Conservation Biology

Review

The Potential Conservation Value of Non-Native Species

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Abstract: *Non-native species can cause the loss of biological diversity (i.e., genetic, species, and ecosystem diversity) and threaten the well-being of humans when they become invasive. In some cases, however, they can also provide conservation benefits. We examined the ways in which non-native species currently contribute to conservation objectives. These include, for example, providing habitat or food resources to rare species, serving as functional substitutes for extinct taxa, and providing desirable ecosystem functions. We speculate that non-native species might contribute to achieving conservation goals in the future because they may be more likely than native species to persist and provide ecosystem services in areas where climate and land use are changing rapidly and because they may evolve into new and endemic taxa. The management of non-native species and their potential integration into conservation plans depends on how conservation goals are set in the future. A fraction of non-native species will continue to cause biological and economic damage, and substantial uncertainty surrounds the potential future effects of all non-native species. Nevertheless, we predict the proportion of non-native species that are viewed as benign or even desirable will slowly increase over time as their potential contributions to society and to achieving conservation objectives become well recognized and realized.*

Keywords: evolution, exotic species, invasive species, management, non-native species, restoration

El Valor de Conservación Potencial de Especies No Nativas

Resumen: *Las especies exóticas pueden causar la pérdida de diversidad biológica (i. e., diversidad genética, de especies y ecosistemas) y amenazar el bienestar de humanos cuando se vuelven invasoras. Sin embargo, en algunos casos también pueden proporcionar beneficios de conservación. Examinamos las formas en que las especies exóticas contribuyen actualmente a objetivos de conservación. Estos incluyen, por ejemplo, proporcionar hábitat o recursos alimenticios para especies raras, fungir como sustitutos funcionales de taxa extintos y proporcionar funciones ecosistémicas deseables. Especulamos que las especies exóticas pueden contribuir a lograr metas de conservación en el futuro porque su probabilidad de persistir y proporcionar servicios ecosistémicos es mayor que la de especies nativas en áreas donde el clima y el uso de suelos están cambiando rápidamente y porque pueden evolucionar hacia taxa nuevos y endémicos. El manejo de especies exóticas y su potencial integración en planes de conservación depende de cómo se definen las metas de conservación en el futuro. Una fracción de especies exóticas continuará causando daños biológicos y económicos, y una considerable incertidumbre rodea a los futuros efectos potenciales de todas las especies exóticas. Sin embargo, pronosticamos que la proporción de especies exóticas que son vistas como benignas*

Paper submitted May 29, 2010; revised manuscript accepted November 3, 2010.

Conservation Biology, Volume 25, No. 3, 428–437

DOI: 10.1111/j.1523-1739.2010.01646.x

o aun deseables incrementará lentamente con el tiempo a medida que sus contribuciones potenciales a la sociedad y al logro de objetivos de conservación sean bien reconocidas y entendidas.

Palabras Clave: especies exóticas, especies invasoras, especies no nativas, evolución, manejo, restauración

Introduction

Non-native species present a range of threats to native ecosystems and human well-being. Non-native predators and herbivores can cause extinctions of native species, particularly on islands and in freshwater ecosystems (Wilcove et al. 1998; Mooney & Hobbs 2000; Sax & Gaines 2008). Furthermore, they can alter the functioning of ecosystems and can carry infectious diseases that can endanger native species and human health (Vitousek et al. 1996; Daszak et al. 2000; Ehrenfeld 2003). By damaging commercial crops and interfering with industrial activities, non-native species are responsible for annual economic losses on the order of billions of U.S. dollars per year (Pimentel et al. 2005). As a result governmental agencies and nongovernmental organizations are frequently mandated or have chosen to prevent the introduction of non-native species and minimize their negative effects (Millennium Ecosystem Assessment 2005; Lodge et al. 2006).

Not all non-native species cause biological or economic harm, and only a fraction become established and have an effect that is considered harmful (Williamson & Fitter 1996; Davis 2009). But non-native species can also have desirable effects on an ecosystem. For example, numerous species have been repeatedly and deliberately introduced outside their native range for agricultural, ornamental, and recreational purposes (Ewel et al. 1999). As a result non-native species are integral to the culture and economies of most countries. There have also been numerous recent examples of non-native species contributing to achievement of conservation objectives (e.g., Westman 1990; D'Antonio & Meyerson 2002; Gozlan 2008).

Subjective Views of Non-Native Species

Scientific and societal perceptions of non-native species have likely impeded consideration of the potential beneficial effects of non-native species. Most scientists investigating the effects of non-native species try to conduct their work objectively; nevertheless, several authors have demonstrated that a bias persists against non-native species among scientists (Slobodkin 2001; Gurevitch & Padilla 2004; Stromberg et al. 2009). These biases are reflected in the assumptions commonly made about the intrinsic and instrumental values of non-native species, the language used when describing them, and in the types of studies conducted (Sagoff 2005). For example, in a landmark study in which the response of biological diversity (encompassing genetic, species, and ecosystem diversity) to several natural and anthropogenic drivers were predicted, Sala et al. (2000) considered non-native species only as potential threats, not as contributors to a region's species richness. Furthermore, in studies in which an index of biotic integrity was used, the presence of non-native species decreases the index value even if the non-native species have no or little detectable biological effect (Parker et al. 1999). Finally, the language used to describe non-native species in the scientific literature is frequently scattered with militarized and xenophobic expressions (e.g., "war on aliens" and "American ecosystems under siege by alien invaders") (e.g., Peretti 1998; Krajick 2005; Larson 2005).

The consequences of these biases are difficult to quantify, but they almost certainly have resulted in an emphasis on documenting the negative economic and biological effects of non-native species (Pyšek et al. 2008). Studies that fail to find a negative effect (e.g., Nielsen et al. 2008) are likely underreported. Furthermore, numerous researchers have evaluated the economic costs associated with non-native species, and syntheses that estimate the total economic effect of non-native species (e.g., Pimentel et al. 2005; McIntosh et al. 2009) attract substantial attention. By contrast, relatively few researchers have quantified the economic benefits (e.g., value of pollination by non-native bees, fees paid to hunt non-native game) derived from non-native species (but see Southwick & Southwick 1992; Ackefors 1999; Pascual et al. 2009). As a result, there has not been a comprehensive review of the economic benefits provided by non-native species. The direct economic costs associated with wild and feral non-native species may well be greater than the income they generate, but we think both costs and income should be quantified.

We had two aims here. First, we sought to catalog the possible ways in which non-native species can help achieve conservation objectives. We did not review all the known negative effects of non-native species because these have been described exhaustively (e.g., Mooney & Hobbs 2000; Lodge et al. 2006). We also did not focus on economic or human-health effects. Instead, we considered examples of unplanned and intentional introductions of non-native species that contributed to achieving conservation objectives. We use the term *non-native* for species that occur outside of their historic range and *invasive* for cases in which these species cause biological, social, or economic harm.

Second, we investigated the role of non-native species in the broader context of setting conservation objectives. Traditionally, conservation goals have been defined by historical, static benchmarks aimed at protecting flagship species and "pristine" ecosystems and their putative integrity and stability (Forum 2004). But many non-native species are firmly established in their recipient ecosystems and cannot be eradicated; thus, novel approaches are required to manage them (Schlaepfer et al. 2005; Norton 2009). Furthermore, the negative and positive effects of non-native species vary over time, as will the manner in which these effects are perceived by humans, which in turn will have large effects on how non-native species are managed (Maris & Béchet 2010).

Current Uses of Non-Native Species to Conserve and Restore Species and Ecosystems

Many conservation efforts focus on the protection of genes, species, ecosystems, and their interactions. Numerous researchers have documented the various ways in which non-native species positively contribute to achieving conservation goals either serendipitously (Table 1) or intentionally (Table 2). Conservation benefits include providing habitat, food, or trophic subsidies for native species, serving as catalysts for the restoration of native species, serving as substitutes for extinct ecosystem engineers, and providing ecosystem services.

Shelter and Food for Native Species

Non-native species can provide shelter (e.g., Wonham et al. 2005; Severns & Warren 2008) or be a nutritional resource (e.g., Bulleri et al. 2006; Carlsson et al. 2009) for native species. The potential role of non-native species in providing resources for rare native species is likely to be particularly important in situations when restoration of the native species that formerly provided shelter or an energy source is impractical due to limited economic resources or changes in the physical environment (e.g., Zavaleta et al. 2001; Hershner & Havens 2008). In the case of the non-native tamarisk (*Tamarix* spp.), preconceived notions appear to have contributed to an underestimation of its potential contributions to conservation. Tamarisk is a non-native woody plant that has become relatively common in riparian areas throughout the southwestern United States as a result of human activity and changes in hydrology (Stromberg et al. 2009). Initial reports suggested tamarisk were causing a drop in water table levels and reducing habitat quantity and quality for native riparian species, including the Southwestern Willow Flycatcher (*Empidonax traillii extimus*), which is listed as endangered under the U.S. Endangered Species Act. As a result millions of U.S. dollars were spent removing tamarisk with mechanical treatments, herbicides, and a herbivorous beetle (*Diorabda elongate*) (DeLoach et al. 2006). Nevertheless, results of recent field studies reveal that in some areas up to 75% of the Southwestern Willow Flycatchers nest in tamarisk and that fledgling success associated with nests built in tamarisk was indistinguishable from success associated with nests built in native trees (Ellis et al. 2008; Sogge et al. 2008). In a recent review Stromberg et al. (2009) argue that many undesirable changes to water tables and displacement of native biota attributed to tamarisk are exaggerated or unfounded.

Given the substantial modification to flooding regimes by dams throughout the southwestern United States, it may be difficult in many areas to reestablish native taxa that formerly supported the Flycatcher. Thus, although removing tamarisk may provide a step toward restoring historic vegetation in these regions, doing so may unexpectedly cause direct harm to an endangered native species that now depends in part on tamarisk (Zavaleta et al. 2001; Shafroth et al. 2008). In locations with multiple non-native species, the control or eradication of one species will not necessarily result in the desired outcome because species interactions may be altered (Courchamp et al. 2003; Norton 2009; Chiba 2010).

Catalysts for Restoration

Non-native species that increase structural heterogeneity or complexity of an area are positively correlated with increases in abundance or species richness (Crooks 2002), and in some instances non-native species may therefore be useful catalysts for ecosystem restoration (Ewel & Putz 2004) (Tables 1 & 2). For example, former pastures with sparse vegetation and eroded soils in Puerto Rico (U.S.A.) are not readily recolonized by native trees. By contrast, non-native plantation trees are able to survive and subsequently attract seed dispersers and establish microclimates in which native plants can reestablish (Lugo 1997; Rodriguez 2006). In one study, 20 native woody species recolonized deforested land 8 years after non-native trees were planted, whereas only one native woody species colonized unplanted control plots (Parrotta 1999).

Substitutes for Extinct Taxa

Non-native species are sometimes deliberately introduced to fill an ecological niche formerly occupied by a closely related species (Donlan et al. 2006; Griffiths et al. 2010) (Table 2). Non-native species do not have the same cultural and historical value as native species, but they have been used as acceptable ecological substitutes in cases where the benefits of their ecological function are perceived to exceed the potential risks of introducing a non-native species. For example, Aldabra giant tortoises (*Aldabrachelys gigantea*) have been introduced to several small islands surrounding Mauritius, where they appear to have successfully

Table 1. Examples of positive (+) and negative (−) roles of non-native species that were not intentionally introduced for conservation purposes.*

Purpose	*Example*	*Reference*
Habitat, shelter, and food for native species	+non-native tamarisk (*Tamarix* spp.) provides nesting habitat for Southwestern Willow Flycatcher (*Empidonax traillii extimus*)	Sogge et al. 2008; Stromberg et al. 2009
	+ native butterflies oviposit or feed on non-native plants in California, U.S.A.	Graves & Shapiro 2003
	+ reclaimed mine grasslands composed of non-native species provide habitat for Henslow's Sparrow (*Ammodramus henslowii*) in Indiana, U.S.A.	Bajema et al. 2009
	+ non-native melaleuca (*Melaleuca quinquinervia*) provides habitat for Snail Kite (*Rostrhamus sociabilis plumbeus*) in the Everglades (Florida, U.S.A.);	Chen 2001
	− non-native melaleuca may cause decrease in the kite's primary food source, apple snail (*Pomacea paladusa*)	Chen 2001
	+ non-native mudsnail (*Potamopyrgus antipodarum*) abundant prey item for native fish in western U.S.A.	Vinson & Baker 2008
	− non-native mudsnail are food for native rainbow trout (*Oncorhynchus mykiss*) but when fish feed exclusively on mudsnails they lose 0.5% of body weight per day	Vinson & Baker 2008
	+ native avian predators in Spain increase in abundance as a result of foraging on non-native crayfish (*Procambarus clarkii*)	Tablado et al. 2010
	+ non-native plant (*Casuarina*) protects native snails (*Ogasawarana optima* and *O. discrpans*) in Japan from predation by non-native black rats (*Rattus rattus*)	Chiba 2010
Catalysts for restoration	+ non-native guava trees (*Psidium guajava*) support native frugivorous birds and promote forest regeneration via seed dispersal in Kenya	Berens et al. 2008
	+ non-native trees established on abandoned pastures facilitate restoration of native tree species in Puerto Rico	Lugo 2004
	+ non-native zebra mussel (*Dreissena polymorpha*) filters water and control toxic cyanobacteria in shallow eutrophic lakes	Elliot et al. 2008; Dionisio Pires et al. 2009
Ecosystem engineers	+ non-native birds in Hawaii disperse native plant seeds	Foster & Robinson 2007
	+ non-native Pacific oyster (*Crassostrea gigas*) colonizes unvegetated tideflats and forms hard reefs thereby increasing densities of native invertebrate species relative to native oyster beds	Ruesink et al. 2005
	+ non-native ascidian in intertidal waters in Chile creates dense three-dimensional structural matrix that increases local and regional species richness	Castilla et al. 2004
Ecosystem services	+ non-native African honey bees (*Apis mellifera*) pollinate native plants in fragmented forest landscapes in Brazil and Australia	Dick 2001; Gross 2001
	+ pollination of the ieie vine (*Freycinetia arborea*) in Hawaii by non-native Japanese White-eye (*Zosterops japonica*) replaces the role formerly held by now-extinct native birds	Cox 1983
	+ biofiltration rates of non-native Pacific oyster (*Crassostrea gigas*) in estuaries may reduce production of phytoplankton caused by anthropogenic nutrient loading	NRC 2004

*Negative roles listed are not exhaustive and include only those that directly oppose the listed positive roles. Many of the non-native species listed have other negative effects on conservation objectives.

Table 2. Examples of positive (+) and unintended negative (−) roles of non-native species that were intentionally introduced for conservation purposes.*

Purpose	*Example*	*Reference*
Habitat, shelter, and food for native species	+ American shad (*Alosa sapidissima*) introduced into the Columbia River Basin and California as a forage fish for Pacific salmonids	Petersen et al. 2003
	+ non-native crayfish introduced across North America to provide forage for recreational fishes (e.g., largemouth bass [*Micropterus salmoides*])	Kats & Ferrer 2003
	− introduced non-native crayfish resulted in declines of several native amphibian taxa	Kats & Ferrer 2003
Catalysts for native species	+ non-native trees planted on abandoned pastures to facilitate restoration of native tree restoration species in Puerto Rico	Lugo 1997
	+ non-native cattle maintain early-successional vegetation that favors native fishes and reptiles	Brown & McDonald 1995; Tesauro & Ehrenfeld 2007
	− removal of cattle may result in proliferation of non-native grasses, which would have detrimental effects on the vulnerable (IUCN Red List) native skink (*Cyclodina whitakeri*)	Norton 2009
	+ non-native black locust (*Robinia pseudoacacia*) provides cover and restores soil fertility on mined lands	Ashby 1987
	+ European legume gorse (*Ulex europaeus*) acts as a nurse plant for native forest regeneration in New Zealand in old fields once livestock grazing stops	Sullivan et al. 2007
	− plant succession under European legume gorse follows a different trajectory resulting in lower species richness of native forest species	Sullivan et al. 2007
Taxon substitution	+ Aldabra giant tortoise (*Aldabrachelys gigantea*) replaces the ecological role of extinct giant *Cylindraspis* tortoises in the Mascarene Islands	Griffiths & Harris 2010
Ecosystem services	+ non-native *Chrysolina* beetles control invasive St. John's wort (*Hypericum perforatum*) in Australia and North America	Morrison et al. 1998
	− failed biocontrol of non-native cane beetle (*Dermolepida albohirtum*) through introduction of non-native cane toad (*Bufo marinus*) in Australia	Lever 2001
Preservation of species	+ species are transplanted to islands outside their historical range to mediate threats from non-native predators or transplanted poleward to mediate concerns about species' ability to shift their distributions in response to changing climate	Jolly & Colbourne 1991; Fontenot et al. 2006; Richardson et al. 2009; Willis et al. 2009

*Negative roles listed here are not exhaustive and include only those that directly oppose the listed positive roles. Many of the non-native species listed have other negative effects on conservation objectives.

substituted the herbivory and seed-dispersal functions of native tortoises that recently became extinct (Griffiths et al. 2010).

In other cases the substitute roles provided by non-native species have been more serendipitous (Table 1). For example, in Hawaii (U.S.A.), non-native species of birds are now the primary dispersers of seeds and fruits of some native plant species with native dispersers that have become extinct or been extirpated from lowland vegetation (Foster & Robinson 2007). Non-native birds may have contributed to the extinction of several native bird species (by serving as vectors of avian malaria to which native bird species are susceptible (Kilpatrick 2006)), but the remaining native species of plants and current ecosystems may now depend on the ecological roles of such substitute species.

Augmenting Ecosystem Services

Non-native species can alter and degrade ecosystem services, but in other cases they can also provide or augment ecosystem services (Pejchar & Mooney 2009). For instance, non-native species can serve as plant pollinators, especially in fragmented landscapes. Dick (2001) found that native pollinators are absent from forest fragments in Amazonia, Brazil, but that non-native African honey bees (*Apis mellifera scutellata*) move between forest fragments. Honey bees therefore not only pollinate the tall, native, canopy-emergent trees, but also ensure long-distance gene flow between forest fragments. In Utah (U.S.A.) non-native plants provide nectar and pollen to insects, thereby increasing the carrying capacity of both generalist and specialist native pollinators (Tepedino et al. 2008). In a review of the ecological effects of 2 non-native wetland plant species (*Hydrilla verticillata* and *Phragmites australis*) in North America, Hershner and Havens (2008) suggest these plants provide as much or more waterfowl habitat, biomass production, and nitrogen retention than native wetland plant species, although *H. verticillata* also decreases habitat quality for native fishes (Hershner & Havens 2008).

Non-native species can function as biocontrol agents to limit undesirable effects of invasive non-native species in both agricultural and natural settings. Introduced natural enemies have prevented the loss of billions of dollars and saved human lives by limiting the abundance of agricultural pests such as cottony cushion scale (*Icerya purchasi*) and cassava mealybug (*Phaenococcus manihoti*) (Messing & Wright 2006). Biocontrol agents, however, are sometimes less host-specific than initially thought and may parasitize native species. There is also the potential than novel host preferences may evolve over time (Messing & Wright 2006; Thomas & Reid 2007).

Future Role of Non-Native Species

A subset of non-native species will undoubtedly continue to cause biological, economic, and social harm. But we venture that other non-native species could become increasingly appreciated for their tolerance and adaptability to novel ecological conditions and their contributions to ecosystem resilience and to future speciation events.

Ecological Roles in Rapidly Changing Ecosystems

Non-native species could come to fill important ecosystem and aesthetic functions, particularly in places where native species cannot persist due to environmental changes. Indeed, some non-native species may be preadapted or adapt rapidly to the novel ecological conditions (Byers 2002). Furthermore, the ability of non-native species to tolerate and adapt to a broad range of biotic and abiotic conditions, as well as to expand their ranges rapidly, suggests they may persist under a variety of future climate scenarios (Dukes & Mooney 1999; Muth & Pigliucci 2007; Williams & Jackson 2007).

Non-native species contribute to local species richness (Sax & Gaines 2008) and thus may also contribute to ecosystem resilience and stability. Research has focused on species interactions (e.g., predation, herbivory) that can lead to declines in abundance of native species. Nevertheless, much less attention has been given to how food webs may be altered by the presence of non-native species (although see Byrnes et al. 2007) and whether long periods of time are necessary for strong positive links to form among species. Certainly, ecosystems that are composed mostly of non-native species can have complex species interactions and community structure (Wilkinson 2004). Therefore, it seems likely that non-native species will often contribute to some of the putative benefits of species-rich ecosystems, such as increased productivity and stability (Hooper et al. 2005; Cardinale et al. 2007), but this proposition has not been tested.

Novel Evolutionary Lineages

Given sufficient time, non-native species can increase global species richness through speciation. In situations in which gene flow is absent or low between a species' native and introduced populations, the combination of adaptation to novel selective regimes in the introduced region and drift (particularly with small founder populations) is expected to result in genetic divergence between native and introduced populations (Hendry et al. 2007). Divergent selective pressures can also rapidly arise among introduced populations (Lee 2002). For example, distinct subpopulations of European house sparrows (*Passer domesticus*) have evolved since 1850 in ecosystems in North America that range from deserts to moist, temperate forests (Johnston & Selander 1964).

Non-native species can also contribute to the formation of novel evolutionary lineages among native species. For instance, native soapberry bugs (*Jadera haematoloma*) have colonized non-native plants in the soapberry family in North America, where their lineages have diverged from bugs that remained on the original host (Carroll et al. 1997). Ultimately, such distinct lineages are likely to give rise to reproductively isolated, endemic species. Although speciation is generally believed to occur over centuries or longer, evidence of reproductive isolation was documented in allopatric populations of introduced salmonids after fewer than 13 generations (Hendry et al. 2000).

Non-native species can also catalyze hybridization events between native species that result in novel evolutionary lineages. For example, the *Lonicera* fly is a novel native species that resulted from the hybridization of two native *Rhagoletis* fly species. The parental fly species normally specialize on different native host plants and so rarely encounter each other. But both parental species occasionally visit the invasive honeysuckle (from the *Lonicera tatarica* complex) since its introduction to North America (Schwarz et al. 2007). Thus, the invasive plant provides a location for hybridization to occur. The plant now also serves as a resource on which the novel *Rhagoletis* hybrid species has become specialized.

Speciation events can also result from hybridization between certain non-native and native species and between pairs of non-native species (Vellend et al. 2007). For example, repeated speciation events of salsify (*Tragopogon* spp.) plants have occurred following their hybridization with multiple species introduced to the United States (e.g., Tate et al. 2006). Thus, although non-native species initially contribute to the homogenization of the world's biota (Olden et al. 2004) and may cause a delayed extinction debt (Jackson & Sax 2010), they also represent the source material for future speciation events and could eventually result in instances of evolutionary diversification. A conservation strategy that eradicates species simply because they are non-native could undermine the very biological entities that may be the most likely to succeed in a rapidly changing world.

Managing Non-Native Species

Efforts to manage non-native species generally focus on two approaches that have proven effective: preventing the introduction of novel species that are likely to become invasive and, in the event a non-native species is introduced and rapidly detected, controlling or eradicating the species (Lodge et al. 2006). Challenges to managing non-native species that are firmly established include uncertainties over future effects of a non-native species, divergent values among stakeholders, varying interpretations of sometimes sparse historical records, and dynamic conservation goals.

The future effects of a non-native species are uncertain because biotic interactions are notoriously difficult to predict and because current and future environmental conditions may differ substantially (Walther et al. 2009). For example, expected positive effects will not necessarily be realized. In addition, non-native species may become invasive at some point in the future and potentially result in the extirpation or extinction of other species. These uncertainties have led some to assume all non-native species undesirable until proven otherwise (e.g., Ricciardi & Simberloff 2009). We disagree with this perspective because it assumes the magnitude of negative effects will always be greater than the positive effects. Risk analyses may reveal that some non-native species are more likely to have positive impacts.

Major sources of uncertainty are not only whether a species will become invasive in the future, but also for how long negative effects will persist. Theoretically, there will be strong selective advantage for species that exploit an abundant non-native species; thus, initial negative effects are not expected to endure indefinitely. Empirically, the abundance of some non-native species declines after a period of initial growth (Simberloff & Gibbons 2004; Hawkes 2007), but there is insufficient data to predict how long this growth period will last.

Cost-benefit analyses of any management option for non-native species must include the subjective valuation of species (Evans et al. 2008; Sandler 2010). Stakeholders frequently have different value systems and prefer different management outcomes. There may be strong differences in opinion even among individual conservation professionals. For example, some place a premium on the integrity of native ecosystems or fear the future negative effects of non-native species (Ricciardi & Simberloff 2009), whereas others may value the ecosystem function provided by a non-native species (Dudgeon & Smith 2006) or the potential of translocation to preserve species in the wild (Hoegh-Guldberg et al. 2008).

A recurring issue in the valuation of non-native species is whether a species "belongs" to a given region. Strong opposition to non-native species comes from those who wish to retain the historical character of a region. We argue that the character of a region is likely to change over time as a non-native species becomes naturalized and humans grow accustomed to its presence. Evidence of such changes in normative values is already apparent in citizen groups that mobilize for the protection of non-native species such as the dingo (*Canis lupus dingo*) in Australia and *Eucalyptus* trees and Red-masked Parakeets (*Aratinga erythrogenys*) in California (U.S.A.). Philosophically, we question how human actions differ from those of other species. In other words, why is a dispersal event that is facilitated by, say, a migratory bird or storm event (e.g., Censky et al. 1998) considered natural, whereas a human-transported species is non-native and thus undesirable (Brown & Sax 2005; Cassey et al. 2005)? Furthermore, the past distributions and dispersal events of most species are poorly known, and this reduces one's ability to clearly distinguish native from non-native species, especially for lesser-known taxonomic groups (Carlton 1996). Because of these uncertainties and philosophical differences, we believe it is preferable to distinguish species on the basis of how long they have been present with terms such as *long-term resident species*, *recently arrived species*, and *new species* (Pyšek et al. 2004; Davis 2009). We surmise that species will increasingly be evaluated for reasons independent of their recent range distributions.

Because communities and species characteristics are so dynamic (e.g., Mace & Purvis 2008; Hobbs et al. 2009), we anticipate that conservation professionals will increasingly look toward the future rather than to the past when setting benchmarks and devising strategies. Instead of determining what species formerly occurred in an area and how to restore these species, they might determine what they want the area to look like in the future. Species that are economically or biologically damaging will likely be controlled, regardless of their historic origin. Conversely, species that are considered desirable for their aesthetic beauty, rarity, economic, or intrinsic value will likely be protected, subsidized, or left alone, regardless of whether their former status was native or non-native (Briggs 2008; Hoegh-Guldberg et al. 2008). In the past, risk analyses focused on negative events associated with non-native species, and a species was termed invasive if any significant negative effect was documented. Here, we suggest that both negative and positive potential effects of non-native species should be tallied. We also suggest that a more meaningful definition of an invasive species would be one for which there is a *net* negative effect. A dynamic view of nature that recognizes that species characteristics and human valuations thereof change over time, not only reflects ongoing evolutionary processes, but also leads to a more balanced and objective approach to the management of non-native species.

Acknowledgments

We thank B. Blossey and his laboratory group, K. Schulz and the Aqua-lunch group, T.A. Gavin, P. Kareiva, K. Smith, J. Fridley, J. Stella, and two anonymous reviewers for discussion and comments on previous versions of this manuscript.

Literature Cited

Ackefors, H. 1999. The positive effects of established crayfish introductions in Europe. Pages 49–61 in F. Gherardi and D. M. Holdich, editors. Crayfish in Europe as alien species. A.A. Balkema, Rotterdam, The Netherlands.

Ashby, W. C. 1987. Forests in W. R. Jordan III, M. E. Gilpin, and J. D. Aber, editors. Restoration ecology. Cambridge University Press, New York.

Bajema, R. A., T. L. DeVault, P. E. Scott, and S. L. Lima. 2009. Reclaimed coal mine grasslands and their significance for Henslow's Sparrows in the American Midwest. The Auk **118:**422–431.

Berens, D. G., N. Farwig, G. Schaab, and K. Böhning-Gaese. 2008. Exotic guavas are foci of forest regeneration in Kenyan farmland. Biotropica **40:**104–112.

Briggs, J. C. 2008. The North Atlantic Ocean: need for proactive management. Fisheries **33:**180–185.

Brown, J. H., and W. McDonald. 1995. Livestock grazing and conservation on southwestern rangelands. Conservation Biology **9:**1644–1647.

Brown, J. H., and D. F. Sax. 2005. Biological invasions and scientific objectivity: reply to Cassey et al. Austral Ecology **30:**481–483.

Bulleri, F., L. Airoldi, G. M. Branca, and M. Abbiati. 2006. Positive effects of the introduced green alga, *Codium fragile* ssp. *tomentosoides*, on recruitment and survival of mussels. Marine Biology **148:**1213–1220.

Byers, J. E. 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos **97:**449–458.

Byrnes, J. E., P. L. Reynolds, and J. J. Stachowicz. 2007. Invasions and extinctions reshape coastal marine food webs. Public Library of Science ONE **2:**e295. DOI:10.1371/journal.pone.0000295.

Cardinale, B. J., J. P. Wrigh, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau, and J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. Proceedings of the National Academy of Sciences of the United States of America **104:**18123–18128.

Carlsson, N. O., O. Sarnelle, and D. L. Strayer. 2009. Native predators and exotic prey – an acquired taste? Frontiers in Ecology and the Environment **7:**525–532.

Carlton, J. T. 1996. Biological invasions and cryptogenic species. Ecology **77:**1653–1655.

Carroll, S. P., H. Dingle, and S. P. Klassen. 1997. Genetic differentiation of fitness-associated traits among rapidly evolving populations of the soapberry bug. Evolution **51:**1182–1188.

Cassey, P., T. M. Blackburn, R. P. Duncan, and S. L. Chown. 2005. Concerning invasive species: reply to Brown and Sax. Austral Ecology **30:**475–480.

Castilla, J. C., N. A. Lagos, and M. Cerda. 2004. Marine ecosystem engineering by the alien ascidian *Pyura praeputialis* on a mid-intertidal rocky shore. Marine Ecology Progress Series **268:**119–130.

Censky, E. J., K. Hodge, and J. Dudley. 1998. Over-water dispersal of lizards due to hurricanes. Nature **395:**556.

Chen, L. Y. 2001. Cost savings from properly managing endangered species habitats. Natural Areas Journal **21:**197–203.

Chiba, S. 2010. Invasive non-native species' provision of refugia for endangered native species. Conservation Biology **24:**1141–1147.

Courchamp, F., J.-L. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: impact, control and control impact. Biological Reviews **78:**347–383.

Cox, P. A. 1983. Extinction of the Hawaiian avifauna resulted in a change of pollinators for the ieie, *Freycinetia arborea*. Oikos **41:**195–199.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos **97:**153–166.

D'Antonio, C., and L. A. Meyerson. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restoration Ecology **10:**703–713.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife- threats to biodiversity and human health. Science **287:**443–449.

Davis, M. A. 2009. Invasion biology. Oxford University Press, Oxford, United Kingdom.

DeLoach, C. J., et al. 2006. Overview of saltcedar biological control. Pages 92–99 in C. Aguirre-Bravo, P. J. Pellicane, D. P. Burns, and S. Draggan, editors. Monitoring science and technology symposium: unifying knowledge for sustainability in the Western Hemisphere. Proceedings RMRS-P-42CD. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Dick, C. W. 2001. Genetic rescue of remnant tropical trees by an alien pollinator. Proceedings of the Royal Society B-Biological Sciences **268:**2391–2396.

Dionisio Pires, L. M., B. W. Ibelings, and E. van Donk. 2009. Zebra mussels as a potential tool in the restoration of eutrophic shallow lakes, dominated by toxic cyanobacteria. Pages 361–372 in G. Van der Velde, S. Rajagopal, and A. A. bij de Vaate, editors. The zebra mussel in Europe. Backhuys Publishers, Leiden, The Netherlands.

Donlan, J., et al. 2006. Pleistocene rewilding: an optimistic agenda for twenty-first century conservation. The American Naturalist **168:**660–681.

Dudgeon, D., and R. E. W. Smith. 2006. Exotic species, fisheries and conservation of freshwater biodiversity in tropical Asia: the case of the Sepik River, Papua New Guinea. Aquatic Conservation: Marine and Freshwater Ecosystems **16:**203–215.

Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? Trends in Ecology & Evolution **14:**135–139.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems **6:**503–523.

Elliot, P., D. C. Aldridge, and G. D. Moggridge. 2008. Zebra mussel filtration and its potential uses in industrial water treatment. Water Resources **42:**1664–1674.

Ellis, L. A., D. M. Weddle, S. D. Stump, H. C. English, and A. E. Graber. 2008. Southwestern willow flycatcher final survey and monitoring report. Research technical guidance bulletin 10. Arizona Game and Fish Department, Phoenix.

Evans, J. M., A. C. Wilkie, and J. Burkhardt. 2008. Adaptive management of nonnative species: moving beyond the "either-or" through experimental pluralism. Journal of Agricultural & Environmental Ethics **21:**521–539.

Ewel, J. J., et al. 1999. Deliberate introductions of species: research needs. BioScience **49:**619.

Ewel, J. J., and F. E. Putz. 2004. A place for alien species in ecosystem restoration. Frontiers in Ecology and the Environment **2:**354–360.

Fontenot, D. K., S. P. Terrel, K. Malakooti, and S. Medina. 2006. Health assessment of the Guam rail (*Gallirallus owstoni*) population in the Guam Rail Recovery Program. Journal of Avian Medicine and Surgery **20:**225–233.

Forum. 2004. Restoration ecology: the challenge of social values and expectations. Frontiers in Ecology and the Environment **2:**43–48.

Foster, J. T., and S. K. Robinson. 2007. Introduced birds and the fate of Hawaiian rainforests. Conservation Biology **21:**1248–1257.

Gozlan, R. E. 2008. Introduction of non-native freshwater fish: is it all bad? Fish and Fisheries **9:**106–115.

Graves, S. D., and A. M. Shapiro. 2003. Exotics as host plants of the California butterfly fauna. Biological Conservation **110:**413–433.

Griffiths, C. J., and S. Harris. 2010. Prevention of secondary extinctions through taxon substitution. Conservation Biology **24:**645–646.

Griffiths, C. J., C. G. Jones, D. M. Hansen, M. Puttoo, R. V. Tatayah, C. B. Müller, and S. Harris. 2010. The use of extant non-indigenous tortoises as a restoration tool to replace extinct ecosystem engineers. Restoration Ecology **18:**1–7.

Gross, C. L. 2001. The effect of introduced honeybees on native bee visitation and fruit-set in *Dillwynia juniperina* (Fabaceae) in a fragmented ecosystem. Biological Conservation **102:**89–95.

Gurevitch, J., and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? Trends in Ecology & Evolution **19:**470–474.

Hawkes, C. V. 2007. Are invaders moving targets? The generality and persistence of advantages in size, reproduction, and enemy release in invasive plant species with time since introduction. The American Naturalist **170:**832–843.

Hendry, A. P., P. Nosil, and L. H. Rieseberg. 2007. The speed of ecological speciation. Functional Ecology **21:**455–464.

Hendry, A. P., J. K. Wenburg, P. Bentzen, E. C. Volk, and T. P. Quinn. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. Science **290:**516–518.

Hershner, C., and K. J. Havens. 2008. Managing invasive aquatic plants in a changing system: strategic consideration of ecosystem services. Conservation Biology **22:**544–550.

Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology & Evolution **24:**599–605.

Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D. B. Lindenmayer, C. Parmesan, H. P. Possingham, and C. D. Thomas. 2008. Assisted colonization and rapid climate change. Science **321:**345–346.

Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs **75:**3–35.

Jackson, S. T., and D. F. Sax. 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. Trends in Ecology & Evolution **25:**131–198.

Johnston, R. F., and R. K. Selander. 1964. House Sparrows: rapid evolution of races in North America. Science **144:**548–550.

Jolly, J. N., and R. M. Colbourne. 1991. Translocations of the little spotted kiwi (*Apteryx owenii*) between offshore islands of New Zealand. Journal of the Royal Society of New Zealand **21:**143–149.

Kats, L. B., and R. P. Ferrer. 2003. Alien predators and amphibian declines: review of two decades of science and the transition to conservation. Diversity and Distributions **9:**99–110.

Kilpatrick, A. M. 2006. Facilitating the evolution of resistance to avian malaria in Hawaiian birds. Biological Conservation **128:**475–485.

Krajick, K. 2005. Winning the war against island invaders. Science **310:**1410–1413.

Larson, B. M. H. 2005. The war of the roses: demilitarizing invasion biology. Frontiers in Ecology and the Environment **3:**495–500.

Lee, C. E. 2002. Evolutionary genetics of invasive species. Trends in Ecology & Evolution **17:**386–391.

Lever, C. 2001. The cane toad: the history and ecology of a successful colonist. Westbury Academic and Scientific, Yorkshire, United Kingdom.

Lodge, D. M., et al. 2006. Biological invasions: recommendations for U.S. policy and management. Ecological Applications **16:**2035–2054.

Lugo, A. E. 1997. The apparent paradox of re-establishing species richness on degraded lands with tree monocultures. Forestry Ecology and Management **99:**9–19.

Lugo, A. E. 2004. The outcome of alien tree invasions in Puerto Rico. Frontiers in Ecology and the Environment **2:**265–273.

Mace, G., and A. Purvis. 2008. Evolutionary biology and practical conservation: bridging a widening gap. Molecular Ecology **17:**9–19.

Maris, V., and A. Béchet. 2010. From adaptive management to adjustive management: a pragmatic account of biodiversity values. Conservation Biology **24:**966–973.

McIntosh, C. R., D. C. Finnoff, C. Settle, and J. F. Shogren. 2009. Economic valuation and invasive species. Pages 151–179 in R. P. Keller, D. M. Lodge, M. A. Lewis, and J. F. Shogren, editors. Bioeconomics of invasive species. Oxford University Press, Oxford, United Kingdom.

Messing, R. H., and M. G. Wright. 2006. Biological control of invasive species: solution or pollution. Frontiers in Ecology and the Environment **4:**132–140.

Millennium Ecosystem Assessment. 2005. Ecosystems and well-being: biodiversity synthesis. World Resources Institute, Washington, D.C.

Mooney, H. A., and R. J. Hobbs 2000. Invasive species in a changing world. Island Press, Washington, DC.

Morrison, K. D., E. G. Reekie, and K. I. N. Jensen. 1998. Biocontrol of common St. Johnswort (*Hypericum perforatum*) with *Chrysolina hyperici* and a host-specific *Colletotrichum gloeosporioides*. Weed Technology **12:**426–435.

Muth, N. Z., and M. Pigliucci. 2007. Implementation of a novel framework for assessing species plasticity in biological invasions: responses of *Centaurea* and *Crepis* to phosphorus and water availability. Journal of Ecology **95:**1001–1013.

Nielsen, C., C. Heimes, and J. Kollmann. 2008. Little evidence for negative effects of an invasive alien plant on pollinator services. Biological Invasions **10:**1353–1363.

Norton, D. A. 2009. Species invasions and the limits to restoration: learning from the New Zealand experience. Science **325:**569–571.

NRC. 2004. Nonnative oysters in the Chesapeake Bay. National Academy, Washington, DC.

Olden, J. D., N. LeRoy Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology & Evolution **19:**18–24.

Parker, I. M., et al. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions **1:**3–19.

Parrotta, J. A. 1999. Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. Forest Ecology and Management **124:**45–77.

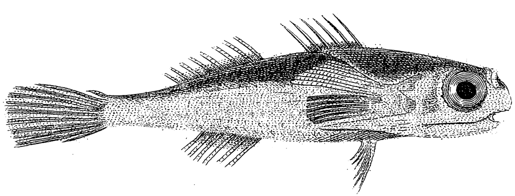
Pascual, M. A., J. L. Lancelotti, B. Ernst, J. E. Ciancio, E. Aedo, and M. García-Asorey. 2009. Scale, connectivity, and incentives in the introduction and management of non-native species: the case of exotic salmonids in Patagonia. Frontiers in Ecology and the Environment **7:**533–540.

Pejchar, L., and H. A. Mooney. 2009. Invasive species, ecoystem services and human well-being. Trends in Ecology & Evolution **24:**497–504.

Peretti, J. H. 1998. Nativism and nature: rethinking biological invasion. Environmental Values **7:**183–192.

Petersen, J. H., R. A. Hinrichsen, D. M. Gadomski, D. H. Feil, and D. W. Rondorf. 2003. American shad in the Columbia River. Pages 141–155 in K. E. Limburg and J. R. Waldman, editors. Biodiversity,

status, and conservation of the world's shads. American Fisheries Society, Bethesda, Maryland.
Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics **52:**273–288.
Pyšek, P., D. M. Richardson, J. Pergl, V. Jarosík, Z. Sixtová, and E. Weber. 2008. Geographical and taxonomic biases in invasion ecology. Trends in Ecology & Evolution **23:**237–244.
Pyšek, P., D. M. Richardson, M. Rejmánek, G. L. Webster, M. Williamson, and J. Kirschner. 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon **53:**131–143.
Ricciardi, A., and D. Simberloff. 2009. Assisted colonization is not a viable conservation strategy. Trends in Ecology & Evolution **24:**248–253.
Richardson, D. M., et al. 2009. Multidimensional evaluation of managed relocation. Proceedings of the National Academy of Sciences **107:**9721–9724.
Rodriguez, L. F. 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biological Invasions **8:**927–939.
Ruesink, J. L., H. S. Lenihan, A. C. Trimble, K. W. Heiman, F. Micheli, J. E. Byers, and M. C. Kay. 2005. Introduction of non-native oysters: Ecosystem effects and restoration implications. Annual Review of Ecology, Evolution, and Systematics **36:**643–689.
Sagoff, M. 2005. Do non-native species threaten the natural environment? Journal of Agricultural & Environmental Ethics **18:**215–236.
Sala, O. E., et al. 2000. Global biodiversity scenarios for the year 2100. Science **287:**1770–1774.
Sandler, R. 2010. The value of species and ethical foundations of assisted colonization. Conservation Biology **24:**424–431.
Sax, D. F., and S. D. Gaines. 2008. Species invasions and extinction: the future of native biodiversity on islands. Proceedings of the National Academy of Sciences **105:**11490–11497.
Schlaepfer, M. A., P. W. Sherman, B. Blossey, and M. C. Runge. 2005. Introduced species as evolutionary traps. Ecology Letters **8:**241–246.
Schwarz, D., K. D. Shoemaker, N. L. Botteri, B. A. McPheron, and M. Noor. 2007. A novel preference for an invasive plant as a mechanism for animal hybrid speciation. Evolution **61:**245–256.
Severns, P. M., and A. D. Warren. 2008. Selectively eliminating and conserving exotic plants to save an endangered butterfly from local extinction. Animal Conservation **11:**476–483.
Shafroth, P. B., V. B. Beauchamp, M. K. Briggs, K. Lair, M. L. Scott, and A. A. Sher. 2008. Planning riparian restoration in the context of *Tamarix* control in western North America. Restoration Ecology **16:**97–112.
Simberloff, D., and L. Gibbons. 2004. Now you see them, now you don't! Population crashes of established introduced species. Biological Invasions **6:**161–172.
Slobodkin, L. B. 2001. The good, the bad, and the reified. Evolutionary Ecology Research **3:**1–13.
Sogge, M. K., S. J. Sferra, and E. H. Paxton. 2008. Tamarix as habitat for birds: implications for riparian restoration in the southwestern United States. Restoration Ecology **16:**146–154.
Southwick, E. E., and L. Southwick. 1992. Estimating the economic value of honey bees as agricultural pollinators in the United States. Economic Entomology **85:**621–633.
Stromberg, J. C., M. K. Chew, P. L. Nagler, and E. P. Glenn. 2009. Changing perceptions of change: the role of scientists in *Tamarix* and river management. Restoration Ecology **17:**177–186.
Sullivan, J. J., P. A. Williams, and S. M. Timmins. 2007. Secondary forest succession differs through naturalised gorse and native kanuka near Wellington and Nelson. New Zealand Journal of Ecology **31:**22–38.
Tablado, Z., J. L. Tella, J. A. Sanchez-Zapata, and F. Hiraldo. 2010. The paradox of long-term positive effects of a North American crayfish on a European community of predators. Conservation Biology DOI: 10.1111/j.1523-1739.2010.01483.x.
Tate, J. A., Z. Ni, A.-C. Scheen, J. Koh, C. A. Gilbert, D. Lefkowitz, Z. J. Chen, P. S. Soltis, and D. E. Soltis. 2006. Evolution and expression of homeologous loci in *Tragopogon miscellus* (Asteraceae), a recent and reciprocally formed allopolyploid. Genetics **173:**1599–1611.
Tepedino, V., B. Bradley, and T. Griswold. 2008. Might flowers of invasive plants increase native bee carrying capacity? Intimations from Capitol Reef National Park, Utah. Natural Areas Journal **28:**44–50.
Tesauro, J., and D. Ehrenfeld. 2007. The effects of livestock grazing on the bog turtle *Glyptemys* (= *Clemmys*) *muhlenbergii*. Herpetologica **63:**293–300.
Thomas, M. B., and A. M. Reid. 2007. Are exotic natural enemies an effective way of controlling invasive plants? Trends in Ecology & Evolution **22:**447–453.
Vellend, M., L. J. Harmon, J. L. Lockwood, M. M. Mayfield, A. R. Hughes, J. P. Wares, and D. F. Sax. 2007. Effects of exotic species on evolutionary diversification. Trends in Ecology & Evolution **22:**481–488.
Vinson, M. R., and M. A. Baker. 2008. Poor growth of rainbox trout fed New Zealand mud snails *Potamopyrgus antipodarum*. North American Journal of Fisheries Management **28:**701–709.
Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist **84:**468–478.
Walther, G.-R., et al. 2009. Alien species in a warmer world: risks and opportunities. Trends in Ecology & Evolution **24:**686–693.
Westman, W. E. 1990. Park management of exotic plant species: problems and issues. Conservation Biology **4:**251–260.
Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience **48:**607–615.
Wilkinson, D. M. 2004. The parable of Green Mountain: Ascension Island, ecosystem construction and ecological fitting. Journal of Biogeography **31:**1–4.
Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment **5:**475–482.
Williamson, M., and A. Fitter. 1996. The varying success of invaders. Ecology **77:**1661–1666.
Willis, S. G., J. K. Hill, C. D. Thomas, D. B. Roy, R. Fox, D. S. Blakeley, and B. Huntley. 2009. Assisted colonization in a changing climate: a test-study using two U.K. butterflies. Conservation Letters **2:**46–52.
Wonham, M. J., M. O'Connor, and C. D. G. Harley. 2005. Positive effects of a dominant invader on introduced and native mudflat species. Marine Ecology Progress Series **289:**109–116.
Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology & Evolution **16:**454–459.



Conservation Biology

Comment

Revisiting the Potential Conservation Value of Non-Native Species

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Human travel and transportation of goods are increasingly changing species distributions (Ricciardi 2007). Non-native species—those introduced beyond their natural ranges—often have undesirable effects at levels from genes to landscapes (Ehrenfeld 2011). However, as has long been acknowledged, not all introduced species have negative effects (Williamson 1996).

Although Schlaepfer et al. (2011) recognize much evidence of undesirable effects of species' introductions, they synthesize information on contributions of non-native species to conservation goals. Schlaepfer et al. contend that non-native species may catalyze restoration of native species and ecosystems, especially if they substitute for extirpated ecosystem engineers (organisms that modulate availability of resources to other species by changing ecosystem components; Jones et al. 1994), and may thus provide ecosystem services. Schlaepfer et al. predict that non-native species will increasingly aid conservation because they are more likely than native species to persist despite changing climate and land use. They further argue that non-native species may evolve into new taxa and thus increase species diversity. Their main message is clear: non-native species should be used for conservation given their potential desirable contributions.

We disagree with Schlaepfer et al.'s main message. It is challenging to understand a species' ecological effects, and current evidence shows that desirable (i.e., positive) effects of non-native species are much less frequent than undesirable (i.e., negative) effects. Even for species Schlaepfer et al. use as examples of the positive effects of non-native species (e.g., gorse [*Ulex europaeus*], African honey bee [*Apis mellifera*], zebra mussel [*Dreissena polymorpha*]), most published effects are negative (Clements et al. 2001; Goulson 2003; Strayer et al. 2004). Schlaepfer et al. do not accurately represent the extent of desirable and undesirable effects of non-native species with respect to conservation. This misrepresentation can suggest that effects of non-native species are mostly positive.

When a non-native species becomes abundant, even when it is highly detrimental to the ecosystem, some native species will likely benefit because it provides an additional resource. One thus expects some positive effects. However, these effects are frequently transient, and calling them *desirable* or *undesirable* is often a consequence of subjective analyses (e.g., Rodewald 2011; Lapointe et al. 2012). Schlaepfer et al.'s examples highlight positive effects of some introduced species. They state, "[w]e did not review all the known negative effects . . . because they have been exhaustively described." Furthermore, they do not acknowledge uncertainty—many effects are difficult to predict or occur only in the long term (Strayer et al. 2006). An example is the phenomenon of time lags (Crooks 2011), in which species do not immediately become problematic. Many effects cannot be detected without extensive, long-term studies (Strayer et al. 2006; Traveset & Richardson 2006; Arbačiauskas et al. 2010). Of course, subtle and delayed effects can be positive, although the catalog so far is heavily weighted toward negative effects.

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Paper submitted November 13, 2011; revised manuscript accepted April 17, 2012.

Conservation Biology, Volume 26, No. 6, 1153–1155

DOI: 10.1111/j.1523-1739.2012.01950.x

Although we disagree with some views of Schlaepfer et al., we agree that some invasions can aid conservation, as when they functionally replace an extinct species. Ship rats (*Rattus rattus*) have multiple undesirable effects (Pascal 2011). Yet ship rats pollinate some native species in New Zealand, where native pollinators have been extirpated (Pattemore & Wilcove 2012). Thus, even highly detrimental species can have some desirable local effects. The irony is that rats contributed greatly to extirpating pollinators in the first place (Pattemore & Wilcove 2012), so the net invasion effect was not beneficial.

In addition, Schlaepfer et al. overestimate ecologists' ability to forecast risks and benefits of non-native species. Prediction in ecology is difficult (Lawton 1999). Surprises emerge even in well-studied systems (Lindenmayer et al. 2010). For example, kokanee salmon (*Oncorhynchus nerka*) and lake trout (*Salvelinus namaycush*) were introduced into Flathead Lake, Montana, in the early 20th century, and 50 years later, opossum shrimp (*Mysis diluviana*) were introduced into part of the catchment to increase kokanee production (Ellis et al. 2011). By 1981 shrimp floated downstream into Flathead Lake, causing population crashes of cladoceran and copepod prey. Kokanee, competing with shrimp for prey, declined from 1 to 2 fish per standardized gill net set before shrimp were present to <0.5 fish per net. This decline caused the abundances of Bald Eagles (*Haliaeetus leucocephalus*), grizzly bears (*Ursus arctos*), and other predators to decline. Eagle abundance at one monitored site fell from 639 to 25 (Spencer et al. 1991). Lake trout became the dominant species of fish. Owing to changes in the food web associated with the increase in abundance of lake trout, the lake's population of bull trout (*Salvelinus confluentus*) may be extirpated (Ellis et al. 2011). Such indirect effects of a non-native species are common and difficult to predict, so Schlaepfer et al.'s confidence in recognizing positive effects is unwarranted.

Schlaepfer et al. suggest quantifying net effects of non-native species to define when they become invasive. They also suggest that one should not try to control species with positive net effects and instead should consider them conservation resources. However, the aforementioned difficulties—especially that species have many effects and that these effects may be hard to measure or predict—make quantifying net effects extremely challenging, especially when management action is urgent (e.g., when an introduced species spreads rapidly).

Another point of contention is that Schlaepfer et al. downplay reports of invasion effects from developing countries. In developing countries, Schlaepfer et al.'s thesis might be used to support practices that promote introductions of non-native species that have highly undesirable effects. In many developing countries, introductions of species are promoted on economic grounds and no studies of potential undesirable long-term effects are conducted (e.g., Vitule et al. 2009; Lövei et al. 2012). There are more developing than developed countries, yet most research dealing with invasions is restricted to developed countries (Vázquez & Aragón 2002). Also, in general, economic development accelerates invasions (Lin et al. 2007). Invasions are therefore likely to become more frequent and to generate greater net undesirable effects in developing nations with rapidly growing economies. Such countries are generally located where species diversity is high and less information is available on effects of introductions (Lin et al. 2007; Lövei et al. 2012). These considerations lead us to disagree with Schlaepfer et al.'s prediction that an increasing proportion of non-native species will be benign or even desirable for conservation.

Finally, Schlaepfer et al. (p. 434) say they "question how human actions differ from those of other species. In other words, why is a dispersal event that is facilitated by, say, a migratory bird or storm event considered natural, whereas a human-transported species is non-native and thus undesirable?" Although migration of species is facilitated by the removal of natural barriers (e.g., the opening of the Panamanian corridor between North and South America during the Great American Interchange), these events cannot be compared with the current wave of human-assisted invasions. The rate of human-assisted invasions is orders of magnitude higher than natural or prehistoric rates (Ricciardi 2007). For instance, over the last century mammal genera have been exchanged between North and South America 10,000 times more frequently than during the Great American Interchange (Ricciardi 2007). Furthermore, human-mediated dispersal often carries species between sites that would never have been sites of species exchanges facilitated through tectonic movement or aerial or aquatic transport (Ricciardi 2007; Wilson et al. 2009), and human-mediated dispersal frequently moves more individuals and individuals from multiple sources (Wilson et al. 2009). Human-assisted dispersals are a distinct global change (Ricciardi 2007; Wilson et al. 2009).

Schlaepfer et al. downplay the danger of species introductions, and the absence of a perspective that accounts for the issues we raise here could encourage decision makers, who typically focus on short-term benefits of introductions without concern for potential long-term consequences, to approve introductions that carry a high risk of adverse consequences. The Millennium Ecosystem Assessment is more prudent. It notes that some introductions will be beneficial, but it nevertheless emphasizes that introductions have much more frequently caused loss of biological diversity, ecosystem functions, and ecosystem services (Millennium Ecosystem Assessment 2005). The Convention on Biological Diversity (UNEP 1992) also advocates a precautionary approach to species introduction when information about its effects is highly uncertain; thus, the risk of negative effects puts the burden of proof on those wishing to introduce species. We believe a more sensible alternative to Schlaepfer et al.'s proposal to encourage introductions when predicted net effects are positive is to use the best available knowledge to increase vigilance and to improve management. The issue of species' invasions is complex and necessitates a cautious, balanced view, including consideration of short-term and long-term introduction effects, both positive and negative.

Literature Cited

Arbačiauskas, K., V. Rakauskas, and T. Virbickas. 2010. Initial and long-term consequences of attempts to improve fish-food resources in Lithuanian waters by introducing alien peracaridan species: a retrospective overview. Journal of Applied Ichthyology **26:**28–37.

Clements, D. R., D. J. Peterson, and R. Prasad. 2001. The biology of Canadian weeds. 112. *Ulex europaeus* L. Canadian Journal of Plant Science **81:**325–337.

Crooks, J. A. 2011. Lag times. Pages 404–410 in D. Simberloff, and M. Rejmánek, editors. Encyclopedia of biological invasions. University of California Press, Berkeley.

Ehrenfeld, J. G. 2011. Ecosystem consequences of biological invasions. Annual Review of Ecology, Evolution, and Systematics **41:** 59–80.

Ellis, B. K., J. A. Stanford, D. Goodman, C. P. Stafford, D. L. Gustafson, D. A. Beauchamp, D. W. Chess, J. A. Craft, M. A. Deleray, and B. S. Hansen. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proceedings of the National Academy of Sciences USA **108:**1070–1075.

Goulson, D. 2003. Effects of introduced bees on native ecosystems. Annual Review of Ecology, Evolution, and Systematics **34:**1–26.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos **69:**373–386.

Lapointe, N. W. R., R. M. Pendleton, and P. L. Angermeier. 2012. A comparison of approaches for estimating relative impacts of nonnative fishes. Environmental Management **49:**82–95.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos **84:**177–192.

Lin, W., G. F. Zhou, X. Y. Cheng, and R. M. Xu. 2007. Fast economic development accelerates biological invasions in China. Public Library of Science ONE **2** DOI: 10.1371/journal.pone.0001208.

Lindenmayer, D. B., G. E. Likens, C. J. Krebs, and R. J. Hobbs. 2010. Improved probability of detection of ecological "surprises." Proceedings of the National Academy of Sciences of the United States of America **107:**21957–21962.

Lövei, G. L., T. M. Lewinsohn, and Invasions in Megadiverse Regions Network. 2012. Megadiverse developing countries face huge risks from invasives. Trends in Ecology & Evolution **27:**2–3.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: current state and trends: findings of the Condition and Trends Working Group. Island Press, Washington, D.C.

Pascal, M. 2011. Rats. Pages 571–575 in D. Simberloff and M. Rejmánek, editors. Encyclopedia of biological invasions. University of California Press, Berkeley.

Pattemore, D. E., and D. S. Wilcove. 2012. Invasive rats and recent colonist birds partially compensate for the loss of endemic New Zealand pollinators. Proceedings of the Royal Society B: Biological Sciences **279:**1597–1605.

Ricciardi, A. 2007. Are modern biological invasions an unprecedented form of global change? Conservation Biology **21:**329–336.

Rodewald, A. D. 2011. Spreading messages about invasives. Diversity and Distributions **18:**97–99.

Schlaepfer, M. A., D. F. Sax, and J. D. Olden. 2011. The potential conservation value of non-native species. Conservation Biology **25:**428–437.

Spencer, C. N., B. R. McClelland, and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and eagle displacement. BioScience **41:**14–21.

Strayer, D. L., K. A. Hattala, and A. W. Kahnle. 2004. Effects of an invasive bivalve (*Dreissena polymorpha*) on fish in the Hudson River estuary. Canadian Journal of Fisheries and Aquatic Sciences **61:**924–941.

Strayer, D. L., V. T. Eviner, J. M. Jeschke, and M. L. Pace. 2006. Understanding the long-term effects of species invasions. Trends in Ecology & Evolution **21:**645–651.

Traveset A., and D. M. Richardson. 2006. Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology & Evolution **21:**208–216.

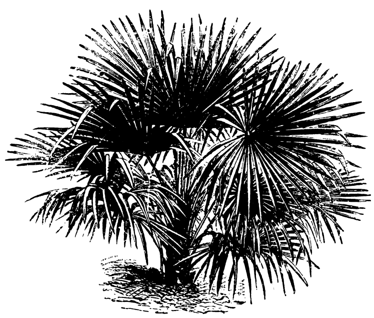
UNEP (United Nations Environmental Programme). 1992. Rio declaration on environment and development. United Nations, New York. Available from http://www.unep.org/Documents.Multilingual/Default.asp?documentid=78&articleid=1163 (accessed May 2012).

Vázquez, D. P., and R. Aragón. 2002. Introduction [to special issue on biological invasions in southern South America]. Biological Invasions **4:**1–5.

Vitule, J. R. S., C. A. Freire, and D. Simberloff. 2009. Introduction of non-native freshwater fish can certainly be bad. Fish and Fisheries **10:**98–108.

Williamson, M. 1996. Biological invasions. Chapman & Hall, London.

Wilson, J. R. U., E. E. Dormontt, P. J. Prentis, A. J. Lowe, and D. M. Richardson. 2009. Something in the way you move: dispersal pathways affect invasion success. Trends in Ecology & Evolution **24:**136–144.



Comment

Toward a More Balanced View of Non-Native Species

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We thank Vitule et al. (2012) for responding to our review "The Potential Conservation Value of Non-Native Species for Conservation." Although scientists have long known that non-native species could be benign or beneficial in some regards, in practice most scientists and managers have treated all non-native species by definition as problematic. Gross inefficiencies and misguided programs have arisen in cases where policy was driven by such dogmatic views on non-native species (Stromberg et al. 2009). We are happy to read that Vitule et al. are in agreement with us that such biases should be actively eliminated, and we whole-heartedly agree with the last sentence in their reply, which reads: "The issue of species' invasions is complex and necessitates a cautious, balanced view, including consideration of short-term and long-term introduction effects, both positive and negative." We look forward to such assertions being put into practice. Indeed, we maintain that the vast majority of studies on non-native species conducted to date fail to properly consider any potential positive effects.

We disagree with Vitule et al. on numerous other points. For example, we believe they erroneously interpreted our primary message when they stated: "Their main message is clear: non-native species should be used for conservation given their potential desirable contributions." We do not believe *all* non-native species should be used for conservation, and we do not even imply such a notion in our paper. In fact, we argued that the desirable and undesirable aspects of any non-native species must be evaluated carefully when deciding whether (and how) it should be managed. We further argued that it is important to do so for the sake of scientific objectivity and effective policy. It may well be that many non-native species have a sum negative effect, but this cannot be asserted until both potential positive and negative effects have been estimated. Our main point is clearly summed up in the last sentences of our paper: "In the past, risk analyses focused on negative events associated with non-native species, and a species was termed invasive if any significant negative effect was documented. Here, we suggest that both negative and positive potential effects of non-native species should be tallied. We also suggest that a more meaningful definition of an invasive species would be one for which there is a net negative effect. A dynamic view of nature that recognizes that species characteristics and human valuations thereof change over time, not only reflects ongoing evolutionary processes, but also leads to a more balanced and objective approach to the management of non-native species." We, therefore, disagree with Vitule et al.'s interpretation of our main message.

We further believe that Vitule et al. misrepresent or misinterpret several points we raised in our article. We never discussed (explicitly or implicitly) the issue of intentional introductions. It is, therefore, a misrepresentation of our work to say that we put forth a "proposal to encourage introductions when predicted net effects are positive." In fact, we believe that novel introductions—intentional and unintentional—are associated with great uncertainty and risk and that priority should, therefore, be given to preventing such introductions under most circumstances, with exceptions being granted, for example, to prevent extinction of certain species.

The authors also state we did not consider the uncertainty surrounding the long-term effects of non-native species, when they write: " . . . they do not acknowledge uncertainty – many effects are difficult to predict or occur only in the long term (Strayer et al. 2006)." In fact, in our abstract we state, "A fraction of non-native species will continue to cause biological and economic damage, and substantial uncertainty surrounds the potential future effects of all non-native species." We also wrote, "The future effects of a non-native species are uncertain

Paper submitted June 7, 2012; revised manuscript accepted July 19, 2012.

Conservation Biology, Volume 26, No. 6, 1156–1158

DOI: 10.1111/j.1523-1739.2012.01948.x

because biotic interactions are notoriously difficult to predict and because current and future environmental conditions may differ substantially (Walther et al. 2009)." We, therefore, fail to understand how the authors reached the conclusion that this perspective was missing in our paper.

Finally, we disagree with their statement that "introductions have much more frequently caused loss of biological diversity, ecosystem functions, and ecosystem services . . . " They base these claims on the Millennium Ecosystem Assessment (2005), but much data has become available over the last decade that shows that these statements are not generally true. First, any discussion of loss or gain of biodiversity must be related to the spatial scale of interest (Sax & Gaines 2003). Although species diversity is declining globally, in part because of non-native species, the net effect of regional species introductions is generally an increase in diversity. Such an increase has occurred with plants, mammals, birds, fishes, and many other groups on both islands and continents worldwide (Sax et al. 2002; Sax & Gaines 2003). Locally the effects of non-native species on alpha diversity are likely to be more idiosyncratic, but net increases are still the expectation in most cases because of the positive association between local and regional species richness (Sax & Gaines 2003). Second, introduced species typically lead to an increase, not a decrease, in ecosystem function (Ehrenfeld 2010). Results of two recent meta-analyses show this to be the general case for most ecosystem functions that have been measured (Liao et al. 2008; Vila et al. 2011). Third, non-native species can provide many ecosystem services that are desirable to humans (e.g., clean water, erosion control, food provisioning). Although we are unaware of any study that has tallied the number of services provided versus amount of harm associated with introduced species (clearly not a small task), the provision of ecosystem services by such species certainly occurs and may be more frequent than is appreciated. Non-native species may produce many different undesirable effects, but it is important to use the existing data to distinguish between disproven assumptions and real consequences.

Vitule et al. criticize us on issues we did not address in our paper. For example, they claim we misrepresented the frequency of positive effects of non-native species. In our paper, we reviewed the numerous ways in which non-native species can potentially contribute to conservation efforts. We never wrote or implied that we quantitatively measured the number of studies documenting positive versus negative effects. We concede that a reader could come away with an incomplete picture of the field if our article was the first they ever read on the topic of non-native species. But our target audience was conservation professionals who read *Conservation Biology* and who, by contrast, have been hearing almost exclusively about the negative effects of non-native species for years or even decades. We even clarified that our aim was "to catalog the possible ways in which non-native species can help achieve conservation objectives. We did not review all the known negative effects of non-native species because these have been described exhaustively (e.g., Mooney & Hobbs 2000; Lodge et al. 2006)." We are, therefore, uncertain how the authors concluded that our aim was to provide a quantitative measure of the number of each type of study. Such a comparison would be difficult given the historical bias in the literature that favors descriptions of negative effects of non-native species.

Vitule et al. also state that we "downplay reports of invasion effects in developing countries." Given that we sought examples for our review indiscriminately and that our paper had no geographic or sociopolitical focus, we fail to understand the origin of this criticism. Nevertheless, the question of whether the nature and magnitude of positive and negative effects differ according to a country's development path is an interesting one that should be pursued.

The world is rapidly changing, as are the ways we view non-native species. How we manage these species and whether we even chose to maintain a distinction between native and non-native species in the future is a wide-open question. One the one hand, the distinction may sometimes prove to be distracting from the larger issue of the positive and negative effects that both native and non-native species can have relative to any particular conservation goal (e.g., Davis et al. 2011; Carey et al. 2012). On the other hand, information on a species' origin may provide useful information in some cases, for example, on islands and in other insular settings where non-native species regularly have negative effects on native biota (Sax & Gaines 2008). We look forward to future work by Vitule et al. and others as they carefully document both the positive and negative potential effects of non-native species, and we thank them for their contributions to this interesting debate.

Literature Cited

Carey, M. P., B. L. Sanderson, K. A. Barnas, and J. D. Olden. 2012. Native invaders create novel challenges for science, management, society and policy. Frontiers in Ecology and the Environment **10:**373–381.

Davis, M.A., et al. 2011. Don't judge a species on their origins. Nature **474:**153–154.

Ehrenfeld, J. G. 2010. Ecosystem consequences of biological invasions. Annual Review in Ecology, Evolution and Systematics **41:**59–80.

Liao, C. Z., et al. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New Phytologist **177:**706–714.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: current state and trends: findings of the Condition and Trends Working Group. Island Press, Washington, D.C.

Sax, D. F., and S. D. Gaines. 2003. Species diversity: from global decreases to local increases. Trends in Ecology & Evolution **18:**561–566.

Sax, D. F., and S. D. Gaines. 2008. Species invasions and extinction: the future of native biodiversity on islands. Proceedings of the National Academy of Sciences **105:**11490–11497.

Sax, D. F., S. D. Gaines, and J. H. Brown. 2002. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. The American Naturalist **160:**766–783.

Stromberg, J. C., M. K. Chew, P. L. Nagler, and E. P. Glenn. 2009. Changing perceptions of change: the role of scientists in Tamarix and river management. Restoration Ecology **17:**177–186.

Vila, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarosik, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pysek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters **14:**702–708.

Vitule, J. R. S., C. A. Freire, D. P. Vazquez, M. A. Nuñez, and D. Simberloff. 2012. Revisiting the potential conservation value of non-native species. Conservation Biology, in press.