Over-invasion by functionally equivalent invasive species

JAMES C. RUSSELL,1,2,4 NURUL S. SATARUDDIN,2 AND ALLISON D. HEARD3

1School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand
2Department of Statistics, University of Auckland, Private Bag 92019, Auckland, New Zealand
3Department of Mathematics, University of Auckland, Private Bag 92019, Auckland, New Zealand

Abstract. Multiple invasive species have now established at most locations around the world, and the rate of new species invasions and records of new invasive species continue to grow. Multiple invasive species interact in complex and unpredictable ways, altering their invasion success and impacts on biodiversity. Incumbent invasive species can be replaced by functionally similar invading species through competitive processes; however the generalized circumstances leading to such competitive displacement have not been well investigated. The likelihood of competitive displacement is a function of the incumbent advantage of the resident invasive species and the propagule pressure of the colonizing invasive species. We modeled interactions between populations of two functionally similar invasive species and indicated the circumstances under which dominance can be through propagule pressure and incumbent advantage. Under certain circumstances, a normally subordinate species can be incumbent and reject a colonizing dominant species, or successfully colonize in competition with a dominant species during simultaneous invasion. Our theoretical results are supported by empirical studies of the invasion of islands by three invasive Rattus species. Competitive displacement is prominent in invasive rats and explains the replacement of R. exulans on islands subsequently invaded by European populations of R. rattus and R. norvegicus. These competition outcomes between invasive species can be found in a broad range of taxa and biomes, and are likely to become more common. Conservation management must consider that removing an incumbent invasive species may facilitate invasion by another invasive species. Under very restricted circumstances of dominant competitive ability but lesser impact, competitive displacement may provide a novel method of biological control.

Key words: competition; ecosystem management; incumbent advantage; invasive species; island colonization; logistic equations; New Zealand; over-invasion; population dynamics; priority effect; propagule pressure; Rattus spp.

INTRODUCTION

The number of species being introduced to new locations outside their native range continues to increase, and with it so does the number of these species that naturalize and become invasive (Blackburn et al. 2011). Most locations throughout the world are now invaded by multiple invasive species, causing major alteration to biodiversity and ecosystem processes. The impact of these invasive species on native species and ecosystem function is well documented (Simberloff et al. 2013), but the interactions of these invasive species among themselves can be complex (White et al. 2006). Direct interactions among invasive species can take the form of positive mutualisms (e.g., invasional meltdown; Simberloff and Von Holle 1999, Grosholz 2005), but more often are negative via processes such as predation, competition, or parasitism (Duncan and Forsyth 2006, Russell 2011). Most work on multiple interacting invasive species has focused on inter-trophic interac-

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considered an “over-invasion” of the first species. Such “over-invasion” should most commonly occur as a competitive outcome among species sharing similar functional identities and, hence, niches. The incumbent species could be completely replaced (i.e., driven extinct) or coexist with the new species but experience changes in abundance, behavior, or trophic level. Competition by an introduced species as the primary mechanism of complete exclusion of another species is rare (Davis 2003), but reduction (e.g., control) of an incumbent invasive species can often lead to replacement by another invasive species (Buckley et al. 2007).

Functional identity has an important influence on invasive species impacts on native species, with greater niche diversity and differing functional identity elevating impacts as invasive species complement one another (Blackburn et al. 2005, McCoy et al. 2012). However, some invasive species have a high similarity. The three most invasive rat species all come from the genus *Rattus* (in decreasing body size: *R. norvegicus*, *R. rattus*, and *R. exulans*) and are present on over 80% of the world’s island groups (by species: 25% *R. exulans*, 36% *R. norvegicus*, 50% *R. rattus*; Atkinson 1985). Although they are morphologically very similar (Rowe et al. 2011), and in comparison to other invasive mammals have almost identical impacts (Towns et al. 2006), among themselves their impacts are subtly different (Jones et al. 2008). Their invasion across the Pacific Islands, where all three species co-occur, is marked by a checkerboard distribution (Atkinson 1985). Generally, *R. exulans* first established with Polynesians on islands in the absence of competing mammals. With Europeans came two larger and more aggressive species of rats, *R. rattus* and *R. norvegicus*, generally leading to the extinction of the incumbent *R. exulans* populations. However, there are documented cases of a subordinate rat species retaining an incumbent advantage over an invading dominant rat species (e.g., Roberts 1991) and of a greater number of colonizing propagules from a subordinate rat species over a dominant rat species during co-occurring colonizations (e.g., Russell et al. 2010).

The causal mechanisms regulating the different population outcomes in competition among the invasive rat species on islands remains elusive, but are likely related to all of several factors, including resources, habitat, climate, competitors, and stochasticity/historical contingency (Taylor 1975, King et al. 2011), as is the case for other invasive congeneres (Rauschert and Shea 2012). Body size alone is not a strong predictor of competitive dominance (Yom-Tov et al. 1999), and coexistence varies with island size and competition–dispersal trade-offs (Russell and Clout 2004). These relationships further covary with latitude, where at high latitudes multiple species rarely coexist, except on very large islands with spatial heterogeneity (Russell and Clout 2004). In contrast, at low latitudes, multiple species can coexist on very small islands (e.g., Russell et al. 2011a). The outcome of these multiple invasions by very functionally similar species is a mixture of native species extinctions and current rat distributions (Towns et al. 2006). Whatever the mechanisms of coexistence, it clearly leads to very different outcomes in species persistence, as evidenced by *R. rattus* dominance in New Zealand but *R. norvegicus* dominance in the United Kingdom (King et al. 2011).

Species invasions are likely to increase, including more introductions of known invasive species and recognition of new invasive species (Essl et al. 2011). The likelihood of invasive species with similar niches coexisting is also expected to increase (LeBrun et al. 2007). Similar species may interact negatively with one another, leading to reduction in the abundance or even complete exclusion of the competitively subordinate species, and shared impacts on any prey. However, nuances in this interaction may perhaps create unique management situations (Taylor 1975). When both species are present, managing only one may allow the other to expand. An incumbent invasive species of low impact may be able to exclude a functionally similar high-impact invasive species. Alternatively, a dominant species with fewer impacts might reduce the impact of an incumbent invasive species, effectively a form of “bio-control,” although such a project would have to be embarked on cautiously, given the legacy of bio-control (Simberloff 2012). We modeled the interaction of two invasive species with similar niches and functional identities during their respective invasions, and the impact that invasion has on a shared prey of conservation concern. In particular, we investigated the roles of incumbent advantage and propagule pressure on the invasion outcome of each species, respectively.

Extensive previous work has investigated the inter-trophic interactions of invasive and native species using a series of three coupled logistic differential equations (see Courchamp et al. 1999, 2000, Caut et al. 2007, Russell et al. 2009). Much of this work has focused on investigating the equilibrium (stable) states of these systems, but for conservation management, such states can be trivial where native species are extinct and invasive species dominate (Russell et al. 2009). We examined the case in which two invasive species are functionally equivalent or very similar, and impact a shared prey. We investigated the conditions in which a subordinate species may have an invading propagule pressure effect over a dominant species during their simultaneous invasion, and where a subordinate incumbent species may exclude invasion of a dominant colonizing species. We finally considered empirical observations as case studies to validate the different model outcomes.

**Methods**

We modeled a deterministic dual-competitor shared prey system (Fig. 1) using ordinary logistic differential equations incorporating realistic population dynamics among the competing invasive species, mediated by a
between rat species is \( P_{ij} \) and vegetation (subscript \( v \)). The annual intrinsic growth rate model where available on the population dynamics of rates. We parameterized this system with field data competition coefficient and small variations in growth rates. We parameterized this system with field data available on the population dynamics of \( R.\ ratus \) and \( R.\ exulans \); two species of rats that have similar niches and commonly coexist. We also examined a prey of conservation concern, an insular bird species such as the Kakerori (\( Pomarea \ dimidiata; \) Saul et al. 1998), typically vulnerable to rat predation (Towns et al. 2006). We also included an alternative vegetative food base for the omnivorous rats that provides an ongoing resource once birds are extinct. Vegetation typically dominates the diet of invasive rats (Ruscoe et al. 2013). Competition between the two invasive species is incorporated with a competition coefficient altering the density dependence of each competing species, and we included control terms for each species of rat, to simulate pest control. We verified the equilibrium (stable) states of this series of equations through mathematical derivation (see Appendix), and then investigated the nonequilibrium (transient) dynamics through numerical simulation using software MATLAB (MathWorks, Natick, Massachusetts, USA).

For each species, we used typical logistic population growth models. Both rat and bird species can breed in their first year, so we do not distinguish age classes or age-related fecundity. Following previous work (Russell et al. 2009), the presence of alternative prey (viz., vegetation) is set at an arbitrarily large fixed abundance. This allows biologically realistic population persistence despite bird extinction. We defined simple predator functional responses using estimates from previously published models (Russell et al. 2009), in which predation is relative to prey availability and all prey items have equal value (Table 1). Population biology parameters of rats and insular birds are generally consistent across regions, whereas predation rates can depend more on available prey (St Clair 2011).

Hence, for \( B \), the population size of birds, and \( R \), the population size of rats:

\[
\frac{dB}{dt} = r_b B \left( 1 - \frac{B}{K_b} \right) - \frac{B}{B + V} \mu_b (R_i + R_j)
\]

\[
\frac{dR_i}{dt} = r_i R_i \left( 1 - \frac{\mu_b \mu_i (R_i + \delta_i R_i)}{\mu_b B + \mu_i V - \mu_b \mu_i R_i} \right) - (1/\delta_i) \tau R_i
\]

\[
\frac{dR_j}{dt} = r_j R_j \left( 1 - \frac{\mu_b \mu_i (R_i + (1/\delta_i) R_j)}{\mu_b B + \mu_i V - \mu_b \mu_i R_j} \right) - \delta_j \tau R_j
\]

where rat species \( i \) and \( j \) are \( R.\ exulans \) and \( R.\ ratus \), respectively, \( r \) is the intrinsic growth rate of rat species \( i \) and \( j \) and of birds, \( b \), \( V \) is vegetation as an alternative food source, \( \mu \) is the predation rate upon birds (subscript \( b \)) and vegetation (subscript \( v \)), \( \delta \) is the competition coefficient between invasive species, and \( \tau \) is the removal rate (simulated control) of the invasive species.

Carrying capacity of the bird population was arbitrarily fixed, reflecting habitat availability, while the functionally similar rat species shared a derived carrying

**TABLE 1.** Biological parameters for the \( Rattus \) spp. over-invasion model, following Russell et al. (2009).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bird population growth rate</td>
<td>( r_b )</td>
<td>0.03</td>
</tr>
<tr>
<td>Rat population growth rate for species ( i ) (( Rattus ) ( exulans ))</td>
<td>( r_i )</td>
<td>3</td>
</tr>
<tr>
<td>Rat population growth rate for species ( j ) (( Rattus ) ( ratus ))</td>
<td>( r_j )</td>
<td>4</td>
</tr>
<tr>
<td>Bird carrying capacity</td>
<td>( K_b )</td>
<td>100,000</td>
</tr>
<tr>
<td>Vegetation abundance</td>
<td>( V )</td>
<td>100,000</td>
</tr>
<tr>
<td>Rat predation on birds (no. prey eaten)</td>
<td>( \mu_b )</td>
<td>8</td>
</tr>
<tr>
<td>Rat predation on vegetation (no. prey eaten)</td>
<td>( \mu_v )</td>
<td>5</td>
</tr>
<tr>
<td>Competition coefficient (where ( j ) is the superior species)</td>
<td>( \delta_j )</td>
<td>1.1</td>
</tr>
<tr>
<td>Control rate</td>
<td>( \tau )</td>
<td>3.95</td>
</tr>
</tbody>
</table>

*Note:* The value for \( \tau \) was derived by simulation of control to low density and finally eradication.
capacity, $K_{r^*}$, based on the abundance of their available prey (birds and vegetation), which is incorporated directly into their logistic equations, and derived by the following:

$$K_{r^*} = \frac{B}{\mu_b} + \frac{V}{\mu_v} - \frac{\mu_b B + \mu_v V}{\mu_b \mu_v}$$

$$K_i = K_{r^*} - R_i = \frac{\mu_b B + \mu_v V - \mu_b \mu_v R_j}{\mu_b \mu_v}$$

where $i$ and $j$ are $R. exulans$ and $R. rattus$, respectively.

We treated competition as an asymmetrical relationship between the invasive species, incorporated in the equations through a density-dependent modifier $\delta_j$, which is the relative density-dependent effect of one individual of species $j$ on species $i$, where $\delta_i > 1$ for the dominant species $j$ (intraspecific stronger than interspecific competition), and the reciprocal, $1/\delta_j$ (equivalently $\delta_i$), is the effect of one individual of species $i$ on species $j$ (interspecific stronger than intraspecific competition). Typical competition for invasive species control devices (such as access to traps or poison bait for rats) is also reflected by modifying the control rate, $\tau$, by the relative competition coefficients, where the dominant species has prioritized access (sensu Caut et al. 2007).

For parsimony, we do not model any spatial or temporal variability in this system, such as spatial heterogeneity in habitat and resources, or temporal heterogeneity such as seasonality or interannually, where alternative food sources can increase by orders of magnitude and hence alter the carrying capacity of rats. Previous work suggests that such heterogeneity alters the timing, but not final outcome, of interactions (Dumont et al. 2010). For simplicity, we also do not consider small variations in the impact (predation rate) between invasive species. Any such variation will alter the nature of the impact on the prey species, but will not directly alter the relationship between the invasive species.

The models are numerically simulated for the prey population at demographic equilibrium and an invasion by either one or both functionally similar invasive species. We examine the nonequilibrium system dynamics over time during the process of bird extinction, or rat invasion, leading to the final equilibrium outcome. We first simulate invasion by only one of the invasive species, to observe the impact on the prey species. The bird (prey) population starts at equilibrium prior to the introduction of rats. In the standard case, invasion occurs by one pregnant female (i.e., $n = 1$). We then simulate nonequilibrium system dynamics over time, including predator control for conservation. Rat control (eradication) occurs at time $t = 3$ years following invasion. We then wish to determine the circumstances under which the competitively inferior (subordinate) rat species may establish in the presence of the dominant rat species, or alternatively reject an invasion of the dominant rat species. We first simulate the simultaneous colonization of an island by both invasive species with different numbers of founding propagules, to investigate any propagule pressure effect between the two invasive species. We then simulate the colonization of an island by one invasive species when the other is already established close to carrying capacity, to investigate any incumbent advantage effect between the two invasive species. All results are tested for robustness to ±10% sensitivity in demographic and predation rate parameters, given that these parameters will have had associated statistical variation from the studies in which they were estimated.

**RESULTS**

For our models, the persistence of more than one species is only ever possible under precise control strategies upon any rat species present. Generally, invasion by invasive *Rattus rattus* leads to the extinction of the vulnerable bird species (Fig. 2a), and only with a strong control ($\tau > r$; essentially eradication) of the invasive rat does the bird species survive, albeit with a slow recovery typical of long-lived insular...
species (Fig. 2b). This conservation outcome is now routinely achieved via rat species eradication. This result is qualitatively identical for invasion by *R. exulans* (results not shown), but because of its lesser impact on the bird species, the extinction of the bird species is delayed, but not avoided. Altering the amount of alternative food available, as a proxy for bottom-up regulation in the system, merely alters the carrying capacity of the rat species (results not shown), and again only alters the time to bird extinction, but not its inevitability.

**Propagule pressure**

Only one invasive rat species successfully establishes during the simultaneous colonization of an island by both species. For $1.0 < \delta_j < 1.1$, *R. rattus* typically competitively displaces *R. exulans* in a consistent manner (Fig. 3a). However, when the number of *R. exulans* introduced at the outset is greater than the number of *R. rattus*, *R. exulans* can numerically dominate (Fig. 3b), giving it a propagule pressure effect.

**Incumbent advantage**

When one invasive rat species is already established at close to carrying capacity, it can resist invasion by another invasive rat species, even when the latter arrives in large numbers. When *R. exulans* is established in high abundance, it can resist invasion by *R. rattus*, giving it an incumbent advantage effect (Fig. 4a). However, this incumbent advantage for *R. exulans* is lost when the invasion front of *R. rattus* increases (Fig. 4b).

**Case studies**

All of the model outcomes theoretically demonstrated are supported by rat invasion case studies. Invasion of rat-free Big South Cape Island (939 ha) off southern New Zealand by *R. rattus* in 1962 was rapid, with rats widespread across the entire island in 2–3 years (Bell 1978). By the time conservation agencies could respond, five bird species were already extirpated and a further two were greatly depleted in numbers (e.g., Fig. 2a). Three invasive rat species coexisted on Pearl Island (512 ha) off southern New Zealand prior to their simulta-
neous eradication in 2005. Nine months following rat eradication, R. rattus and R. norvegicus were detected reinvading from the adjacent mainland (Russell et al. 2010). Although R. rattus was previously the dominant rat species on the island, the greater number of reinvading R. norvegicus apparently had a propagule advantage, which led to their eventual dominance across the island (e.g., Fig. 3b). Parasitological investigation of invasive rats on islands off northern New Zealand found evidence from shared parasites that the competitively subordinate R. exulans had resisted colonization by rats arriving from Europe on up to nine islands (Roberts 1991), presumably due to an incumbent advantage (e.g., Fig. 4a), whereas R. exulans was displaced by an R. rattus invasion front across mainland New Zealand (e.g., Fig. 4b).

**DISCUSSION**

The models presented here are simple and deterministic, but encapsulate the essence of the interaction between two competing species in a biological invasions context. We found variable invasion outcomes from interactions between functionally similar invasive species and show that one invasive species can displace another invasive species with a very similar niche through a process that we term “over-invasion.” We do not exhaustively explore all possible outcomes of the competitive interaction between two similar invasive species; equilibrium dynamics yield only a small set of realistic outcomes, but it is the richness of nonequilibrium dynamics that provides the more interesting results for conservation. In practice, stochastic dynamics at low or declining population sizes also contribute to alternative invasion outcomes (Orrock and Fletcher 2005), and in the most extreme stochastic case, neither invasive species may establish.

Competitive displacement by functionally similar invasive species is fairly common, and examples can be found across taxa and biomes. Displacement has been documented in Vespula wasps in New Zealand (Harris et al. 1991), Aedes mosquitoes in Brazil (Braks et al. 2004), Vulpes foxes in Alaska (Bailey 1993), nectar-thieving ants in Hawaii (Lach 2005), freshwater amphipods in the Rhine (van Riel et al. 2009), freshwater crayfish in The Netherlands (Hudina et al. 2011), freshwater fish in Kenya (Britton et al. 2010), Cardurus thistles in Pennsylvania, USA (Rauschert et al. 2012), and Passiflora vines in New Zealand (Williams and Buxton 1995). In many of these examples, the invading species come from the same genus. In such cases, the displacement might then incorporate elements of hybridization in the swamping of the incumbent by the new invader (Prentis et al. 2008). However, in other examples functional similarity can exist between phylogenetically dissimilar invasive species, and still result in competitive exclusion. Phylogenetic relatedness alone is not a good predictor of competition intensity (Kaplan and Denno 2007, Cahill et al. 2008). At broader taxonomic levels, introduction success among invaders, such as passerine birds, also depends on competition and priority effects, but coexistence can occur due to adaptations such as morphological displacement (Duncan and Forsyth 2006).

We have focused on negative interaction between two invasive species that occupy a common niche, but positive interaction through commensalism and facilitation have also been as commonly observed between invasive species (Simberloff and Von Holle 1999). These positive interactions typically occur between dissimilar invasive species (Simberloff 2006). The more similar two species are, the more they are expected to engage in competition, but functionally similar invasive species might also facilitate the invasion of one another. This could occur through ecosystem-engineering that benefits both species (Crooks 2002). Among invasive rats, R. rattus is able to open coconuts; this may benefit the coexistence of R. exulans, which is unable to do so. Determining the overall nature of the relationship between two invasive species during over-invasion will require consideration of the full range of impacts that each species has on the other, and recognition that these may include both positive and negative effects on different aspects of the population biology of either or both species (Russell 2011).

Population size is crucial in determining the outcome of over-invasion scenarios. During initial invasion at low population sizes, especially with only a single pregnant female propagule, stochastic dynamics will play an important role (Lande 1993, Duncan and Forsyth 2006). For simultaneous colonization, the respective propagule pressure of each colonizing species determines which will become established, and small plausible changes within the bounds of stochasticity may change the invasion outcome. Propagule pressure during simultaneous initial invasions can thus alter the final invaded community composition, and potentially interact with already established invasive species to facilitate further invasion (Grosholz 2005). Once an invasive species is established, a much larger propagule pressure is required to displace the incumbent species, even if it is normally subordinate. Nevertheless, such large propagule pressures have almost certainly happened via shipping or through invasion fronts during the colonization of large archipelagos.

The competition model presented here shares many similarities with models of apparent competition (e.g., Oliver et al. 2009), and the inclusion of an invasive species control term with variable specificity effectively creates apparent competition dynamics through altering the abundances of only one invasive species. This was observed in the “competitor-release effect” model of Caut et al. (2007), where an intra-trophic competition between invasive rats and mice (Mus musculus) on islands was modeled during control operations. Because rats are consistently dominant over mice on islands, Caut et al. (2007) focused mostly on the optimal control
strategies for the rodent competitors, rather than the form of the competitive relationship or impact on any shared prey. Unlike symmetrical competition between invasive rats, which can have alternative states of species coexistence, rats always dominate mice through asymmetrical competition (Bridgman et al. 2013).

Both spatial and temporal heterogeneity within an island will also alter invasion outcomes. We only focus on the case of complete exclusion by one invasive species, such as on a small island. However, spatial heterogeneity in resources is likely to increase the probability of coexistence among functionally similar invasive species. Indeed, on islands in the Pacific, competing invasive rats are able to coexist (Yom-Tov et al. 1999), although this coexistence is mediated by island size and latitude (Russell and Clout 2004, Russell et al. 2011), much like other characteristics of island populations. Over-invasion may subsequently induce niche partitioning among invasive species, such as different habitat and food preferences observed in coexisting invasive rats (King et al. 2011). Temporal heterogeneity, such as seasonal or interannual interruptions or population crashes, may also give a short-term advantage to one species that allows it to persist or invade in circumstances under which the species would otherwise be excluded. Finally, the interactions among functionally similar invasive species will also be affected by the presence of other dissimilar species, both native and invasive, in the ecosystem. The population dynamics of invasive rats is known to be altered by the presence of other competing rodents and predatory mammals (Russell et al. 2011b), and many instances of competitive displacement in other commensal rodents on islands have been documented (Taylor 1975).

In some cases, even native Rattus can forestall the establishment of invasive species in the same genus (Stokes et al. 2009). In all cases, though, the functional similarity in both invading species suggests that they probably would respond identically to sources of environmental variation and stochasticity (Adler and Drake 2008). Nonetheless, ongoing empirical work is required to fully understand the competitive mechanisms by which invasive rat species compete and coexist among one another (e.g., King et al. 2011).

Over-invasion should be an outcome of direct interference or exploitative competition between two invasive species, but other indirect effects during species invasion may induce species displacement. Replacement of incumbent Aedes aegypti mosquitos by Aedes albopictus has been experimentally explained by resource competition alone, and apparent competition mediated by shared parasites did not play an important role (Juliano 1998). Further experimental work of this nature will help to explain the exact mechanisms by which competitive displacement occurs between particular invasive species pairs. Nonetheless, complex situations may occur in which direct competition as well as indirect interactions mediate the outcome of invasion by a functionally similar invasive species. As for other indirect interactions in invasion biology, these outcomes may be difficult to predict, and necessitate a “whole-ecosystem” or “ecosystem management” approach (White et al. 2006; Russell 2011).

Over-invasion has particular relevance to conservation management, when removing an incumbent invasive species may facilitate invasion by a more detrimental species (Buckley et al. 2007, Rauschert and Shea 2012). Manipulating an incumbent invasive species with less impact to maintain an alternative stable state may prove to be the most effective management regime (Finn et al. 2010). On Tetiaroa atoll, the presence of R. exulans on the main nesting islands for seabirds may provide some protection against R. rattus invasion from nearby islands (Russell et al. 2011a). Under certain circumstances, displacement of an incumbent invasive species by a competitively dominant invasive species with less impact may be a viable impact mitigation option. This is not the case for invasive rats, where the competitively dominant R. rattus also has the greater impact on native fauna (Townes et al. 2006, Jones et al. 2008). However, Oriental fruit flies (Bactrocera dorsalis) are competitively dominant to Mediterranean fruit flies (Ceratitis capitata) (Keiser et al. 1974), but are considered less of an agricultural pest (Harris 1977), and over-invaded in Hawaii. Common wasps (Vespula vulgaris) over-invaded German wasps (V. germanica) in New Zealand, but have less impact on the bee-keeping industry (Clapperton et al. 1989). Similarly, red foxes experimentally introduced to Alaskan islands previously invaded by arctic foxes eventually competitively excluded the incumbent arctic foxes (Bailey 1993). However, we do not recommend this as a control strategy unless all other avenues of control have been exhausted (Hoddlle 2004), and even then it still may not be advisable (Taylor 1975, Simberloff 2012). In most cases, the best control strategy for multiple invasive species is to target all species simultaneously. Competitive interactions between functionally similar invasive species will only increase as invasive species expand their introduced ranges and spread to new locations (LeBrun et al. 2007). During this era of increased global mobility and elevated invasion risk, we recommend that conservation managers focus foremost on preventing invasions at the outset through responsible biosecurity.

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