towards more sexual reproduction produce larger numbers of successful invaders. Such an analysis would need to take phylogenetic relatedness into account, an approach so far missing from such analyses (e.g. Rambuda & Johnson, 2004; Sutherland, 2004). Complementary experimental work could then assess whether more rapid adaptation is evident in sexual species versus asexual congeners, and whether this process can be documented in particular cases of introduced species. Finally, these analyses should examine the possibility of non-linear relationships between outcrossing rate and invasiveness. Baker's (1955) hypothesis that uniparental reproduction may be important for early colonization suggests a potential scenario in which species with low and high levels of outcrossing show high invasiveness (via colonizing success and adaptability, respectively), while those with intermediate levels show low invasiveness.

3 Greater caution is needed in interpreting the outcome of ISPS and in allowing introductions. Evolution has a large stochastic component as a result of forces such as random mutation and genetic drift, and no predictive schemes will ever reach 100% accuracy. The accuracy of ISPS needs to be re-evaluated over time to take into account species that evolve greater or lesser invasiveness, and communities that evolve altered levels of invasibility. Importantly, global change will exacerbate the issue of predictive power. Apart from direct effects of global change altering the ecological 'match' between a potential invader and a community/ecosystem (Hobbs & Mooney, 2005), global change has already influenced the evolutionary trajectories of both invaders and native species (Bradshaw & Holzapfel, 2006; Franks *et al.*, 2007). This could have the effect of making the traits of all participants in the invasion process (the invader and members of the recipient community) more dynamic through time, decreasing our ability to predict invasive potential. As several workers have pointed out (Smith *et al.*, 1999), the high cost:benefit ratio associated with invasive species risk assessments (cost of allowing an invasion:benefit of allowing introduction of a presumed non-invasive) strongly suggests erring on the side of caution.

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REFERENCES

- Abbott, R.J. (1992) Plant invasions, interspecific hybridization and the evolution of new plant taxa. *Trends in Ecology and Evolution*, **7**, 401–405.
- Anderson, E. (1949) *Introgressive Hybridization*. Chapman & Hall, London.
- Ashley, M.V., Willson, M.F., Pergams, O.R.W., O'Dowd, D.J., Gende, S.M. & Brown, J.S. (2003) Evolutionarily enlightened management. *Biological Conservation*, **111**, 115–123.
- Baker, H.G. (1955) Self compatibility and establishment after long-distance dispersal. *Evolution*, **9**, 347–349.
- Baker, H.G. (1974) The evolution of weeds. *Annual Review of Ecology and Systematics*, **5**, 1–24.
- Baker, R., Hulme, P., Copp, G.H., Thomas, M., Black, R. & Haysom, K. (2005) *UK non-native organism risk assessment scheme user manual*, v. 3.3. Central Science Laboratory, York, UK.
- Barrett, S.C.H., Colautti, R.I. & Eckert, C.G. (2008) Plant reproductive systems and evolution during biological invasion. *Molecular Ecology*, **17**, 373–383.
- Blair, A.C. & Wolfe, L.M. (2004) The evolution of an invasive plant: an experimental study with *Silene latifolia*. *Ecology*, **85**, 3035–3042.
- Blair, A.C., Hanson, B.D., Brunk, G.R., Marrs, R.A., Westra, P., Nissen, S.J. & Hufbauer, R.A. (2005) New techniques and

- findings in the study of a candidate allelochemical implicated in invasion success. *Ecology Letters*, **8**, 1039–1047.
- Bleeker, W., Schmitz, U. & Ristow, M. (2007) Intraspecific hybridization between alien and native plant species in Germany and its consequences for native biodiversity. *Biological Conservation*, **137**, 248–253.
- Blossey, B. & Nötzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants – a hypothesis. *Journal of Ecology*, **83**, 887–889.
- Bomford, M. (2003) *Risk assessment for the import and keeping of exotic vertebrates in Australia*. Bureau of Rural Sciences, Canberra, ACT, Australia.
- Bomford, M., Kraus, F., Braysher, M., Walter, L. & Brown, L. (2005) *Risk assessment model for the import and keeping of exotic reptiles and amphibians*. Bureau of Rural Sciences, Canberra, ACT, Australia.
- Bossdorf, O., Auge, H., Lafuma, L., Rogers, W.E., Siemann, E. & Prati, D. (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, **144**, 1–11.
- Bradshaw, W.E. & Holzapfel, C.M. (2006) Climate change – evolutionary response to rapid climate change. *Science*, **312**, 1477–1478.
- Brown, A.H.D. & Marshall, D.R. (1981) Evolutionary changes accompanying colonization in plants. *Evolution today, proceeding of the second international congress of systematic and evolutionary biology* (ed. by G.G.T. Scudder and J.L. Reveal), pp. 351–363. Carnegie-Mellon University, Pittsburgh, PA.
- Caley, P. & Kuhnert, P.M. (2006) Application and evaluation of classification trees for screening unwanted plants. *Austral Ecology*, **31**, 647–655.
- Callaway, R.M., Ridenour, W.M., Laboski, T., Weir, T. & Vivanco, J.M. (2005) Natural selection for resistance to the allelopathic effects of invasive plants. *Journal of Ecology*, **93**, 576–583.
- Campbell, L.G., Snow, A.A. & Ridley, C.E. (2006) Weed evolution after crop gene introgression: greater survival and fecundity of hybrids in a new environment. *Ecology Letters*, **9**, 1198–1209.
- Carroll, S.P., Loye, J.E., Dingle, H., Mathieson, M., Famula, T.R. & Zalucki, M.P. (2005) and the beak shall inherit – evolution in response to invasion. *Ecology Letters*, **8**, 944–951.
- CFIA. (2001) *Canadian PHRA rating guidelines*. Unpublished report. Canadian Food Inspection Agency, Ottawa, Ontario, Canada.
- Champion, P.D. & Clayton, J.S. (2001) A weed risk assessment model for aquatic weeds in New Zealand. *Weed risk assessment* (ed. by R.H. Groves, F.D. Panetta and J.G. Virtue), pp. 194–202. CSIRO Publishing, Collingwood, Victoria, Australia.
- Cody, M.L. & Overton, J.M. (1996) Short-term evolution of reduced dispersal in island plant populations. *Journal of Ecology*, **84**, 53–61.
- Cornell, H.V. & Hawkins, B.A. (1993) Accumulation of native parasitoid species on introduced herbivores: a comparison of hosts as natives and hosts as invaders. *The American Naturalist*, **141**, 847–865.
- Cousyn, C., De Meester, L., Colbourne, J.K., Brendonck, L., Verschuren, D. & Volckaert, F. (2001) Rapid, local adaptation of zooplankton behavior to changes in predation pressure in the absence of neutral genetic changes. *Proceedings of the National Academy of Sciences USA*, **98**, 6256–6260.
- Cox, G.W. (2004) *Alien species and evolution*. Island Press, Washington.
- Crooks, J.A. & Soule, M.E. (1999) Lag times in population explosions of invasive species: causes and implications. *Invasive species and biodiversity management* (ed. by O.T. Sandlund, P.J. Schei and A. Viken). Kluwer, New York.
- Daehler, C.C. (1998) The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. *Biological Conservation*, **84**, 167–180.
- Daehler, C.C., Denslow, J.S., Ansari, S. & Kuo, H.C. (2004) A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific Islands. *Conservation Biology*, **18**, 360–368.
- Darwin, C. (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, London.
- Dietz, H. & Edwards, P.J. (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. *Ecology*, **87**, 1359–1367.
- Dlugosch, K.M. & Parker, I.M. (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology*, **17**, 431–449.
- Ellstrand, N.C. & Schierenbeck, K.A. (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences USA*, **97**, 7043–7050.
- EPPO. (2006) *Guidelines on pest risk analysis: decision-support scheme for quarantine pests*, v. 2. European and Mediterranean Plant Protection Organization, Paris, France.
- Facon, B., Jarne, P., Pointier, J.P. & David, P. (2005) Hybridization and invasiveness in the freshwater snail *Melanooides tuberculata*: hybrid vigour is more important than increase in genetic variance. *Journal of Evolutionary Biology*, **18**, 524.
- Fox, A.M., Gordon, D.R., Dusky, J.A., Tyson, L. & Stocker, R.K. (2005) *IFAS assessment of the status of non-native plants in Florida's natural areas*. Agronomy Department, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL, USA. Available at <http://plants.ifas.ufl.edu/assessment.html>.
- Franks, S.J., Sim, S. & Weis, A.E. (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences USA*, **104**, 1278–1282.
- Fritts, T.H. & Rodda, G.H. (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annual Review of Ecology and Systematics*, **29**, 113–140.
- Goodwillie, C., Kalisz, S. & Eckert, C.G. (2005) The evolutionary enigma of mixed mating systems in plants: occurrence, theoretical explanations, and empirical evidence. *Annual Review of Ecology Evolution and Systematics*, **36**, 47–79.
- Goodwin, B.J., McAllister, A.J. & Fahrig, L. (1999) Predicting invasiveness of plant species based on biological information. *Conservation Biology*, **13**, 422–426.
- Groves, R.H. (2006) Are some weeds sleeping? Some concepts and reasons. *Euphytica*, **148**, 111–120.

- Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T. & Fox, J.A. (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters*, **8**, 1114–1127.
- Hegde, S.G., Nason, J.D., Clegg, J.M. & Ellstrand, N.C. (2006) The evolution of California's wild radish has resulted in the extinction of its progenitors. *Evolution*, **60**, 1187–1197.
- Hiebert, R.D. & Stubbendieck, J. (1993) *Handbook for ranking exotic plants for management and control*. Natural Resources Report NPS/NRMWRO/NRR-93/08. In United States Department of the Interior, National Park Service, Denver, CO, USA.
- Hobbs, R.J. & Mooney, H.A. (2005) Invasive species in a changing world: the interactions between global change and invasives. *Invasive alien species: a new synthesis* (ed. by H.A. Mooney, R.N. Mack, J.A. McNeely, L.E. Neville, P.J. Schei and J.K. Waage), pp. 310–331. Island Press, Washington DC, USA.
- Holt, J., Barfield, M. & Gomulkiewicz, R. (2005) Theories of niche conservatism and evolution: could exotic species be potential tests? *Species invasions: insights into ecology, evolution, and biogeography* (ed. by D.F. Sax, J.J. Stachowicz and S.D. Gaines), pp. 259–290. Sinauer, Sunderland, MA, USA.
- Hufbauer, R.A. & Roderick, G.K. (2005) Microevolution in biological control: mechanisms, patterns, and processes. *Biological Control*, **35**, 227–239.
- International Plant Protection Convention (IPPC) (2004) *ISPM No. 11. Pest risk analysis for quarantine pests including analysis of environmental risks and living modified organisms*. International Plant Protection Convention. Food and Agriculture Organization, Rome.
- Keller, R.P., Drake, J.M. & Lodge, D.M. (2007) Fecundity as a basis for risk assessment of nonindigenous freshwater molluscs. *Conservation Biology*, **21**, 191–200.
- Keller, R.P., Lodge, D.M. & Finnoff, D.C. (2007) Risk assessment for invasive species produces net bioeconomic benefits. *Proceedings of the National Academy of Sciences USA*, **104**, 203–207.
- Kinnison, M.T., Unwin, M.J. & Quinn, T.P. (2008) Eco-evolutionary vs. habitat contributions to invasion in salmon: experimental evaluation in the wild. *Molecular Ecology*, **17**, 405–414.
- Kolar, C.S. & Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution*, **16**, 199–204.
- Kolar, C.S. & Lodge, D.M. (2002) Ecological predictions and risk assessment for alien fishes in North America. *Science*, **298**, 1233–1236.
- Kolbe, J.J., Glor, R.E., Schettino, L.R.G., Lara, A.C., Larson, A. & Losos, J.B. (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature*, **431**, 177–181.
- Lambrinos, J.G. (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology*, **85**, 2061–2070.
- Lau, J.A. (2006) Evolutionary responses of native plants to novel community members. *Evolution*, **60**, 56–63.
- Lee, C.E. (2002) Evolutionary genetics of invasive species. *Trends in Ecology and Evolution*, **17**, 386–391.
- Mack, R.N. (1996) Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biological Conservation*, **78**, 107–121.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.
- Maillet, J. & Lopez-Garcia, C. (2000) What criteria are relevant for predicting the invasive capacity of a new agricultural weed? The case of invasive American species in France. *Weed Research*, **40**, 11–26.
- Marchetti, M.P., Moyle, P.B. & Levine, R. (2004) Alien fishes in California watersheds: characteristics of successful and failed invaders. *Ecological Applications*, **14**, 587–596.
- Maron, J.L., Vila, M., Bommarco, R., Elmendorf, S. & Beardsley, P. (2004) Rapid evolution of an invasive plant. *Ecological Monographs*, **74**, 261–280.
- Mealor, B.A. & Hild, A.L. (2007) Post-invasion evolution of native plant populations: a test of biological resilience. *Oikos*, **116**, 1493–1500.
- Mooney, H.A. & Cleland, E.E. (2001) The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences USA*, **98**, 5446–5451.
- Nairn, M.E., Allen, P.G., Inglis, A.R. & Tanner, C. (1996) *Australian quarantine: a shared responsibility*. Department of Primary Industries and Energy, Canberra, ACT, Australia.
- Novak, S.J. & Mack, R.N. (2005) Genetic bottlenecks in alien plant species: influences of mating systems and introduction dynamics. *Species invasions: insights into ecology, evolution, and biogeography* (ed. by D.F. Sax, J.J. Stachowicz and S.D. Gaines), pp. 201–228. Sinauer, Sunderland, MA, USA.
- NRC. (2002) *Predicting invasions of nonindigenous plants and plant pests*. Committee on the scientific basis for predicting the invasive potential of nonindigenous plants and plant pests in the United States, National Academy Press, Washington, DC, USA.
- O'Dowd, D.J., Green, P.T. & Lake, P.S. (2003) Invasional 'meltdown' on an oceanic island. *Ecology Letters*, **6**, 812–817.
- Panetsos, C.A. & Baker, H.G. (1967) Origin of variation in wild *Raphanus sativus* (Cruciferae) in California. *Genetica*, **38**, 243–274.
- Panetta, F.D. (1993) A system of assessing proposed plant introductions for weed potential. *Plant Protection Quarterly*, **8**, 10–14.
- Panetta, F.D., Mackey, A.P., Virtue, J.G. & Groves, R.H. (2001) Weed risk assessment: core issues and future directions. *Weed risk assessment* (ed. by R.H. Groves, F.D. Panetta and J.G. Virtue), pp. 231–240. CSIRO Publishing, Collingwood, Victoria, Australia.
- Perrins, J., Williamson, M. & Fitter, A. (1992) Do annual weeds have predictable characters? *Acta Oecologica*, **13**, 517–533.
- Pheloung, P.C., Williams, P.A. & Halloy, S.R. (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management*, **57**, 239–251.

- Phillips, B.L. & Shine, R. (2004) Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. *Proceedings of the National Academy of Sciences USA*, **101**, 17150–17155.
- Phillips, B.L. & Shine, R. (2005) The morphology, and hence impact, of an invasive species (the cane toad, *Bufo marinus*): changes with time since colonisation. *Animal Conservation*, **8**, 407–413.
- Phillips, B.L. & Shine, R. (2006) An invasive species induces rapid adaptive change in a native predator: cane toads and black snakes in Australia. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **273**, 1545–1550.
- Phillips, B.L., Brown, G.P., Webb, J.K. & Shine, R. (2006) Invasion and the evolution of speed in toads. *Nature*, **439**, 803–803.
- Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T. & Tsomondo, T. (2000) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems, and Environment*, **84**, 1–20.
- Pyšek, P. & Richardson, D.M. (2007) Traits associated with invasiveness in alien plants: where do we stand? *Biological invasions* (ed. by W. Nentwig), pp. 97–125. Springer, Heidelberg, Germany.
- Pyšek, P., Prach, K. & Smilauer, P. (1995) Relating invasion success to plant traits: an analysis of the Czech alien flora. *Plant invasions – general aspects and special problems* (ed. by P. Pyšek, K. Prach, M. Rejmánek and M. Wade), p. 263. SPB Academic, Amsterdam, The Netherlands.
- Rambuda, T.D. & Johnson, S.D. (2004) Breeding systems of invasive alien plants in South Africa: does Baker's rule apply? *Diversity and Distributions*, **10**, 409–416.
- Randall, J.M., Benton, N. & Morse, L.E. (2001) Categorizing invasive weeds: the challenge of rating the weeds already in California. *Weed risk assessment* (ed. by R.H. Groves, F.D. Panetta and J.G. Virtue), pp. 203–216. CSIRO Publishing, Collingwood, Victoria, Australia.
- Reed, D.H. & Frankham, R. (2001) How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. *Evolution*, **55**, 1095–1103.
- Reichard, S.H. & Hamilton, C.W. (1997) Predicting invasions of woody plants introduced into North America. *Conservation Biology*, **11**, 193–203.
- Rejmánek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655–1661.
- Rejmánek, M., Richardson, D.M., Higgins, S.I., Pitcairn, M.J. & Grotkopp, E. (2005) Ecology of invasive plants: state of the art. *Invasive alien species: a new synthesis* (ed. by H.A. Mooney, R.N. Mack, J.A. McNeely, L.E. Neville, P.J. Schei and J.K. Waage), pp. 104–161. Island Press, Washington DC, USA.
- Reznick, D.N. & Ghalambor, C.K. (2001) The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica*, **112**, 183–198.
- Rhymer, J.M. & Simberloff, D. (1996) Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics*, **27**, 83–109.
- Richardson, D.M. & Rejmánek, M. (2004) Conifers as invasive aliens: a global survey and predictive framework. *Diversity and Distributions*, **10**, 321–331.
- Rosenheim, J.A., Johnson, M.W., Mau, R.F.L., Welter, S.C. & Tabashnik, B.E. (1996) Biochemical preadaptations, founder events, and the evolution of resistance in arthropods. *Journal of Economic Entomology*, **89**, 263–273.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N. & Weller, S.G. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305–332.
- Scott, J.K. & Panetta, F.D. (1993) Predicting the Australian weed status of Southern African plants. *Journal of Biogeography*, **20**, 87–93.
- Simberloff, D. & Alexander, M. (1998) Assessing risks to ecological systems from biological introductions (excluding genetically modified organisms). *Handbook of environmental risk assessment and management* (ed. by P. Calow), pp. 147–176. Blackwell, Oxford, UK.
- Singer, M.C., Thomas, C.D. & Parmesan, C. (1993) Rapid human-induced evolution of insect host associations. *Nature*, **366**, 681–683.
- Smallwood, K.S. & Salmon, T.P. (1992) A rating system for potential exotic bird and mammal pests. *Biological Conservation*, **62**, 149–159.
- Smith, C.S., Lonsdale, W.M. & Fortune, J. (1999) When to ignore advice: invasion predictions and decision theory. *Biological Invasions*, **1**, 86–96.
- Snow, A.A., Pilson, D., Rieseberg, L.H., Paulsen, M.J., Pleskac, N., Reagon, M.R., Wolf, D.E. & Selbo, S.M. (2003) A Bt transgene reduces herbivory and enhances fecundity in wild sunflowers. *Ecological Applications*, **13**, 279–286.
- Stebbins, G.L. (1959) The role of hybridization in evolution. *Proceedings of the American Philosophical Society*, **103**, 231–251.
- Stockwell, C.A., Hendry, A.P. & Kinnison, M.T. (2003) Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution*, **18**, 94–101.
- Strauss, S.Y., Lau, J.A. & Carroll, S.P. (2006) Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters*, **9**, 354–371.
- Suarez, A.V. & Tsutsui, N.D. (2008) The evolutionary consequences of biological invasions. *Molecular Ecology*, **17**, 351–360.
- Sutherland, S. (2004) What makes a weed a weed: life history traits of native and exotic plants in the USA. *Oecologia*, **141**, 24–39.
- Timmins, S.M. & Owen, S.-J. (2001) Scary species, superlative sites: assessing weed risk in New Zealand's protected natural areas. *Weed risk assessment* (ed. by R.H. Groves, F.D. Panetta and J.G. Virtue), pp. 217–227. CSIRO Publishing, Collingwood, Victoria, Australia.
- Tucker, K.C. & Richardson, D.M. (1995) An expert-system for screening potentially invasive alien plants in South African fynbos. *Journal of Environmental Management*, **44**, 309–338.

- USDA. (2000) *Guidelines for pathway-initiated pest risk assessments*, v. 5.02. United States Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine, Riverdale, MD, USA.
- Veltman, C.J., Nee, S. & Crawley, M.J. (1996) Correlates of introduction success in exotic New Zealand birds. *The American Naturalist*, **147**, 542–557.
- Virtue, J.G., Groves, R.H. & Panetta, F.D. (2001) Towards a system to determine the national significance of weeds in Australia. *Weed risk assessment* (ed. by R.H. Groves, F.D. Panetta and J.G. Virtue), pp. 124–150. CSIRO Publishing, Collingwood, Victoria, Australia.
- Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Muellerdombois, D. & Matson, P.A. (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science*, **238**, 802–804.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.
- Weber, E. & Gut, D. (2004) Assessing the risk of potentially invasive plant species in central Europe. *Journal for Nature Conservation*, **12**, 171–179.
- White, P.S. & Schwarz, A.E. (1998) Where do we go from here? The challenges of risk assessment for invasive plants. *Weed Technology*, **12**, 744–751.
- Whitney, K.D., Ahern, J.R. & Campbell, L.G. (in press) Hybridization-prone plant families do not generate more invasive species. *Biological Invasions*.
- Whitney, K.D., Randell, R.A. & Rieseberg, L.H. (2006) Adaptive introgression of herbivore resistance traits in the weedy sunflower *Helianthus annuus*. *The American Naturalist*, **167**, 794–807.
- Widrechner, M.P., Thompson, J.R., Iles, J.K. & Dixon, P.M. (2004) Models for predicting the risk of naturalization of non-native woody plants in Iowa. *Journal of Environmental Horticulture*, **22**, 23–31.
- Wolfe, L.M. (2002) Why alien invaders succeed: support for the escape-from-enemy hypothesis. *The American Naturalist*, **160**, 705–711.
- Wolfe, L.M., Blair, A.C. & Penna, B.M. (2007) Does intraspecific hybridization contribute to the evolution of invasiveness? An experimental test. *Biological Invasions*, **9**, 515–521.
- Wolfe, L.M., Elzinga, J.A. & Biere, A. (2004) Increased susceptibility to enemies following introduction in the invasive plant *Silene latifolia*. *Ecology Letters*, **7**, 813–820.
- Zangerl, A.R. & Berenbaum, M.R. (2005) Increase in toxicity of an invasive weed after reassociation with its coevolved herbivore. *Proceedings of the National Academy of Sciences USA*, **102**, 15529–15532.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article

Appendix S1 Examples of rapid evolutionary change in 10 traits associated with invasiveness.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1472-4642.2008.00473.x>

(This link will take you to the article abstract).

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