Assisted colonization is not a viable conservation strategy

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A potential conservation strategy increasingly discussed by conservation biologists is the translocation of species to favorable habitat beyond their native range to protect them from human-induced threats, such as climate change. Even if preceded by careful risk assessment, such action is likely to produce myriad unintended and unpredictable consequences. Accurate risk assessment is impeded by contingency: the impacts of introduced species vary over time and space under the influence of local environmental variables, interspecific interactions and evolutionary change. Some impacts, such as native species extinctions, are large and irrevocable. Here we argue that conservation biologists have not yet developed a sufficient understanding of the impacts of introduced species to make informed decisions regarding species translocations.

A new conservation bandwagon?

Conservation biologists are conflicted by the need for both rigorous scientific research and immediate action on the growing biodiversity crisis. In recent years, several biologists have suggested that proactive mass translocations of species will conserve those species or enhance the biodiversity of a target region. 'Translocation' normally refers to the intentional reintroduction of a species within the range in which it evolved [1]. However, the schemes discussed here entail large-scale transfers of species outside their natural ranges—in other words, planned invasions. These include proposals to (i) re-wild the North American continent with large African mammals [2]; (ii) introduce large numbers of nonnative marine invertebrates and fishes to increase the fishery potential of the North Atlantic Ocean [3]; and (iii) conserve species threatened by climate change and other stressors by transferring them to favorable habitats in another region, a process called 'assisted colonization' or 'assisted migration' [4–6]. Similar schemes have been suggested as early as the 1980s [7], but the threat of global warming in particular has given great impetus to the concept of assisted colonization. Shifts in species ranges associated with prehistoric episodes of climate change occurred over much longer time periods and allowed for coevolution with recipient communities (e.g. [8]), whereas contemporary climate change appears to be much more rapid and could act as a major cause of extinction [9].

The possibility of rescuing threatened populations through translocations guided by decision frameworks and risk assessments [6] no doubt appeals to many practitioners of a field that has long been preoccupied with documenting a gloomy litany of species losses and habitat destruction. Despite a general awareness of the dangers of introducing species to new regions, these schemes are being given attention and credibility in highly respected journals (e.g. *Science* and *Nature*) and at scientific conferences (e.g. a workshop in the 2008 annual meeting of the Ecological Society of America). A recent position paper by the Ecological Society of Australia supports assisted colonization as a management response to climate change (http://www.ecolsoc.org.au/Position_papers/Climate-Change.htm). Other organizations could follow, driven by desperation in the face of anticipated species loss. Indeed, some scientists have claimed that rejecting assisted colonization will 'greatly increase the threat of climate-driven extinction' [4]. At least one private group has already taken matters into its own hands: the 'Torreya Guardians' (http://www.torreyaguardians.org) are planting seeds and seedlings across the eastern USA to expand the range of an endangered conifer, *Torreya taxifolia*, whose modern distribution is confined to the Florida panhandle.

These events signal the emergence among some conservationists of a new philosophy regarding species introductions that is at odds with the traditional objective of preservation. We believe that much of the literature on assisted colonization pays little attention to the importance of evolutionary context in conservation biology and places too much faith in risk assessment. Here we explain why the current predictive understanding of invasions is inadequate to forecast and prevent negative, potentially disastrous, consequences associated with species translocations.

Species translocations can erode biodiversity and disrupt ecosystems

Impacts of most biological invasions are unknown [10], but a burgeoning number of case studies demonstrate a broad range of ecological risks, which we briefly summarize here. Although most invasions appear to have only minor impacts, some cause substantial changes to biotic communities [11] and have a major role in global animal extinctions [12,13]. Biological invasions, regardless of whether they are unintentional or planned, can profoundly affect the composition, development and functioning of ecosystems by altering fundamental processes such as nutrient

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0169-5347/$ – see front matter doi:10.1016/j.tree.2008.12.006

cycling, primary and secondary production, hydrology and disturbance (e.g. fire, erosion and sedimentation) [11,14,15]. They disrupt key ecological interactions, including the plant–animal mutualisms that drive pollination and seed dispersal (e.g. [16]). They also spread parasites and diseases; a notable example is the recent occurrence in northern Europe of the tropical virus 'bluetongue disease,' apparently as a result of climate change and the introduction of infected livestock from a Mediterranean country [17].

The large-scale movement of animals and plants by humans not only spreads pathogens but also promotes their transfer into new host species [18,19]. For example, the introduction of West Nile virus into the USA, probably through unauthorized importation of infected birds from the Middle East [20], appears to have precipitated the declines of several species of North American birds (e.g. the American crow *Corvus brachyrhynchos*) that lacked immunity to the pathogen [21]. Similarly, the introduction of chestnut blight fungus *Cryphonectria parasitica* with Asian nursery stock caused the near extinction of the American chestnut *Castanea dentata*, formerly one of the dominant trees in eastern North America [14]. Human-assisted introductions of predators have also caused species loss in insular habitats worldwide [22–24]. The largest vertebrate mass extinction in modern times occurred in Lake Victoria following the intentional introduction of the Nile perch *Lates niloticus*, which contributed to the disappearance of nearly 200 endemic fish species [23].

Planned introductions carry high risks

Scientists who advocate considering assisted colonization suggest that these serious risks can be reduced by translocations of species within the same continent, particularly if the species is moved into regions where ecologically similar organisms already exist [4,6]. Some argue that the risk of creating novel invasive threats through intracontinental assisted colonization is small, and suggest that careful risk management could render this an effective conservation tool [6,25]. However, even planned introductions can have nonnegligible ecological consequences, as demonstrated by deleterious impacts resulting from the release of carefully selected biological control agents [26,27], organisms meant to enhance fishery potential [23,28] and plants introduced for ornamental or economic reasons [11,14]. A conservation-oriented example is the deliberate introduction of the American red squirrel *Tamiasciurus hudsonicus* to Newfoundland to augment the diet of the pine marten *Martes americana*, a declining species. The squirrels competed with birds for black spruce cones as a primary food source and thus caused the near total extinction of the Newfoundland red crossbill *Loxia curvirostra percna* [29].

Although the most severe impacts are often associated with continent-to-continent and continent-to-island translocations (Figure 1), organisms transferred within a continent can sometimes extirpate native species and disrupt food webs [23,28,30]. Aquatic animals in particular can cause strong impacts, regardless of whether they are introduced within or between continents (Box 1). For example, a North American freshwater shrimp, *Mysis relicta*, was deliberately introduced by wildlife managers into Flathead Lake (Montana, USA) to enhance the diet of another introduced species, kokanee salmon *Oncorhynchus nerka*. The shrimp is nocturnal and spends daylight hours on the bottom of the lake, whereas the salmon feed in shallower waters. Upwelling currents could have made the shrimp accessible to salmon, but these do not occur in Flathead Lake; consequently, the shrimp avoided predation by the

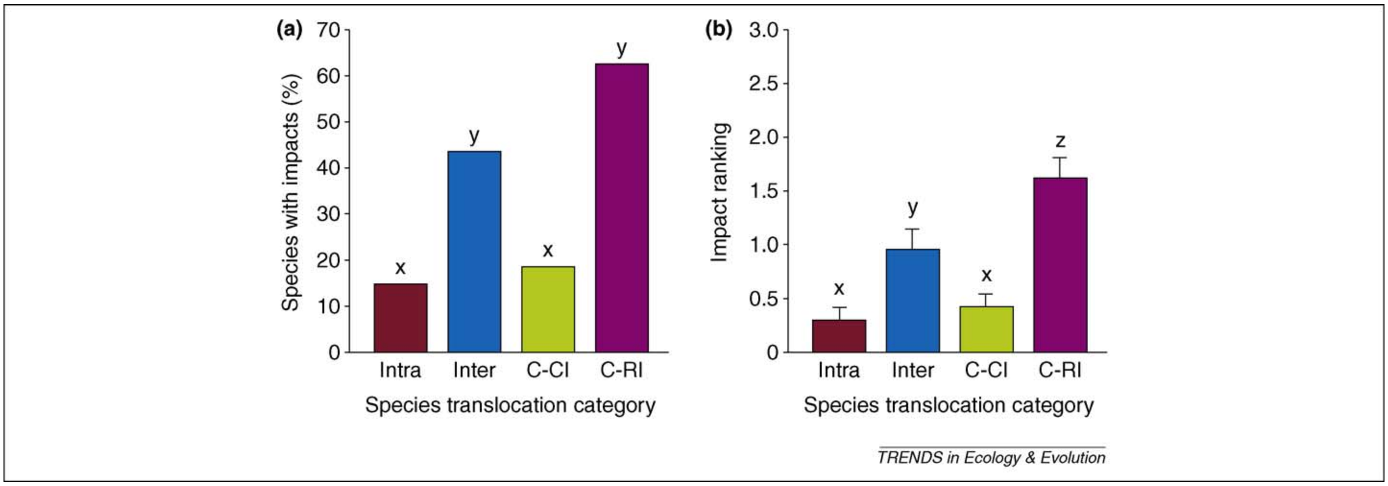

Figure 1. Frequency and severity of impacts of successful translocations of mammals. Translocation categories: Intra = intracontinental; Inter = intercontinental; C-CI = continent-to-coastal island (translocations to islands on the coastal shelf of the native continent of the translocated species); C-RI = continent-to-remote island (oceanic islands or islands on the coastal shelf of a continent beyond the native range of the translocated species). A total of 204 translocations of 152 species were analyzed using data from Ref. [67]. **(a)** Percentage of invading species causing a decline in one or more native species populations. Bars marked with distinct letters differ significantly from each other (Fisher test, $p < 0.05$). **(b)** Mean ranked impact of translocated species, derived from the maximum impact of each species recorded anywhere in the invaded range within each translocation category. Ranks were assigned as follows: 0 = no reported effect on native species abundance; 1 = significant decline of one native species population; 2 = extirpation of one native species population; 3 = multiple declines or extirpations in one or more biogeographic regions it has invaded. Standard error bars are shown. Bars marked with distinct letters differ significantly from each other (Wilcoxon, $p < 0.05$). Intracontinental invasions (Intra) by mammals have a lower risk of strong impacts on biodiversity than intercontinental and continent-to-remote island invasions, but the risk is not negligible; at least 15% of species invading intracontinentally are considered to have negatively affected native populations. Therefore, even if assisted colonization schemes are restricted to intracontinental translocations (as proposed by some advocates, e.g. Ref. [6]), they will not necessarily avoid damaging native species populations in the recipient region (see also Box 1 and Ref. [25]).

Box 1. Impacts of intercontinental versus intracontinental invasions by freshwater fishes

Freshwater fishes are declining more rapidly than are land animals in North America [53] and, therefore, could be prioritized for translocation. In terms of the ecological impacts of introduced fishes, two of the best-studied regions are California (48 nonnative species) and the Great Lakes (22 nonnative species). Statistical analysis suggests that fish invasions, rather than habitat alteration, are the primary driver of population declines and extinctions of native California fishes [54]. The impacts of fish invasions on native species populations in these regions are independent of the origin of the invader (Figure I), suggesting that intracontinental translocations do not pose a lower risk.

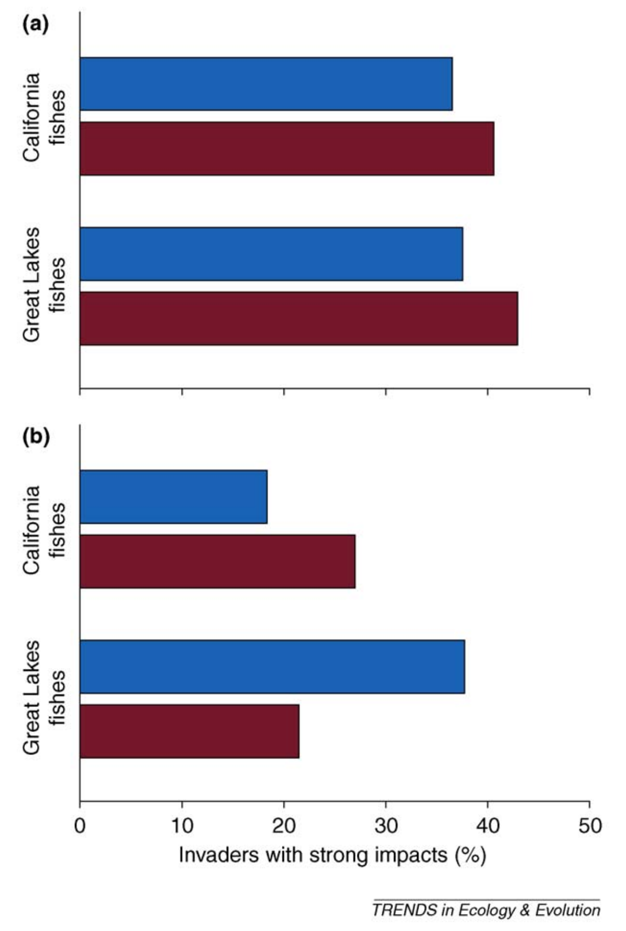

Figure I. Data on the percentage of invaders implicated in **(a)** severe ($>50\%$) decline or extirpation of at least one native species population, and **(b)** declines or extirpations of multiple native species, in California [55–57] and the Great Lakes [58,59]. For either region, intracontinental (brown bars) and intercontinental (blue bars) invaders had similar proportions of species with strong negative impacts (Fisher test, $p > 0.05$).

salmon and effectively became their competitor for food resources. The kokanee population subsequently crashed, followed by a crash in the eagle population that depended on the salmon as a major prey item [28].

The most damaging invaders tend to be those that represent novel life forms in the recipient environment [31], but we cannot safely assume that an introduced plant or animal will be benign solely because it appears similar to a resident species. A case in point is the devastation of native populations of lake trout *Salvelinus namaycush* and other salmonine fishes following the introduction of the predatory sea lamprey *Petromyzon marinus* from the North American Atlantic coast to the upper Great Lakes, where native species of lamprey already existed [30]. Competition with native species is also more likely to occur when a functionally similar species is introduced, and can cause the exclusion of the native species [11,32]. Furthermore, the introduction of nonindigenous species into regions containing close relatives promotes hybridization and introgression that can erode native populations and create new invasive pests (see Box 2 for examples).

Uncertainty and contingency confound risk assessment

Hoegh-Guldberg *et al.* [6] propose that decisions regarding assisted colonization schemes can be guided by an assessment of the costs and benefits of translocation, but fail to recognize that our ability to forecast ecological costs is still

Box 2. The risk of hybridization and introgression

Among the serious ecological risks posed by assisted colonization is increased hybridization. Many cases involving birds, fishes, mammals and plants have demonstrated the potential for extinction by genetic dilution and assimilation when species are brought into contact with relatives from which they had previously been isolated [60–63]. Of greatest concern are threatened species that hybridize so extensively with a common invader that they lose their genetic integrity and thus disappear as distinct species [60]. For example, an endemic fish, the Amistad gambusia *Gambusia amistadensis*, was hybridized to extinction when the freshwater spring it inhabited was submerged in a newly constructed reservoir and it hybridized with introduced mosquitofish [63]. Hybridization with introduced relatives is thought to be at least partially responsible for 15 (31%) of the 48 North American freshwater fish species considered extinct in the wild, including the Amistad gambusia [12,64].

Hybridization events can occur long after a species is introduced. For example, a Japanese smelt, the wakasagi *Hypomesus nipponensis*, intentionally introduced to reservoirs in California in 1959, was assumed to be innocuous until 35 years later, when it appeared in the Sacramento-San Joaquin estuary and began to hybridize with the endangered delta smelt *H. transpacificus* (Figure I) [55,56]. Another danger is that hybridization between an invader and a native can create a new invasive taxon [65,66]. The most famous such case is the globally invading cordgrass *Spartina anglica*, a new species produced in England by hybridization between the introduced North American *Spartina alterniflora* and the native *Spartina maritima*, followed by a spontaneous chromosomal mutation that rendered the sterile hybrid fertile [66]. Such events are among the risks associated with translocations of species into areas where closely related taxa exist.

Figure I. Hybridizing exotic and native species. **(a)** The wakasagi *Hypomesus nipponensis* and **(b)** the endangered delta smelt *Hypomesus transpacificus*. Reproduced with permission from René C. Reyes.

weak [10]. The complex interspecific interactions in the kokanee–shrimp–eagle case described above would have stymied attempts to predict risk by existing methods. Standard techniques for assessing environmental risks posed by chemical pollutants, for example, are not easily extended to introduced species, a stressor that can self-propagate, spread autonomously over large distances and evolve [33]. Until we develop more accurate and general methods of predicting the impact of introduced species, cost–benefit analyses will be dangerously misleading (Figure 2). It is not yet possible to quantify the probability that a given species will go extinct because of climate change, or that a translocated species will harm one or more native species in a recipient community. To compare two such illusory numbers would lead to a false sense of scientific certainty.

At present, conservation managers have few tools that enable them to recognize and prioritize the worst invasion threats reliably. The best predictor is the history of impacts of an invader throughout its invaded range [10,34], but even species with extensive invasion histories can have unpredictable effects. Zebra and quagga mussels (*Dreissena* spp.), which have been spreading across North America for two decades and across Europe for over a century, are deemed largely responsible for outbreaks of avian botulism that have caused the deaths of nearly 80 000 waterfowl in the Great Lakes since 1999 [35]; this impact could not have been anticipated, because it was not previously documented in Europe.

Most candidate species that will be considered for assisted colonization will lack a documented invasion history, as they will not have had previous opportunities for introduction elsewhere. In such cases, procedures for risk assessment for invasions often count as important the question of whether a closely related species has been found to be invasive (e.g. [36]), but even close relatives have sometimes differed enormously in their invasion success and impact [37–39]. For example, two congeneric Eurasian species, the tree sparrow *Passer montanus* and the house sparrow *Passer domesticus*, were deliberately introduced into North America during the 19th century; subsequent range expansion by the former has been slow and limited, whereas the latter has spread through most of North America and has proven to be highly invasive and an aggressive competitor of native birds [40]. Another example is the rusty crayfish *Orconectes rusticus*, which has expanded its range from the Ohio River into the Great Lakes region, where it has displaced native crayfishes, whereas several other *Orconectes* species are declining in North American watersheds [39]. In fact, many high-impact invaders lack similarly harmful relatives and, thus, might have been deemed innocuous by risk assessment if they had no previous invasion history.

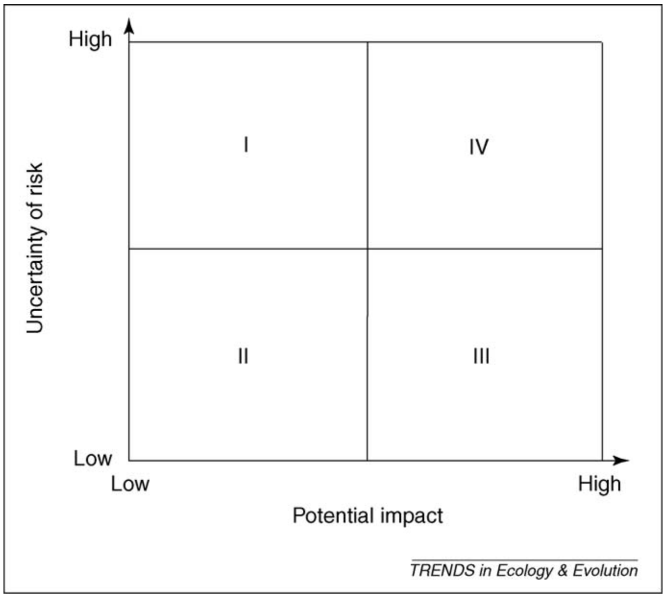

Figure 2. Risk uncertainty versus the potential impact of a species translocation. In principle, translocations should be performed only when uncertainty of risk and the potential impact are minimal, that is, state II. However, given our current predictive power and the context-dependent nature of impact [10] our cost–benefit assessments are likely to be misleading, and many translocations would be performed under the high-risk conditions of state IV (i.e. high uncertainty, high potential impact).

Even species that are threatened in their native ranges could become invasive in a new evolutionary context. For example, the singida tilapia *Oreochromis esculentus* is considered critically endangered in Lake Victoria, where it is endemic, but an invasive pest in some African reservoirs, where it has been introduced [41]. Similarly, the Australian paperbark tree *Melaleuca quinquenervia*, one of the most invasive and damaging plants in Florida, is considered threatened in its native Australia (http://www.invasive.org/eastern/biocontrol/8AutralianPaperbarkTree.html). These cases reflect the fact that the biological traits that promote endangerment are not simply the opposite of those that favor invasiveness [42]. Moreover, invasiveness is not a good predictor of impact; a species that is a poor colonizer could nonetheless exert profound impacts when placed in a particular environment [43].

As the above examples demonstrate, contingency is the largest impediment to prediction. Impacts vary across time and space; an invader can cause the loss of native species from a particular area, while coexisting with the same species in other areas, owing to the influence of local environmental variables [10,34,44]. In addition, interactions with other species [45,46] or other stressors [47,48] can produce a multitude of indirect effects, nonlinearities and synergistic impacts that are difficult to forecast. Introduced species can facilitate each other's establishment or population expansion (e.g. when an animal pollinates and disperses a plant), with significant consequences for the entire community; such interactions can cause previously benign species to become invasive and disruptive quickly [45].

Lag times in the spread or onset of impacts of invaders are a common phenomenon [49]. The impacts of an introduction might not be fully realized until decades after the human-assisted transfer and cultivation of a species [50]. Thus, introductions that initially seem inconsequential can later prove to be harmful when it is no longer feasible to control them. One factor contributing to this phenomenon is the interaction of the invader with multiple environmental drivers that change with time, including climate change. For example, a combination of unrelated human-induced changes caused a nonindigenous plant (tree mallow, *Lavatera arborea*) along the Scottish coastline to become invasive suddenly after several decades, resulting in a loss of native vegetation and a >50% decline in a breeding population of seabirds [48]. Another factor contributing to lags is evolution, sometimes rapid, of the invader or native species in the invaded range. Immersed in novel habitat conditions, introduced species are frequently able to undergo swift adaptations involving their behavior, physiology, morphology and life history [51], all of which modulate their impacts in the invaded region. Native species can experience similar adaptive changes that are largely unpredictable [51,52]. All of these factors contribute to tremendous uncertainty in the outcome of a species introduction and, thus, render risk assessments and decision frameworks unreliable.

Ecological gambling versus the precautionary principle

Those proposing assisted colonization as a conservation tool have argued that the risks of large-scale species translocations must be 'weighed against those of extinction and ecosystem loss' [6], but the latter risks are precisely those posed by introducing species outside their historical range. At present, these risks cannot be reliably estimated or anticipated, which underscores our need to develop a predictive understanding of invasions and their impacts. Given this lack of predictive power, assisted colonization is tantamount to ecological roulette and should probably be rejected as a sound conservation strategy by the precautionary principle. Despite initial intentions to use such a strategy only as a 'tool of last resort,' there could be growing pressure to move species long before their populations begin to decline and their densities become low, because these conditions reduce the success of translocation [1]. We are concerned that increasing consideration of assisted colonization will promote unauthorized introductions of species by well-intentioned individuals, impede efforts to preserve habitat and, ultimately, create more conservation problems than it solves.

In attempting to facilitate the persistence of threatened species, it is crucial to develop methods to increase the effectiveness of existing conservation measures (e.g. captive breeding, local population enhancement, habitat restoration) and, above all, mitigate human-induced stressors such as climate change; but there are many reasons to be skeptical about future conservation schemes that rely upon large-scale species translocation.

Acknowledgements

We thank Jessica Hellmann and two anonymous reviewers for their comments. Funding to A.R. by the Canadian Aquatic Invasive Species Network is gratefully acknowledged.

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