Translocation strategies for multiple species depend on interspecific interaction type

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Abstract. Conservation translocations, anthropogenic movements of species to prevent their extinction, have increased substantially over the last few decades. Although multiple species are frequently moved to the same location, current translocation guidelines consider species in isolation. This practice ignores important interspecific interactions and thereby risks translocation failure. We model three different two-species systems to illustrate the inherent complexity of multispecies translocations and to assess the influence of different interaction types (consumer-resource, mutualism, and competition) on translocation strategies. We focus on how these different interaction types influence the optimal founder population sizes for successful translocations and the order in which the species are moved (simultaneous or sequential). Further, we assess the effect of interaction strength in simultaneous translocations and the time delay between translocations when moving two species sequentially. Our results show that translocation decisions need to reflect the type of interaction. While all translocations of interacting species require a minimum founder population size, which is demarked by an extinction boundary, consumer–resource translocations also have a maximum founder population limit. Above the minimum founder size, increasing the number of translocated individuals leads to a substantial increase in the extinction boundary of competitors and consumers, but not of mutualists. Competitive and consumer–resource systems benefit from sequential translocations, but the order of translocations does not change the outcomes for mutualistic interaction partners noticeably. Interspecific interactions are important processes that shape population dynamics and should therefore be incorporated into the quantitative planning of multispecies translocations. Our findings apply whenever interacting species are moved, for example, in reintroductions, conservation introductions, biological control, or ecosystem restoration.

Key words: assisted migration; coextinction; competition; conservation introduction; consumer–resource system; mitigation translocation; mutualism; reintroduction; restoration.

INTRODUCTION

Translocations are human-mediated movements of organisms from one location to another, and they commonly occur in fields such as biological control, invasion ecology, ecosystem restoration, conservation biology, and mitigating development. In recent years, translocations have increasingly been used as ex situ conservation tools to prevent the loss of threatened species (Seddon et al. 2014) and are applied in several different ways (IUCN 2013). Population restorations aim to reinforce existing populations (population augmentation) or to reestablish species in a habitat where they previously occurred (reintroduction). Managers may move species to a new habitat to perform lost ecological functions (ecological replacement) or to establish insurance populations (conservation introduction). And finally, an increasingly common practice, which is not primarily for conservation purposes, is to mitigate detrimental effects to species’ populations from development projects (mitigation translocations; Germano et al. 2015). Generally, conservation translocations aim to establish self-sustaining populations in the release habitat (Griffith et al. 1989, IUCN 2013).

Although a variety of organisms have been successfully translocated, reported success rates are generally low (Griffith et al. 1989, Seddon 1999, Fischer and Lindenmayer 2000, Seddon et al. 2007) and even these likely reflect a publication bias towards successes (Miller et al. 2014). To increase the success rate of translocations, a range of decision frameworks and guidelines have been proposed (Hoegh-Guldberg et al. 2008, Richardson et al. 2009, McDonald-Madden et al. 2011, Chauvenet et al. 2012, Schwartz and Martin 2013). These frameworks consider multiple factors that influence translocation success: particularly the suitability of the destination habitat (Griffith et al. 1989, Wolf et al. 1996), the size of the founder population (Griffith et al. 1989, Lubow 1996, Fischer and Lindenmayer 2000), the origin of founder populations (Fischer and Lindenmayer 2000), and their demographic and genetic characteristics (Griffith et al.
The plant can survive in the absence of its pollinator, but shows a much higher seed set when *R. gigas* is present (Steiner and Whitehead 1996). In consumer–resource interactions, the absence of suitable or sufficient resource individuals can jeopardize the successful translocation of the consumer, and managers may therefore need to translocate individuals from each species to ensure that both survive, or they may need to translocate the consumer into locations with large existing resource populations (Miller et al. 1999). The strongest interactions occur when species are specialized; for example, host-specific parasites are unable to survive without their hosts (Colwell et al. 2012) and some orchid species depend on specialized pollinators for reproduction (Pemberton 2010).

Although ignored in translocation guidelines, multispecies translocations already occur frequently. Predator-free areas are scarce and expensive to create (Bode and Wintle 2010), and the increasing number of threatened species encourages managers to move competing species into the same reserves. In New Zealand, three threatened reptile species, *Sphenodon punctatus*, *Hoplodactylus duvaucelii*, and *Oligosoma smithi*, were reintroduced to Tiritiri Matangi Island, an island that already held other native and possibly competing reptile species (Baling et al. 2013). The desire to recreate historical ecosystems often leads to species being translocated to the same destinations, such as translocations of marsupial herbivores to Peron Peninsula, Australia (Richards 2003). But even in such ecosystem restorations, the translocations are planned and implemented for each individual species in isolation, without quantitatively considering the potential interaction between them. Mitigation translocations, in which organisms are moved to reduce their mortality due to anthropogenic development, often require moving several species to the same destination (Germano et al. 2015). To allow a large port development in London, approximately 24000 animals, mostly reptiles but also water voles and newts, were moved to a single site (Williams 2011). The interactions between species are generally not considered in mitigation translocations.

In this study, we analyze the influence of interspecific interactions on translocation strategies for two species. Our aim is to identify management decisions that allow the successful translocation of two interacting species, across different interaction scenarios. We are particularly interested in whether the type of interaction affects two fundamental decisions: (1) How many founder individuals of each species are necessary for their successful establishment? and (2) In what order should the translocations occur: simultaneous (both species at the same time) or sequential (one species before the other)? We use models for three common types of interspecific interactions: consumer–resource, competition, and mutualism. For competitive and mutualistic systems, we analyze symmetric and asymmetric interaction strengths. Finally, for all interaction types, we analyze the sensitivity of the
models to increasing interaction strength and to an increasing delay between sequential translocations of the two species.

**Methods**

We assume that conservation managers face the following problem: two interacting species are threatened in their original location (source). The species would therefore benefit from establishing insurance populations, since occupying two sites will markedly reduce the species’ global extinction risk. Individuals of both species are removed from the source to become founder populations at a new site (destination). We define that a successful translocation includes the establishment of founder populations at the destination, as well as the survival of the source population. As the removal of individuals from the source will increase the populations’ local extinction risk, we seek to minimize this risk by translocating the smallest number of individuals that still allows population establishment at the destination. There are risks from introducing organisms to new habitats, such as invasion risk, disruption of ecosystems, host switching, or disease introduction (Ricciardi and Simberloff 2009), and while important, we do not focus on these risks in our analyses.

**Interaction models**

To assess the influence of interaction types, strength, and symmetry on the decisions about founder size and translocation order, we model deterministic systems of two interacting species. We consider the dynamics of founder populations at the destination only and identify those translocation decisions that result in persisting founder populations of both species. We assume no dispersal between source and destination sites, hence, the population dynamics of both patches are spatially independent and contingent only on local abundances.

We use previously published models for three different interspecific interaction types: consumer–resource (Eqs. 1a, 1b), competition (Eqs. 2a, 2b), and mutualism (Eqs. 3a, 3b). We specifically choose these models because they are density dependent processes, which are known to strongly influence population growth (Hixon and Johnson 2009), interspecific interactions (Courchamp et al. 1999), and translocation success (Deredec and Courchamp 2007, Somers et al. 2008). These processes reduce the population’s growth rate at high abundances (i.e., high density-dependent process) and at low abundance (i.e., low density-dependent process or Allee effect). The interactions between species have an influence on the high density-dependent process, resulting in a change of the populations’ realized carrying capacities. For example, flour beetles reached higher population sizes in experiments without the presence of a competing species (Park 1962). Further, interspecific interactions influence Allee effects, and theory predicts that a consumer’s Allee effect increases a resource’s equilibrium density (Zhou et al. 2005). For example, parasites may find it more difficult to locate hosts when the host is at low densities (Courchamp et al. 1999), leading to reduced reproductive success. Cooperative hunters are less effective if their pack size is below a critical threshold (Creel 1995), which decreases the predation pressure on their prey, and smaller prey groups suffer more from predation than larger groups (Courchamp et al. 1999).

For consumer–resource systems, such as predator–prey, herbivore–plant, or parasite–host systems (Eqs. 1a, 1b), we base our models on those by Zhou et al. (2005). The consumer dynamics depend on a numerical response, which is determined by a strike rate s, a conversion rate c of the resource N by the consumer P, and an intrinsic death rate dP (Eq. 1a). The Allee effect is incorporated as P/(P + AP), where P is the consumer density and AP is an Allee constant. There is no specific formulation for the high density-dependent process in the consumer equation, because its high-density dynamics are regulated by resource availability. The resource dynamics are a function of its birth rate bN, a high density-dependent process I = N/KN, where KN is a constant for the carrying capacity, and an Allee effect N(N + AN), which is an equivalent formulation to the consumer equation. Here, N represents the resource density and AN is a constant. The growth of the resource is then decreased by a per capita mortality rate dN and a consumption term that depends on the strike rate s and the abundance of both consumers and resource, P and N, respectively.

\[
\frac{dP}{dt} = cNP \left( \frac{P}{P + AP} \right) - d_P P, \tag{1a}
\]

\[
\frac{dN}{dt} = N \left( b_N \left( 1 - \frac{N}{KN} \right) \left( \frac{N}{N + AN} \right) - d_N \right) - sNP. \tag{1b}
\]

**Fig. 1.** Translocation scenarios for two interacting species with (a, b) consumer–resource, (c, d) competitive, and (e, f) mutualist interactions. Left column (a, c, e) shows a phase space of founder populations, with trajectory arrows superimposed. The gray shading shows the final outcome of each combination of founder population. Dark gray represents unsuccessful translocated population combinations (failure region). Light gray areas indicate successful combinations (success region). Right column (b, d, f) shows the differences between simultaneous translocations (gray scale) and sequential translocations (black line denotes the extinction boundary). The following parameter sets were used for the simulations: consumer–resource, KN = 45, bN = 2.5, dN = 0.2, dP = 0.5, AN = 6, AP = 5, s = 0.1, c = 0.05, tP = 1; competition, KCI = KDi = 45, ACi = ACi = 0.11, bDi = bCi = 0.01, dDi = dCi = 0.021; mutualism, KDi = KDi = 45, aDi = aDi = 0.5, bDi = bDi = 0.11, dDi = dDi = 12. The parameter combinations for the competition model originate from Wang et al. (1999) and are replicated in the mutualism model for consistency. Translocation delay for the consumer–resource system is one time step, between competitors and mutualists it is five time steps.
For competitive and mutualistic interactions, we use models by Wang et al. (1999). Here, the population growth of two competitors, $C_1$ and $C_2$, is defined by their birth rates, $b_{C1}$ and $b_{C2}$, and their death rates, $d_{C1}$ and $d_{C2}$, respectively (Eqs. 2a, 2b). Both species are linked through competition by interaction terms, $\alpha_{C1}C_2$ and $\alpha_{C2}C_1$, which affect their carrying capacities $K_{C1}$ and $K_{C2}$ and reduce the realized equilibrium of the competitive system. The introduction of an Allee effect, $C_1/(C_1 + A_{C1})$ and $C_2/(C_2 + A_{C2})$, leads to several alternative stable states in the two-species system, but may inhibit coexistence if the interaction is sufficiently strong (Wang et al. 1999).

\[
\frac{dC_1}{dt} = C_1 \left( b_{C1} \left( 1 - \frac{C_1 + \alpha_{C1}C_2}{K_{C1}} \right) \left( \frac{C_1}{C_1 + A_{C1}} \right) - d_{C1} \right), \tag{2a}
\]

\[
\frac{dC_2}{dt} = C_2 \left( b_{C2} \left( 1 - \frac{C_2 + \alpha_{C2}C_1}{K_{C2}} \right) \left( \frac{C_2}{C_2 + A_{C2}} \right) - d_{C2} \right). \tag{2b}
\]

We assume that mutualistic systems (Eqs. 3a, 3b) mirror competitive dynamics, but with interaction coefficients of the opposite sign, such that $\alpha_{M1}$ and $\alpha_{M2}$ are both negative. The parameters are similar to the competitive system: the population growth of both mutualist $M_1$ and $M_2$ is defined by their birth rates $b_{M1}$ and $b_{M2}$, and their death rates $d_{M1}$ and $d_{M2}$, respectively. We are modeling a facultative mutualism, where species are able to survive without their partner, but can utilize more resources in the presence of their partner. Hence, the interaction terms $\alpha_{M1}M_2$ and $\alpha_{M2}M_1$ are only found in the high-density process.

\[
\frac{dM_1}{dt} = M_1 \left( b_{M1} \left( 1 - \frac{M_1 - \alpha_{M1}M_2}{K_{M1}} \right) \left( \frac{M_1}{M_1 + A_{M1}} \right) - d_{M1} \right), \tag{3a}
\]

\[
\frac{dM_2}{dt} = M_2 \left( b_{M2} \left( 1 - \frac{M_2 - \alpha_{M2}M_1}{K_{M2}} \right) \left( \frac{M_2}{M_2 + A_{M2}} \right) - d_{M2} \right). \tag{3b}
\]

**The translocation process**

To demonstrate a translocation, we simulate founder population dynamics after their translocation to the destination until they reach equilibrium density (all of the systems we analyze exhibit asymptotic stability). The population equations have many potential parameterisations. To maintain clarity, we consider a more tractable set of five scenarios with different interaction types and strengths. We model one consumer–resource system (scenario I) and two different scenarios for competition (scenario II and III) and mutualism (scenario IV and V), with symmetric and asymmetric interactions between the partners. Asymmetric interaction is achieved by introducing a difference in the competitive pressure (scenario III) between a superior competitor $C_1$ and an inferior competitor $C_2$ ($\alpha_{C1} < \alpha_{C2}$) and a different mutualistic benefit (scenario V) that a superior mutualist $M_1$ receives by an inferior mutualist $M_2$ ($\alpha_{M1} > \alpha_{M2}$). We explore how the order of the translocations affects outcomes by modeling both simultaneous and sequential translocations. In sequential translocations, we delay the translocation of one of the species (i.e., delayed is the consumer, competitor 2, and mutualist 2). In addition, we explore how outcomes change with increasing interaction strength: attack rate for consumers ($c = 0.7–1.3$ in steps of 0.2) and interaction strength for competitors ($\alpha_{C1} = 0.1; 0.2; 0.3; 0.5$) and mutualists ($\alpha_{M1} = 0.1; 0.2; 0.3; 0.5$). We also investigate the effect of increasing time delays (time steps between sequential translocations = 0; 1; 2; 5) by delaying the translocation of the consumer, competitor 2, and mutualist 2. We use Matlab 8.4.0 (R2014b) to simulate the population dynamics.

We present the population dynamics in phase spaces for a range of possible founder population sizes (e.g., Fig. 1). For each combination of founder population sizes, we map the outcome of a translocation as one of two possibilities: success when both populations establish and coexist (Fig. 1, light gray area, hereafter the success region) and failure if either population goes extinct (dark gray area, hereafter the failure region). In this translocation space, the success and failure regions are divided by a boundary line (i.e., a separatrix sensu Murray 2002), which we hereafter call extinction boundary. To present the outcome of sequential translocations, we superimpose the new extinction boundary (black line) in the phase space of simultaneous translocations (Fig. 1). The extinction boundary actually reflects each species’ individual extinction boundary separately. To increase simplicity and because we are only interested in the success or failure of a two-species system, we combine these extinction boundaries to a single continuous line.

**RESULTS**

**Effects of interaction types**

The consumer–resource phase space (scenario I) shows a distinct shape, with the success region for founder populations surrounded by the failure region (Fig. 1a). This is caused by the cyclic nature of Lotka-Volterra consumer–resource dynamics (e.g., Murray 2002) and is visible in the population trajectories (i.e., arrows in Fig. 1a). While increasing initial resource abundances decreases the lower extinction boundary for the consumer, increasing consumer abundances increases the lower extinction boundary of the resource. With increasing resource abundances, the upper extinction boundary decreases, thereby reducing the total region for successful translocations (Fig. 1a). The lower and upper extinction boundaries imply that translocations can fail if the number of consumers is too low, but also if their
number is too high. In the latter case, extinction is caused by the consumer population first overshooting its resource population and then declining rapidly to extinction through starvation and passing its extinction boundary (Fig. 1a).

Delays in the consumer translocation changes the location and shape of the success region, so that the lower and the upper extinction boundaries are decreased. Sequential translocations therefore allow moving fewer resource individuals, because the delay permits the resource population to increase rapidly in the temporary absence of its consumer (Fig. 1b). However, the reduced upper extinction boundary of the consumer population requires lower consumer founder populations than in simultaneous translocations. As a result, some combinations of consumer and resource numbers will succeed if translocated simultaneously, but fail if translocated sequentially. This phenomenon occurs when the delay allows resources to establish sufficiently high numbers so that the consumer population overshoots and then crashes.

In contrast to consumer–resource systems, the success region of competitors and mutualists is only limited by an extinction boundary for small founder populations of either species (Fig. 1c–f). When translocating symmetric competitors (scenario II) simultaneously, the failure region increases with growing founder abundances (Fig. 1c), which implies that larger numbers of one competitor require larger numbers of its interaction partner for them to establish successfully. This result is common to all competitor translocations. The equilibrium density of interacting competitors is lower than their equilibrium when they are alone in the ecosystem (indicated by the crossing point of the arrows in Fig. 1c). When translocating symmetric competitors sequentially by delaying competitor two ($C_2$), the extinction boundary of both changes (Fig. 1d). Competitor one ($C_1$) arrives at the destination with a lower extinction boundary, while competitor two experiences a slight increase in its extinction boundary. The delayed competitor has to overcome greater competitive pressure, because it arrives at a destination where another competitor has already established the overall success region for sequential translocations is larger due to a more substantial decrease in the extinction boundary of the competitor translocated first (Fig. 1d).

When translocating asymmetrical competitors simultaneously (scenario III; $\alpha_{C1} < \alpha_{C2}$), the translocation boundary of the superior competitor is lower than that of the inferior competitor (Fig 2a, b). Simultaneous translocations of competitors with unequal competitive abilities require much larger founder populations of the inferior than of the superior competitor. Translocating the superior competitor $C_1$ first in sequential translocations, it maintains its extinction boundary, while the extinction boundary of the inferior competitor $C_2$ increases substantially, exacerbating the difficulty of establishing it at the destination site (Fig. 2a). If the inferior competitor is moved first instead, its extinction boundary decreases substantially, while there is no change in the extinction boundary of the superior competitor (Fig. 2b). The increase in translocation success is caused by the temporary absence of competition before the arrival of the superior competitor, indicating that it is optimal to translocate the inferior before the superior competitor.

When translocating symmetric mutualists (scenario IV) simultaneously, the success region expands only marginally with growing founder populations of both mutualistic species (Fig. 1e). The realized equilibrium density of interacting mutualists increases substantially compared to that of single species (Fig. 1e). When delaying the translocation of mutualist two, its extinction boundary shows a very small decrease, while the extinction boundary of the first species increases (Fig. 1f). The resulting overall success region for sequential translocations is slightly smaller than for simultaneous translocations (Fig. 1f). For asymmetrical mutualists, where $\alpha_{M1} > \alpha_{M2}$ (scenario V), the extinction boundary of the superior mutualist $M_1$ is lower compared to that of the inferior mutualist $M_2$ in simultaneous translocations (Fig. 2c, d). Delaying the inferior mutualist leads to a small increase in the extinction boundary of the superior mutualist, while the extinction boundary of the inferior remains similar (Fig. 2e). When delaying the superior mutualist, its extinction boundary decreases only slightly, and the inferior mutualist’s extinction boundary increases marginally for higher founder numbers (Fig. 2d).

Independent of the symmetry of the mutualistic interaction (scenarios IV and V), the overall success region increases little in sequential translocations, hence, the effect of delaying translocations in mutualistic systems is small.

**Exploration of the decision space for different parameter values**

The extinction boundaries for two-species systems of consumer–resource, competitors, and mutualists react differently to increases in the interaction strength $\alpha_i$ (Fig. 3a–c). In the consumer–resource system, an increase in interaction strength substantially decreases the overall success region (Fig. 3a). For competitors and mutualists, increases in interaction strength result in opposite patterns: while the extinction boundary of competitors decreases substantially with increasing competitive pressure and partner’s population size (Fig. 3b), the mutualistic system experiences a small decrease in its extinction boundaries with increasing mutualistic benefit (Fig. 3c). This decrease and the subsequent increase in the success region are less substantial than the changes in competitive systems.

We finally examine the sensitivity of translocation decisions to increasing delays between translocations in a sequential management strategy. The extinction boundaries of the resource decrease with increasing delay time in sequential translocations of consumers (Fig. 3d).
The upper extinction boundary for high consumer numbers, however, exhibits a profound decrease. High initial consumer numbers that succeed for simultaneous translocations are too high for sequential approaches. The initially translocated resource is released from consumption pressure during the delay period, in which it can establish high numbers. The delayed consumer then enters a resource-rich ecosystem, and consequently experiences rapid population growth, which causes population crashes in both species. The competitor species translocated first, $C_1$, exhibits a decrease in its extinction boundary with increased delay (Fig. 3e). The extinction boundary of the delayed competitor, $C_2$, is lowest for simultaneous translocations and increases with increasing delay (Fig. 3e). Sequential translocations facilitate the establishment of the first competitor at the destination site due to a release from competitive pressure during the delay period. The delayed competitor, however, experiences a higher competitive pressure when arriving to a destination where competitor one is already established. Delaying a mutualist, $M_2$, has very little effect on both species’ extinction boundaries (Fig. 3f). There is, however, a slight increase in the extinction boundary of the initial mutualist, $M_1$, and correspondingly a slight decrease in the extinction boundary of the delayed mutualist. Sequential translocations of mutualists disrupt the
positive interaction between the species leading to decreased growth rates of the mutualist arriving first.

**Discussion**

We have demonstrated that management decisions become more complex when accounting for interspecific interactions in multispecies translocations. Our findings are applicable to all decisions that involve the anthropogenic movement of interacting species, such as the introduction of biological controls, restoration of degraded habitats, mitigation of anthropogenic development, or conservation translocations. Management complexity is influenced by both ecological (i.e., interaction strengths, Allee effects, and equilibrium population sizes) and management (i.e., founder population abundances, order of translocation, length of delay between translocations) factors, each of which influences the likely success and failure of a translocation. Across interaction types, there is only one apparent generality for translocation decisions: founder populations have to exceed a lower extinction boundary for successful
translocations. Given that management would want both source and founder populations to persist, translocations should not reduce the source populations below its extinction boundary. For a translocation to be successful without extirpating the source, source populations need to be at least twice as large as the species’ extinction boundaries. If this requirement is not fulfilled, populations at either the source or the destination will go extinct.

Consumer–resource systems are very complex, illustrated by the distinctive shape of the resulting phase space with the success region enveloped by the failure region (Fig. 1a). Our findings suggest that successful translocations of dependent consumers with their resource are possible, but that the interaction needs to be considered quantitatively in the planning stage of the multispecies translocation. In combined translocations of consumers and resources, founder populations of both species must originate from within a feasible region of population sizes to avoid critical population levels: problems cannot be solved or uncertainties avoided by simply translocating more individuals. The failure to establish populations of tuatara ticks (*Amblyomma sphenodonti*) on translocated tuatara (*Sphenodon punctatus*) in New Zealand has been linked to this phenomenon, with the density of tuatara being considered too low to sustain the tick population (Moir et al. 2012). Currently managers are preparing for the reintroduction of eastern quolls (*Dasyurus viverrinus*) into Booderee National Park in Australia (Milman 2015). These small marsupial predators feed on small mammals, reptiles, insects, and birds, and it might therefore be a threat to the endangered Eastern Bristlebird (*Dasyornis brachypterus*). To successfully reintroduce the quoll, without putting the Eastern Bristlebird population at risk, it is important to ensure a large enough bird population and sufficient alternative resources. Insufficient numbers of natural prey at reintroduction sites have caused wolves to switch to preying on livestock (Hayward and Somers 2009), resulting in human–wildlife conflict. To ensure sufficient resources and avoid human–wildlife conflict, sequential translocations of consumers after initial resource establishment could solve these problems. However, delaying consumer translocations will not always increase the translocations success, as indicated by the reductions on the upper extinction boundary of the success region (Fig. 3d).

Translocating competing species in inappropriate ratios can lead to competitive exclusions of species and jeopardize the success of a multispecies translocation project. The reintroduction of red barbed ants (*Formica rufibarbis*) in the UK is an example where unexpected competitive relationships with other ants, specifically *Lasius niger*, and to a lesser extent *F. sanguinea*, prevented translocation success (Dodd et al. 2013). It is thought that for this translocation to succeed, larger founder populations of *F. rufibarbis* would have been necessary (Dodd et al. 2013). Competing species are commonly translocated in situations where a shared threat endangers species within a particular trophic level. Frequently, species in Australia and New Zealand are being moved onto islands and into fenced areas to release them from the threat posed by invasive predators (Hancock et al. 2000, Short 2009), often with limited success (Richards 2003). In central Australia, for example, the Scotia Wildlife Sanctuary received a suite of translocated marsupial herbivores, including bilbies (*Macrois lagotis*), boodies (*Bettongia lesueur*), woylies (*Bettongia penicillata*), bridled nail-tail wallabies (*Onychogalea fraenata*), numbats (*Myrmecobius fasciatus*), and stick-nest rats (*Leporillus apicalis*), all threatened in the wild by predation from introduced cats and foxes (Australian Wildlife Conservancy 2012). Some of these species have very similar habitat requirements and may therefore compete. In such systems, sequential translocations could benefit inferior competitors or small source populations because of...
priority effects, whereby they may offer the first species to arrive at a destination the opportunity to establish robust populations.

As hypothesized, mutualists enjoy a positive benefit from the interaction with a partner, but compared to competitive interactions, this beneficial effect is only small and changes little with translocation timing or interaction strength. Since small mutualist populations near the Allee threshold are unconstrained by resources, the presence or absence of a mutualist partner has no substantial effect on growth rates. Instead, their growth rates are limited by the availability of conspecifics (e.g., for reproduction or foraging success). Our model represents facultative mutualism, whereby the presence of a mutualist increases a species’ carrying capacity, but the species can survive without each other. For example, the inoculation of the endangered plant species, *Abronia macropcarpa*, with arbuscular mycorrhizal fungi has been shown to improve growth and development of germinated plants and is therefore thought to be a viable technique to increase translocation success (Ferrazzano and Williamson 2013). Although we did not model obligate mutualistic interactions, it is conceivable that the positive mutualistic effect is stronger in more specialized interactions.

The survival of the orchid, *Disa draconis*, in the Rondevlei Nature Reserve, South Africa, depends on hand-pollination, because its obligate pollinator, a long-tongued horsefly, disappeared from the reserve due to fragmentation (Milton et al. 1999). This demonstrates the necessity of including mutualists in plant restoration (Menz et al. 2011), particularly orchid conservation (Seaton et al. 2010). Other mutualistic systems are also likely to benefit from the combined translocation of the interaction partners, such as fleshy-fruiting plants and frugivore seed-dispersers (Brodie and Aslan 2011) or native insect pollinators and flowering plants (Aslan et al. 2012).

We have shown that our results are qualitatively robust to some variation in the parameter values and the different decisions available to managers. However, the specific shapes of the success and failure regions will depend on the parameterization and the structure of the interaction models. We focus our investigation on a few key characteristics of deterministic population dynamics because the purpose of this work is to illustrate how interactions add substantial complexity to translocation decisions. In well-understood systems, decision-makers may add other influential processes into the coupled models, such as genetic factors, environmental and demographic stochasticity, and parameter uncertainty. Many of these processes are mentioned in current single-species translocation guidelines (IUCN 2013, Schwartz and Martin 2013), and adding them to our model would increase both the accuracy and complexity of model predictions and management decisions. However, including such complex dynamics for two species would increase the parameterization effort and the additions would only reinforce our central argument: translocating multiple species is much more complex than current guidelines acknowledge.

Some additional considerations that are not accounted in single-species translocation guidelines will have an amplified effect in multispecies projects. Climate change, for instance, is thought to affect species differently in interactive systems (Tylianakis et al. 2008, Singer et al. 2012, Moir et al. 2014). Global warming can disrupt mutualistic interactions when it reduces the phenological overlap of interacting partners (Memmott et al. 2007), leading to shifts in the competitive dominance within species communities and a change in their structure (Araújo and Luoto 2007). Varying dispersal responses, for example, one species may need to migrate further to avoid negative impacts from global warming, could substantially influence the decisions on the optimal timing of translocations (Singer et al. 2012). These issues are particularly important because climate change is a key reason for translocating threatened species in conservation management. Another factor in multispecies translocation planning is the changing extent of interaction strength associated with different life-stages. In many cases only specific life-stages of an organism interact with another species, and even the type of interaction can vary between life stages (de Roux et al. 2013). Such age restrictions will require appropriate distribution of life stages in the founder populations in relation to their interaction partners. For example, the restoration of host-specific hemipteran herbivores in southwest Australia would benefit from planting mature individuals of their only resource, the grasstree *Xanthorrhoea preissii* (Moir et al. 2010). Considering these factors may be necessary for future investigation of multispecies translocations.

**Conclusion**

Anthropogenic movement of interacting species occurs for various different reasons, such as biological control, invasive species, ecosystem restoration, reintroductions, mitigation translocations, and conservation introductions. We have shown that decisions about translocating multiple species are complex and interaction-specific. Our findings indicate that the type of interaction defines the translocation decisions regarding the required founder sizes and the order of translocations. Interacting species that are subject to Allee effects show thresholds for minimum founder population sizes and the position of these thresholds change with interaction type. Simultaneous translocations are possible for all interaction types, provided that appropriate numbers of founders from each population are translocated, and we have shown that higher numbers are not always better (e.g., consumer–resource systems). While competitors and consumer–resource systems benefit from sequential translocations, mutualistic systems show little change in the extinction boundary when one partner is delayed. This complexity in multi-species translocations needs to be acknowledged and emphasized in translocation frameworks and guidelines, which is not occurring at present. Current translocation guidelines either ignore the interdependencies of species (Griffith et al. 1989, Hunter 2007, Hoegh-Guldberg et al. 2008, Richardson et al. 2009, Pérez et al. 2012, Schwartz...
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LITERATURE CITED


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**Data Availability**

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.bh215
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