



UNIVERSITY OF
GLOUCESTERSHIRE

This is a peer-reviewed, post-print (final draft post-refereeing) version of the following published document:

Goodenough, Anne E ORCID: 0000-0002-7662-6670 (2010) Are the ecological impacts of alien species misrepresented? A review of the “native good, alien bad” philosophy. Community Ecology, 11 (1). pp. 13-21. doi:10.1556/ComEc.11.2010.1.3

Official URL: <http://dx.doi.org/10.1556/ComEc.11.2010.1.3>

DOI: <http://dx.doi.org/10.1556/ComEc.11.2010.1.3>

EPrint URI: <https://eprints.glos.ac.uk/id/eprint/3334>

Disclaimer

The University of Gloucestershire has obtained warranties from all depositors as to their title in the material deposited and as to their right to deposit such material.

The University of Gloucestershire makes no representation or warranties of commercial utility, title, or fitness for a particular purpose or any other warranty, express or implied in respect of any material deposited.

The University of Gloucestershire makes no representation that the use of the materials will not infringe any patent, copyright, trademark or other property or proprietary rights.

The University of Gloucestershire accepts no liability for any infringement of intellectual property rights in any material deposited but will remove such material from public view pending investigation in the event of an allegation of any such infringement.

PLEASE SCROLL DOWN FOR TEXT.

This is a peer-reviewed, post-print (final draft post-refereeing) version of the following published document:

Goodenough, A. (2010). *Are the ecological impacts of alien species misrepresented? A review of the “native good, alien bad” philosophy.* Community Ecology, 11 (1), 13-21. ISSN 1585-8553

Published in Community Ecology, and available online at:

<http://www.akademai.com/doi/abs/10.1556/ComEc.11.2010.1.3>

We recommend you cite the published (post-print) version.

The URL for the published version is <http://dx.doi.org/10.1556/ComEc.11.2010.1.3>

Disclaimer

The University of Gloucestershire has obtained warranties from all depositors as to their title in the material deposited and as to their right to deposit such material.

The University of Gloucestershire makes no representation or warranties of commercial utility, title, or fitness for a particular purpose or any other warranty, express or implied in respect of any material deposited.

The University of Gloucestershire makes no representation that the use of the materials will not infringe any patent, copyright, trademark or other property or proprietary rights.

The University of Gloucestershire accepts no liability for any infringement of intellectual property rights in any material deposited but will remove such material from public view pending investigation in the event of an allegation of any such infringement.

PLEASE SCROLL DOWN FOR TEXT

**ARE THE ECOLOGICAL IMPACTS OF ALIEN
SPECIES MISREPRESENTED? A REVIEW OF THE
“NATIVE GOOD, ALIEN BAD” PHILOSOPHY**

Anne E. Goodenough

Department of Natural and Social Sciences, Francis Close Hall Campus, University of Gloucestershire,
Swindon Road, Cheltenham, Glos., GL50 4AZ, UK.

aegoodenough@glos.ac.uk

Suggested running title: Native good, alien bad?

Abstract

The study of invasion ecology usually focuses on the negative impacts of alien species, while potential positive impacts are often overlooked. Understanding of biotic interactions may thus be skewed towards the negative, which could have important implications for ecological management and conservation. This article provides a comprehensive review of all types of impacts, both beneficial and detrimental, that can result from species translocation. An extensive review of literature on species introductions to terrestrial, freshwater and marine ecosystems and involving a wide range of taxa (including microorganisms, plants, insects, reptiles, birds, mammals, fish and crustacea), showed that, despite limited research into facilitative alien-native interactions, such interactions occur surprisingly frequently. Examples were found of introduced species acting as hosts, food sources, pollinators or seed dispersers for native species, as well as providing herbivory, predatory or parasite release. However, research showed that numerous negative interactions also occurred and combination impacts (when an alien benefits some natives but disadvantages others) were common. In many cases the traditional view that biological invasions constitute a significant threat to native biota is both accurate and appropriate. Efforts to prevent translocation and control non-native species can be vital. However, the “native good, alien bad” maxim does not convey the complexity of invasion ecology: alien species do not axiomatically pose a threat to native biota. In order to move understanding of invasion ecology forward and to develop maximally-effective management strategies, facilitative alien-native interactions need to be added into the alien species debate.

Keywords: Contemporary evolution, facilitative interactions, non-native species, species introductions, translocations.

Nomenclature: Integrated Taxonomic Information System database (2009) (see <http://www.itis.gov/>).

24 **Introduction**

Translocation of species from their native range to new environments is an increasingly common phenomenon as the world becomes evermore interconnected. The resulting biological homogenisation means that the number of species of alien origin in many ecological communities is now considerable, such that the concept of a native range is becoming increasingly archaic (McKinney and Lockwood 1999). For example, using the year 1500 to demarcate natives and non-natives (Kornas 1990), it is estimated that 28% of Canadian flora, and 47% of New Zealand flora, is non-native (Heywood 1989, Green 2000). Thus, in many parts of the world, aliens are becoming the rule, rather than the exception.

As a result of this increasing species globalisation, the prevalence and abundance of aliens are topics of considerable research. However, the majority of studies are undertaken on the basis of a fundamental assumption: that species translocation is inevitably problematic (e.g., Rodríguez 2001, Mooney 2005). This can be demonstrated by considering invasion ecology terminology. For example, Middleton (1999) terms species translocation “biological pollution”, Myers and Bazely (2003) discuss the enormity of the invasion “problem”, and Cronk and Fuller (2001), in their book “*Plant invaders: the threat to natural ecosystems*”, only consider invasions that result in problems. The classification of impacts of alien species is also skewed towards the negative. For example, in one classification system, invasive species were graded according to their impact from one (mildly negative) to five (severely negative) (Fuller 1991). Restricting invasion impact assessment to negative interactions automatically biases a supposedly objective classification system. Although it is common ecological knowledge that alien species introductions can benefit native biota, potential facilitative interactions are often ignored during formal ecological research. In a meta-analysis of biotic interactions between aliens and natives from 120 papers published in key journals such as *Conservation Biology*, *Ecology*, and *American Naturalist* between 1981 and 2003, Bruno et al. (2005) found just 33% tested for facilitative interactions as opposed to negative interactions such as competition (61%). Similarly, of the 29 articles in the recent special issue of *Diversity and Distributions* dedicated to invasion ecology (volume 14, issue 2), only two articles examined positive impacts. Disregarding facilitative interactions in this way appears prevalent throughout much ecological research, which often focuses on a few negative cases (Bruno et al. 2003, Gozlan 2008). Even where alien facilitative interactions have been examined, this usually focuses solely upon mutualisms between alien species themselves (e.g., Simberloff and von Holle 1999), while relationships between aliens and natives that are beneficial to the latter are often overlooked (Richardson et al. 2000).

There is no doubt that the introduction of alien species can have a significant detrimental effect on native biota, reducing fitness, decreasing population size or even causing extirpation or extinction, particularly where endemic species are involved (see the comprehensive review by Simberloff 2005). However,

statements by researchers that alien species represent one of the biggest risks to biodiversity worldwide (e.g., Enserink 1999) are increasingly common and serve to reconfirm the traditional view of ALL aliens as a threat. This attitude may cause researchers to overlook occasions when translocation becomes an ecological opportunity. Consideration of the entire spectrum of impacts is a necessary prerequisite in formulating objective and justifiable policies and management initiatives. Indeed, according to Richardson et al. (2000), the discipline of invasion ecology needs a paradigm shift so that it moves away from a sole focus on negative impacts and biotic resistance to recognise that facilitative interactions can also exist.

This article challenges the axiomatic “native good, alien bad” philosophy (Agyeman 1998) by undertaking a comprehensive and balanced synthesis of the impacts of alien species following an extensive review of the literature. After initial consideration of the fact that establishment, and impacts, are not inevitable, numerous positive and negative interactions are outlined, each being illustrated using a wide range of examples involving many different taxa (microbes, parasites, plants, insects, reptiles, birds, mammals, fish and crustacea). These sections are sub-divided into the main types of impact; which are also synthesised in **Figure 1**. Situations where the introduction of an alien species has a positive impact on one native species but a simultaneous negative impact on other native species are also discussed. In these sections, the focus is on the impacts of interactions, rather than the range of processes by which interactions can occur (as covered previously in reviews such as Richardson et al. (2000)). The processes of contemporary evolution and lag effects, and the impact these processes have on alien-native interactions, are then considered. Finally, the question of whether the impact of alien species on native wildlife is misrepresented is discussed, and implications for ecological management are outlined.

Impacts are not inevitable

Significant impacts of alien species (positive or negative) are only likely with the long-term establishment of a self-sustaining population. This is far from guaranteed. According to the well-known ‘tens rule’ (Williamson and Fitter 1996), only one in ten imported species appears in the wild and only one in ten of those become self-sustaining. Although this rule has been challenged for being too conservative (e.g., Jeschke and Strayer 2005), and indeed Williamson himself commented that the figure of ten should only be taken as indicative of a low number (between five and twenty) (Williamson 1993), it reminds us that alien establishment is not axiomatic. Moreover, even where establishment does occur, impacts on native biota are not inevitable. Many native communities are not species-saturated (Sax et al. 2007), such that new species can thrive without significant problems (Lodge 1993), while co-existence can occur where there is no alien-native competition. This usually happens when an invader exploits an unoccupied niche, a situation most likely when there are few ecological and behavioural similarities between natives and non-natives. In the UK, for example, the alien slender speedwell (*Veronica filiformis*) does not compete with native grassland plants

(Akeroyd 1994) as it has different habitat requirements. Even where habitats overlap, alien and native plants often have complementary nutrient resource use, with aliens using nutrients at different soil depths, or at different times of year, than natives (Fargione et al. 2003). Alternatively, native species may be unaffected by non-natives as a result of pre-existing adaptations, such as generalist anti-predator defences that are effective against alien species (Cox and Lima 2006). It should, however, be noted that the likelihood of aliens affecting natives increases with the total number of introductions, both as a function of the larger pool of invaders and because of cumulative effects (Simberloff and von Holle 1999, Ricciardi and Kipp 2008), although these might not always be apparent immediately due to lag-phase effects (see later).

Potential impacts

Where important alien-native interactions do occur, they can take a variety of forms (Fig. 1). Impacts occur at a variety of scales, from gene-level (e.g., hybridisation) and individual-level (e.g., impacts on fitness or behaviour of individuals), to population-level (e.g., competition or predation) and community-level (e.g., herbivory-driven changes in native vegetation). The effect of alien species on native biota can be direct (e.g., new predator-prey or plant-pollinator relationships) or indirect (e.g., modification of habitat) and might be to the advantage or disadvantage of natives.

Positive impacts

Alien species can establish facilitative interactions with species already present at a given location. It should be noted that for an impact to be considered truly positive to a native species, the native should gain a long-term fitness advantage, which would usually result in an increase in abundance. However, because research into alien-native facilitative interactions is not well established, the following section includes not only examples of where positive impacts are known to have a fitness consequence, but also several examples where a fitness consequence is likely, but not yet demonstrated quantitatively. These occasions, which are made clear in the text, may constitute topics for future research.

(1) *Aliens as hosts*: Non-natives frequently act as hosts for native biota, either through aegism or parasitism. In an unusual example of the first, native cased Caddisfly larvae (Trichoptera) in the UK have been found to use introduced swamp stonecrop (*Crassula helmsii*) in the construction of their protective cases (Newman 2002). This is the first example of a non-native being used beneficially by native aquatic macroinvertebrates, although whether there is a fitness advantage to this behaviour is not yet clear. Examples of parasitism interactions include native trematodes, such as *Renicola roscovita*, parasitizing two introduced bivalves (*Crassostrea gigas* and *Ensis americanus*) in the North Sea, an action that has reduced the parasite burden on native bivalves, such as *Cerastoderma edule*, by 20-34% (Krakau et al. 2006). This reduction is likely to be long-term (rather than the short-

124 term parasite release that could occur if parasite numbers increase due to the presence of new hosts
and then revert to native bivalves) since the first intermediate host is a single species, the common
periwinkle (*Littorina littorea*), which limits the overall trematode population size (Lauckner 1984). Any
population-level effects of the reduced parasite burden on native bivalves still needs to be quantified.

128 (2) *Aliens as food sources*: Native fauna frequently feeds on introduced species, and may even come to rely
on them. For example, 82 of California's 236 butterflies (35%) use non-native plants such as buckwheat
(*Eriogonum* spp.) as larval food plants, while more than 40% have no known native hosts for ovipositing
132 in urban and sub-urban environments, such that many species would likely become extirpated in urban
environments if alien plants were removed (Shapiro 2002). There is even evidence to suggest that
natives sometimes depredate aliens preferentially, possibly because they lack co-evolved deterrent
mechanisms. For example, introduced gall flies (*Urophora affinis* and *U. quadrifasciata*) make up 86%
of the diet of deer mice (*Peromyscus maniculatus*) (Pearson et al. 2000). Since deer mice
136 populations are often food-limited (Taitt 1981), it is perhaps not surprising that mouse populations
have increased in habitats with high gall fly abundance (Pearson et al. 2000). Removal of alien
species as part of conservation management may have a detrimental impact on native species if
there are strong producer-herbivore or predator-prey interactions. This makes management
140 decisions more difficult and potentially controversial (see review by Zavaleta et al. 2001).

(3) *Aliens acting as pollinators and seed dispersers*: There are many cases of aliens being important, even
vital, in the reproduction of native plants, either during pollination or seed dispersal. For example,
pollination of the native prickly parrot-pea (*Dillwynia juniperina*) in Australia is undertaken primarily by
144 the alien honeybee (*Apis mellifera*) (Gross 2001), while the introduced brushtail possum (*Trichosurus*
vulpecula) in New Zealand is an increasingly important seed disperser for native plants that produce
larger seeds due to the decline in large-gaped avian frugivores such as the New Zealand pigeon
(*Hemiphaga novaeseelandiae*) (Dungan et al. 2002). Such interactions between aliens and natives
148 mean that management becomes complicated. For example, the red-whiskered bulbul (*Pycnonotus*
jocosus) is now the sole pollinator of the rare Mauritian endemic plant *Nesocodon mauritanus* (Olesen
et al. 2002), while the native Hawaiian ie'ie vine (*Freycinetia arborea*) relies almost exclusively on
pollination by Japanese white-eyes (*Zosterops japonicus*) (Cox and Elmqvist 2000). In both cases,
152 control of the invader, even if justified for other reasons, could cause the extinction of a rare indigenous
species: an example of just how complex formulating effective conservation policies can become.

(4) *Aliens as ecosystem engineers*: Alien species can cause substantial direct modification of a new
environment through allogenic processes (the concept of physical ecosystem engineering: Jones et al.
156 1997). For example, growth of alien Australian pines (*Casuarina equisetifolia*) along urban beaches in

Florida seems to increase the suitability of that beach for nesting by loggerhead sea turtles (*Caretta caretta*) as the trees screen human lights from the beach (Salmon et al. 1995). The population-level importance of this is not clear, but if more beaches become suitable for breeding, this may have implications on nest-site search-cost and could reduce the chances of catastrophic population decline resulting from problems at any one breeding site by spreading the risk. Meanwhile, in the aquatic environment, the continuing spread of the Asian hornsnail (*Batillaria attramentaria*) across the Northeast Pacific ocean floor has stabilised the substrate and facilitated occupation by two native hermit crabs, *Pagurus hirsutiusculus* and *P. granosimanus* (Wonham et al. 2005). The long-term population effects of this habitat provision are currently unknown. In other cases, an alien species can provide opportunities for native species not through physical alteration of an area, but simply by virtue of its presence. For example, on Robben Island off the coast of South Africa, stands of red-eyed wattle (*Acacia cyclops*) provide nest sites for African penguins (*Spheniscus demersus*), a species classified as vulnerable and declining by the IUCN (Crawford et al. 1995). Similarly, eradication of the alien saltcedar *Tamarix* spp. in substantial parts of its non-native range in the USA has been repeatedly delayed because it provides important nesting habitat for the endangered southwestern willow flycatcher *Empidonax traillii extimus* (Zavaleta et al. 2001).

(5) *Aliens reducing native predation pressure*: This is a relatively uncommon interaction, but can be of key ecological significance. An example is found in the Mediterranean where native juvenile slender yellowtail kingfish fish (*Alepes djedaba*) shelter among the tentacles of the introduced scyphozoan jellyfish (*Rhopilema nomadica*), which decreases the risk of predation by native predators (Galil 2000). The population-level impacts of this interaction have still to be established.

Negative impacts

Introduction of alien species can have a negative impact on native biota. A negative impact in this context refers to a reduction in fitness, a decline in abundance, or the triggering of an extirpation or extinction event. An overview of such impacts is presented below (for more specialist reviews, see Lowe et al. (2000), Pimentel et al. (2005), and Simberloff (2005)).

(1) *Aliens as predators*: Predation by aliens can be widespread (affecting many species) or specific (affecting just one or two species, often with substantial impacts). An example of a generalist alien predator is the now infamous case of the brown tree snake (*Boiga irregularis*) on the Island of Guam. The introduction of this species caused widespread avian predation-related extinctions, including the Micronesian honeyeater (*Myzomela rubratra*), and cascade affects on bird-pollinated plant species such as the oriental mangrove (*Bruguiera gymnorhiza*) (Mortensen et al. 2008). More species-specific predators include the American mink (*Mustela vison*), which has reduced the population of

192 native European water voles (*Arvicola terrestris*) in the UK (Bonesi and MacDonald 2004) and the
European hedgehog (*Erinaceus europaeus*), which is an important cause of egg depredation in wading
196 birds on the Isle of Uist, Scotland (Jackson and Green 2000). Predator-prey interactions that have
large impacts on native species are most common when such species lacks appropriate anti-
predator defences owing to a lack of co-evolution with a given predator archetype (Cox and Lima
2006). Because of the detrimental effect that alien predators can have on native prey species,
200 management to remove aliens, although not always feasible, is often considered desirable. However,
this situation can be complicated by mesopredator release, which occurs when elimination of
introduced top predators leads to the counterintuitive decline of native prey populations through the
ecological release of smaller introduced predator species (Zavaleta et al. 2001). This occurred on
Little Barrier Island, New Zealand, where removal of non-native feral cats (*Felis catus*) led to a
substantial increase in the black rat (*Rattus rattus*), which then caused a substantial decline in native
Cook's petrels (*Pterodroma cookii*) (Rayner et al. 2007). This serves as a reminder than
management of alien species must be carefully planned.

204 (2) *Aliens as competitors*: Floristic out-competition occurs most often when aliens form dense
monospecific stands that become light- and/or nutrient-limited, as in the case of Himalayan balsam
(*Impatiens glandulifera*) across Central Europe (Pyšek and Prach 1995). Faunal competition is
exemplified by out-competition of native white-clawed crayfish (*Austropotamobius pallipes*) by the
208 American signal crayfish (*Pacifastacus leniusculus*), which has resulted in the latter undergoing range
contraction (Holdich 1999). Aliens can also induce competition among natives. For example, the
introduction of fish farming in Scottish lochs has attracted flocks of native gulls (*Larus* spp.), which
has lead to native terns (*Sterna* spp.) being outcompeted and ultimately displaced (Carss 1993).
212 However, although competition between new and native species might cause local extirpations and
resultant changes in range, native extinction rarely results (Davis 2003).

(3) *Alien-native hybridisation*: This can reduce genetic integrity in native species, especially where the alien is
relatively more abundant. This can occur through outbreeding depression, which reduces the fitness of
216 native individuals, or via interspecific gene flow (introgression) resulting in genetic swamping (Rhymer
and Simberloff 1996). Ongoing and frequent introgressive hybridisation often occurs when alien and
native congeners are sympatric, as in the case of the alien succulent ice plant *Carpobrotus edulis* and the
native sea fig (*C. chilensis*) in California (Albert et al. 1997). Such hybridisation is widespread among
220 taxonomic groups. For example, there are 70 recognized alien-native plant hybrids in the UK, with over
half showing fertility (Abbott 1992). Impacts can be profound. In Texas, for example, genetic introgression
is present in the entire wild population of the endemic Leon Springs pupfish (*Cyprinodon bovinus*) due to
hybridisation with the introduced sheepshead minnow (*C. variegatus*) (Echelle and Echelle 1997).

224 (4) *Aliens as vectors*: Aliens can affect natives by vectoring parasites. For example, introduction of the
Mediterranean (blue) mussel (*Mytilus galloprovincialis*) into the North Sea allowed it to become a
vector for the parasitic copepod *Mytilicola intestinalis*, which then infected native bivalves (Torchin et
al. 2002). Similarly, the introduced common pheasant (*Phasianus colchicus*) in the UK is acting as a
228 vector for the cecal nematode *Heterakis gallinarum*, which is causing widespread decline in the native
grey partridge (*Perdix perdix*) and extirpation in sympatric populations (Tompkins et al. 2000). Aliens
can also vector disease. For example, native Hawaiian birds are regularly infected with avian
poxvirus and malaria. These diseases were carried to Hawaii with introduced domestic birds and then
232 vectored by alien southern house mosquitoes (*Culex quinquefasciatus*) introduced in 1826. Due to
the absence of co-evolution, the diseases are a primary cause of avian extinction in low-altitude
(mosquito-prevalent) communities (Warner 1968).

(5) *Aliens as ecosystem engineers*: The physical alteration of habitat by aliens can benefit natives, as
236 noted above, but negative impacts also occur. For example, soil salinisation by the ice plant
(*Mesembryanthemum crystallinum*) in California is inhibiting native non-halophytic plants (Vivrette and
Muller 1977), an effect that persists even after the plant's removal (El-Ghareeb 1991). Impacts can
also be indirect. For example, red deer (*Cervus elaphus*) introduced into New Zealand are overgrazing
240 sub-alpine tussock grass that provides an important source of food for the endangered ground-nesting
Takahe bird (*Porphyrio hochstetteri*), which could be contributing to their decline (Parkes et al. 1978).
Alien species that alter their new ecosystem are a particular problem for the conservationist since the
removal of the non-native species concerned does not usually equal the removal of the problem
244 without additional site restoration.

It should be noted that high impact and high invasiveness are two different phenomena, such that an
invasive alien can have a low impact and an alien species that is not invasive can have a substantial
impact on native biota (Colautti and MacIsaac 2004). However, substantial negative impacts are most
248 often associated with invasive aliens (i.e., those at stage IV or V of Colautti and MacIsaac's model) (Lowe
et al. 2000), largely because invasive species have, *de facto*, become established in their new
environment, spread, and increased in abundance (Colautti and MacIsaac 2004). Expansive natives can
cause similar problems. For example, brambles (*Rubus fruticosus agg.*) in British woodland form dense
252 thickets that reduce light levels and restrict ground flora. Thus, while rapid increases in population or
distribution are more common in alien species (due to a lack of predators, pathogens and parasites; a
concept summarised in the enemy release hypothesis), the real issue is often not alien status itself, but
the presence of biological traits that encourage invasiveness/expansiveness. Investigating how expansive
256 native species affect their own ecosystems would be helpful in separating the effects of alien species
from invasive behaviour alone (Valéry et al. 2009).

The over-simplicity of impact types: combination impacts

Simply dividing the impacts of invaders into “positive” and “negative” is often over-simplistic: aliens
260 frequently benefit some natives, but have a detrimental effect on others (Schutzenhofer and Valone 2006).
Indeed, the multivariate complexity and ecological connectivity of many ecosystems means translocations
producing several impacts are common (Carlton 2002). For example, introducing the crested wheat grass
Agropyron cristatum to the Canadian prairies affected natives in different ways (Heidinga and Wilson
264 2002). Of 33 natives studied, one (*Poa sandbergii*) was positively affected due to competitor release (a
tri-tropic level response summarised in the “an enemy of my enemy is a friend of mine” hypothesis: Colautti
et al. 2004) and increased in abundance. Another species (*Bouteloua gracilis*) was unaffected; while the
remaining 31 species were negatively influenced (population size decreased) due to competition. The
268 invasive Japanese knotweed (*Fallopia japonica*) in the UK affords another example. The plant has a
negative impact on many native plants that are out-competed for light and may even become excluded in
areas with high knotweed abundance (Child and Wade 2000). However, its dense stands can act as a
pseudo-woodland habitat for woodland plants such as the bluebell (*Hyacinthoides non-scripta*) (Gilbert
272 1994), while its flowers are a valuable source of nectar for native insects, which could increase winter
survival rates (Bailey 1999), although this has yet to be tested. In an indirect example of mixed effects
caused by alien-modified plant-pollinator relationships, the sugar-rich nectar produced by Himalayan
balsam (*Impatiens glandulifera*) is used by native bumble bees (*Bombus* spp.) in the UK; a behaviour that
276 increases bee abundance (Lopezaraiza-Mikel et al. 2007). The pollinator-switching is, however, detrimental
to native plants, such as marsh woundwort (*Stachys palustris*), which receive fewer pollinator visits in
areas with co-occurring Himalayan balsam and thus suffer significantly lower rates of seed set (Chittka
and Schürkens 2001). The negative impact on native flora is not offset by increasing bee numbers, at
280 least at current population levels, because Himalayan balsam can produce sugar very rapidly, such that
increasing populations can be supported without bees reverting to native species for their nectar needs.

Another commonly-known, but often overlooked, complexity in determining the impacts of alien species is
that the effects of the same alien can vary spatially very substantially (Parker et al. 1999). For example,
284 the introduction of the European rabbit (*Oryctolagus cuniculus*) to Australia caused displacement of many
native plants through herbivory (Williams et al. 1995). However, in the UK, where the rabbit is also non-
native, grazing of chalk grassland often has a positive impact: indeed this decline of the species following
myxomatosis has been implicated in the decline of the native large blue butterfly (*Phengaris (= Maculinea)*
288 *arion*) due to habitat alteration (Sheail 1991). In some parts of the UK, such as South Wales, grazing by
rabbits is specifically encouraged to prevent psammose succession and conserve rare xerophytic plants
(Hodgkin 1984).

Native reactions to aliens: contemporary evolution

292 In the past, there has often been an implicit, if not explicit, suggestion that natives are inherently vulnerable
to aliens and helpless in the wake of invasion. However, ecologists are increasingly recognising that
where aliens have an impact on natives, positive or negative, they exert a selection pressure that can,
with time, stimulate adaptation (e.g., Mooney and Cleland 2001, Carroll 2007, Yoshida et al. 2007). The
296 more intense a new interaction is, the more likely an adaptive response is to occur (providing that the
native species has a population that is large enough, and that has sufficient genetic variation, for this to
occur). Well-studied examples of alien-influenced contemporary evolution are the genetic-based increase
in toxin resistance in the native amphibian-eating red-bellied black snake (*Pseudechis porphyriacus*) in
300 areas of Australia where the poisonous cane toad (*Bufo marinus*) has been introduced (Phillips and Shine
2006) and habitat shift and associated changes in shell morphology of land snails (*Mandarina anijmana*)
in response to black rat (*Rattus rattus*) introduction (Chiba 2007). The speed with which invaders can
modify evolutionary processes of natives is demonstrated by rapid change in stylet lengths of soapberry
304 bugs (*Jadera haemotoloma*) following colonisation of introduced goldenrain trees (*Koelreuteria* spp.) in
Florida (Carroll and Dingle 1996, Carroll et al. 2001). Such phenotypic change may, in the long term,
promote alien-native coexistence and might even result in speciation of plants, or, more likely, of
pollinators. For example, the introduction of honeysuckle (*Lonicera* spp.) into North America encouraged
308 rapid hybridisation of native fruit flies (*Rhagoletis zephyria* and *R. mendax*) to the extent that speciation
occurred (Schwarz et al. 2007). This represents a rare example of homoploid hybrid speciation in animal
taxa as a direct result of the introduction of a novel host species into the native community.

Lag effects

312 It is well known that the impacts of an alien species on its new environment and native biota can change
temporally. There is usually an initial time lag between invader arrival and population growth, as well as a
second, less-reported, lag between invader population growth and native response (see comprehensive
316 review by Crooks 2005). However, many studies are undertaken when invaders are relatively new; i.e.,
before native species have a chance to respond, and may thus conclude prematurely that the introduction
has detrimental impacts for native species. The need for long-term or repeat studies is evidenced by the
red imported fire ant (*Solenopsis invicta*), the invasion of which initially caused a dramatic reduction in
320 population size of native arthropods (Porter and Savignano 1990) in Texas, USA. Twelve years later, a
repeat study by Morrison (2002) showed that populations were back to pre-invasion levels. Long term,
33% of studies that tested for a change in native species richness following the introduction of non-natives
found that, contrary to expectation, it increased (Bruno et al. 2005).

324 **Correlation versus causality**

The complexity of ecological communities means that it can be difficult to ascribe change in native species to an alien species 'cause', particularly when a correlative approach is used (Parker et al. 1999). The difficulty in quantifying community-level effects of invasion independently of other factors is demonstrated by the decline of the European otter (*Lutra lutra*) in the UK. Population decline was mainly caused by pollution, but coincided with a rapid increase in alien American mink (*Mustela vison*) (Chanin and Jefferies 1978). If these events were linked, this was not in the expected direction. Rather than mink out-competing otter (as commonly suggested at the time), the increase in mink numbers is more likely to have been facilitated, at least in part, by competitive release as a result of otter decline (Bonesi and MacDonald 2004). A similar situation has been seen with regard to avian species extinctions on oceanic islands, which usually occurred before exotic avian introductions (Sax and Gaines 2003). Lack of appreciation of such complexity means that links between invasion and extinction of natives are often based on anecdotal evidence and speculation (see review by Gurevitch and Padilla 2004). The problem of establishing causality between native decline and alien dominance is compounded further as disturbed, nutrient-enriched or polluted ecosystems (all factors often associated with native species decline) are also highly susceptible to invasion (Lozon and MacIsaac 1997, Piola and Johnston 2008). Aliens are often better able to tolerate disturbance due to their generalist ecology and their often inherent phenotypic plasticity (Daehler 2003). Thus the dominance of aliens within a community may be, initially at least, a consequence of ecosystem disturbance, not the driving force behind it (Chabrerie et al. 2008). Moreover, the deterioration of habitats is not only conducive to alien establishment, but also works synergistically with the negative effects that aliens may pose to indigenous communities (Peacock et al. 2007). Accordingly, the view that aliens are universally detrimental may stem not only from lack of research into possible benefits, but also from mis-interpretation of "negative" effects.

Summing up the evidence: native good, alien bad?

Species translocations undoubtedly modify biodiversity patterns and it is certainly not the intention of this review (as it seems to have been with others: e.g., Sagoff 2005) to underestimate the severe negative impacts such translocations can have, nor to justify further introductions of alien species into new ecosystems for any reason (aesthetic, economic or biological). Although this review has not provided an exhaustive list of all impacts, it shows that in many cases the traditional view that biological invasions DO constitute a significant threat to natural ecosystems (e.g., Simberloff 2005) is both accurate and appropriate. However, the "native good, alien bad" maxim does not convey the complexity of invasion ecology; it is conceptually over-simplistic to assume all translocations will inevitably negatively affect native biota. With this in mind, we should continue to study ALL alien-native associations so that maximally-effective management plans can be formulated for the benefit of native species. We also need to apply a precautionary approach to prevent further alien species introductions, especially when negative interactions could have devastating consequences.

Acknowledgements

I thank the three individuals who reviewed an earlier version of this paper for their detailed and helpful comments.

360

Reference List

- 364 Abbott, R.J. 1992. Plant invasions, interspecific hybridization and the evolution of new plant taxa. *Trends Ecol. Evol.* 7: 401-405.
- Agyeman, J. 1998. Native Good, Alien Bad? *Green Teacher.* 34: 28-32.
- Akeroyd, J. 1994. *Seeds of destruction? Non-native wildflower seed and British floral diversity.* Plantlife, London.
- 368 Albert, M.E., D'Antonio, C.M. and Schierenbeck, K.A. 1997. Hybridization and introgression in *Carpobrotus* spp. (Aizoaceae) in California: morphological evidence. *Am. J. Bot.* 84: 896–904.
- Bailey, J.P. 1999. The Japanese knotweed invasion of Europe: the potential for further evolution in non-native regions. In: Yano, E., Matsuo, K., Syiyomi, M. and Andow, D.A (eds) *Biological invasions of ecosystems by pests and beneficial organisms.* Japan, Institute of Agro-Environmental Sciences. pp 27-37.
- 372 Bonesi, L. and MacDonald, D.W. 2004. Impact of released Eurasian otters on a population of American mink: a test using an experimental approach. *Oikos.* 106: 9-18.
- Bruno, J.F., Fridley, J.D., Bromberg, K.D. and Bertness, M.D. 2005. Insights into biotic interactions from studies of species invasions. In: Sax, D.F., Stachowicz, J.J. and Gains, S.D. (eds) *Species invasions: insights into ecology, evolution and biogeography.* Sinauer Associates, USA. pp 13-40.
- 376 Bruno, J.B., Stachowicz, J.J and Bertness, M.D. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18: 119-125.
- 380 Carlton, J.T. 2002. Bioinvasion ecology: assessing invasion impact and scale. In: Leppäkoski, E. Gollasch, S. and Olenin, S. (eds) *Invasive aquatic species of Europe: distribution, impacts and management.* Kluwer, Dordrecht. pp. 7–19.
- Carroll, S.P. 2007. Native adapting to invasive species: ecology, genes, and the sustainability of conservation. *Ecol. Res.* 22: 892-901.
- 384 Carroll, S.P. and Dingle, H. 1996. The biology of post-invasion events. *Biol. Conserv.* 78: 207-214.
- Carroll, S.P., Dingle, H., Famula, T.R. and Fox, C.W. 2001. Genetic architecture of adaptive differentiation in evolving host races of the soapberry bug, *Jadera haematoloma.* *Genetica.* 112–113: 257–272.
- 388 Carss, D.N. 1993. Shags *Phalacrocorax aristotelis* at cage fish farms in Argyll, Western Scotland. *Bird Study.* 40: 203-211.

- 392 Chabrierie, O., Verheyen, K., Saguez, R. and Decocq, G. 2008. Disentangling relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest. *Divers. Distrib.* 14: 204–212.
- Chanin, P.R.F. and Jefferies, D.J. 1978. The decline of the otter *Lutra lutra* L. in Britain: an analysis of hunting records and discussion of causes. *Biol. J. Linn. Soc.* 10: 305-328.
- 396 Chiba, S. 2007. Morphological and ecological shifts in a land snail caused by the impact of an introduced predator. *Ecol. Res.* 22: 884-891.
- Child, L.E. and Wade, M. 2000. *The Japanese Knotweed Manual*. Packard Publishing Limited, Chichester.
- 400 Chittka, L. and Schürkens, S. 2001. Successful invasion of a floral market. *Nature* 411: 653.
- Colautti, R.I. and MacIsaac, H.J. 2004. A neutral terminology to define 'invasive' species. *Diversity Distrib.* 10: 135–141.
- 404 Colautti, R.I., Ricciardi, A., Grigorovich, I.A and MacIsaac, H.J. 2004. Is invasion success explained by the enemy release hypothesis? *Ecol. Lett.* 7: 721–733.
- Cox, J.G. and Lima, S.L. 2006. Naiveté and an aquatic–terrestrial dichotomy in the effects of introduced predators. *Trends Ecol. Evol.* 21: 674-680.
- 408 Cox, P. A. and Elmqvist, T. 2000. Pollinator extinction in the Pacific Islands. *Conserv. Biol.* 14: 1237–1239.
- Crawford R.J.M., Boonstra H.G.v.D., Dyer B.M. and Upfold L. 1995. Recolonization of Robben Island by African penguins, 1938–1992. In: Dann, P., Norman, I. and Reilly, P. (eds) *The Penguins: Ecology and Management*. Chipping Norton, Surrey Beatty. pp. 333–363.
- 412 Cronk, Q. and Fuller, J. 2001. *Plant Invaders – The Threat to Natural Ecosystems*. Earthscan, London.
- Crooks, J.A. 2005. Lag times and exotic species: The ecology and management of biological invasions in slow-motion. *Ecoscience* 12: 316-329.
- 416 Daehler, C.C. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annu. Rev. Ecol. Syst.* 34: 183-211.
- Davis, M.A. 2003. Does competition from new species threaten long-term residents with extinction?, *Bioscience*. 53: 481–489.

- 420 Dungan, R.J., O'Cain, M.J., Lopez, M.L. and Norton, D.A. 2002. Contribution by possums to seed rain and subsequent seed germination in successional vegetation, Canterbury, New Zealand. *New Zeal. J. Ecol.* 26: 121-128.
- Echelle, A.A. and Echelle, A.F. 1997. Genetic Introgression of Endemic Taxa by Non-natives: A Case Study with Leon Springs Pupfish and Sheepshead Minnow. *Conserv. Biol.* 11: 153–161.
- 424 El-Ghareeb, R. 1991. Vegetation and soil changes induced by *Mesembryanthemum crystallinum* L. in a Mediterranean desert ecosystem. *J. Arid Environ.* 20: 321–330.
- Enserink, M. 1999. Predicting invasions: biological invaders sweep in. *Science.* 285: 1834-1836.
- Fargione, J., Brown, C.S. and Tilman, D. 2003. Community assembly and invasion: An experimental test of neutral versus niche processes. *P. Nat. Acad. Sci. USA.* 100: 8916–8920.
- 428 Fuller, J.L. 1991. *The Threat of Invasive Plants to Natural Ecosystems*. MPhil thesis, University of Cambridge, UK.
- Galil, B. 2000. A sea under siege: alien species in the Mediterranean. *Biol. Invasions.* 2: 177-186.
- 432 Gilbert, O.L. 1994. Japanese Knotweed – what problem? *Urban Wildlife News.* 11: 1-2.
- Gozlan, R.E. 2008. Introduction of non-native freshwater fish: is it all bad? *Fish and Fisheries.* 9: 106-115.
- Green, W. 2000. *Biosecurity Threats to Indigenous Biodiversity in New Zealand: an Analysis of Key Issues and Future Options*. Parliamentary Commissioner for the Environment (New Zealand Government), Auckland.
- 436 Gross, C.L. 2001. The effect of introduced honeybees on native bee visitation and fruit-set in *Dillwynia juniperina* (Fabaceae) in a fragmented ecosystem. *Biol. Conserv.* 102: 89-95.
- Gurevitch, J. and Padilla, D.K. 2004. Are invasive species a major cause of extinctions? *Trends Ecol. Evol.* 19: 470-474.
- 440 Heidinga, L. and Wilson, S.D. 2002. The Impact of an Invading Grass (*Agropyron cristatum*) on Species Turnover in Native Prairie. *Divers. Distrib.* 8: 249-258.
- Heywood, V.H. 1989. Patterns, modes and extents of invasions by terrestrial plants. In: Drake, J. (ed) *Biological Invasions: A Global Perspective*. John Wiley and Sons, New York. pp 31-51.
- 444 Hodgkin, S.E. 1984. Scrub encroachment and its effects on soil fertility on Newborough Warren, Anglesey, Wales. *Biol. Conserv.* 29: 9-119.

- 448 Holdich, D.M. 1999. The negative effects of established crayfish introductions. In: Gherardi, F. and Holdich, D.M. *Crustacean issues 11: crayfish in Europe as alien species*. Rotterdam, A.A. Balkema. pp 31-47.
- Jackson, D.B. and Green, R.E. 2000. The importance of the introduced hedgehog (*Erinaceus europaeus*) as a predator of the eggs of waders (Charadrii) on the machair in South Uist, Scotland. *Biol. Conserv.* 93: 452 333–348.
- Jeschke, J.M. and D.L. Strayer. 2005. Invasion success of vertebrates in Europe and North America. *P. Nat. Acad. Sci. USA.* 102: 7198-7202.
- Jones, C.G., Lawton, J.H. and Shachak, M. 1997. Positive and negative effects of organisms as physical 456 ecosystem engineers. *Ecology.* 78: 1946-1957
- Kornas, J. 1990. *Plant Invasions in Central Europe*. Kluwer, Dordrecht.
- Krakau, M., Thielges, D.W. and Reise, K. 2006. Native parasites adopt introduced bivalves of the North Sea. *Biol. Invasions.* 8: 919–925.
- 460 Lauckner, G. 1984 Impact of trematode parasitism on the fauna of a North Sea tidal flat. *Helgoland Mar. Res.* 37: 185-199
- Lodge, D.M. 1993. Biological invasions: lessons for ecology. *Trends Ecol. Evol.* 8: 133-136.
- Lopezaraiza–Mikel, M.E., Hayes, R.B., Whalley, M.R. and Memmott, J. 2007. The impact of an alien 464 plant on a native plant–pollinator network: an experimental approach. *Ecol. Lett.* 10: 539–550.
- Lowe S., Browne M., Boudjelas S., De Poorter M. 2000. *100 of the World's Worst Invasive Alien Species A selection from the Global Invasive Species Database*. Invasive Species Specialist Group, Auckland.
- Lozon, J.D. and MacIsaac, H.J. 1997. Biological invasions: are they dependent on disturbance? *Environ. 468 Rev.* 5: 131-144.
- McKinney, M.L. and Lockwood, J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14: 450-453.
- Middleton, N. 1999. *The Global Casino*, 2nd edn. Arnold, London.
- 472 Mooney, H. 2005. Invasive alien species: the nature of the problem. In: Mooney, H.A., Mack, R.N., McNeely, J.A., Neville, L.E., Schei, P.J. and Waage, J. *Invasive Alien Species: A New Synthesis*. Island Press, UK. pp- 1-15.

- 476 Mooney, H.A. and Cleland, E.E. 2001. The evolutionary impact of invasive species. *P. Nat. Acad. Sci. USA*. 98: 5446-5451.
- Morrison, L.W. 2002. Long-term impacts of an arthropod-community invasion by the imported fire ant, *Solenopsis invicta*. *Ecology*. 83: 2337-2345.
- 480 Mortensen, H.S., Dupont, Y.L and Olesen, J.M. 2008. A snake in paradise: Disturbance of plant reproduction following extirpation of bird flower-visitors on Guam. *Biol. Conserv.* 141: 2146-2154
- Myers, J. and Bazely, D. 2003. *Ecology and Control of Introduced Plants*. Cambridge University Press, Cambridge.
- 484 Newman, J.R. 2002. Centre for Aquatic Plant Management Annual Report 2002. Rothamsted Research, Reading.
- Olesen, J.M., Eskildsen, L.I. and Venkatasamy, S. 2002. Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. *Divers. Distrib.* 8: 181-192.
- 488 Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E. and Goldwasser, L. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions*. 1: 3–19.
- Parkes, J., Tustin, K. and Stanley, L. 1978. The history and control of red deer in the takahe area, Murchison Mountains, Fiordland National Park. *New Zeal. J. Ecol.* 1: 145-52.
- 492 Peacock, D.,S. Rensburg, B.J. and Robertson, M.P. 2007. The distribution and spread of the invasive alien common myna, *Acridotheres tristis* L. (Aves: Sturnidae), in southern Africa. *S. Afr. J. Sci.* 103: 465-473.
- Pearson, D.E., McKelvey, K.S. and Ruggiero, L.F. 2000. Nontarget effects of an introduced biological control agent on deer mouse ecology. *Oecologia*. 122: 121–128.
- 496 Phillips, B.L. and Shine, R. 2006. An invasive species induces rapid adaptive change in a native predator: cane toads and black snakes in Australia. *Proc. R. Soc. B*. 273: 1545–1550.
- Pimentel, D., Zuniga, R. and Morrison, D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econ.* 52: 273-288.
- 500 Piola, R.F. and Johnston, E.L. 2008. Pollution reduces native diversity and increases invader dominance in marine hard-substrate communities. *Divers. Distrib.* 14: 329–342.
- Porter, S.D. and Savignano, D.A. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology*. 71: 2095-2106.

- 504 Pyšek, P. and Prach, K. 1995. Invasion dynamics of *Impatiens glandulifera*—a century of spreading reconstructed. *Biol. Conserv.* 74: 41–48.
- Rayner, M.J., Hauber, M.E., Imber, M.J., Stamp, R.K. and Clout, M.N. 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. *P. Nat. Acad. Sci. USA.* 104: 20862-20865.
- 508 Rhymer, J.M. and Simberloff, D. 1996. Extinction by hybridization and introgression. *Annu. Rev. Ecol. Syst.* 27: 83–109.
- Ricciardi, A. and Kipp, R. 2008. Predicting the number of ecologically harmful exotic species in an aquatic system. *Divers. Distrib.* 14: 374–380,
- 512 Richardson, D.M. Allsopp, N., D'Antonio, C.M., Milton, S.J. and Rejmánek, M. 2000. Plant invasions – the role of mutualisms. *Biol. Rev.* 75: 65–93.
- Rodríguez, J-P. 2001. Exotic introductions into South America: an underestimated threat? *Biodiversity and Conservation.* 10: 1983-1996.
- 516 Sagoff, M. 2005. Do non-native species threaten the natural environment? *J. Agr. Environ. Ethic.* 18: 215–236.
- Salmon, M., Reiners, R., Lavin, C. and Wyneken, J. 1995. Behavior of loggerhead sea turtles on an urban beach: correlates of nest placement. *J. Herpetol.* 29: 560-567.
- 520 Sax, D.F. and Gaines, S.D. 2003. Species diversity: from global decreases to local increases. *Trends Ecol. Evol.* 18: 561-566.
- Sax, D.F., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D., Grosberg, R.K., Hastings, A., Holt, R.D., Mayfield, M.M., O'Connor, M.I. and Rice, W.R. 2007. Ecological and evolutionary insights from species invasions. *Trends Ecol. Evol.* 22: 465–471.
- 524 Schutzenhofer, M.R. and Valone, T.J. 2006. Positive and negative effects of exotic *Erodium cicutarium* on an arid ecosystem. *Biol. Conserv.* 132: 376-381.
- Schwarz, D., Shoemaker, K.D., Botteri, N.L. and McPheron, B.A. 2007. A novel preference for an invasive plant as a mechanism for animal hybrid speciation. *Evolution* 61: 245-256.
- 528 Shapiro, A.M. 2002. The Californian urban butterfly fauna dependence on alien plants. *Divers. Distrib.* 8: 31-40.
- Sheail, J. 1991. The management of an animal population: Changing attitudes towards the wild rabbit in Britain. *J. Environ. Manage.* 33: 189-203.
- 532

- Simberloff D. 2005. Non-native species do threaten the natural environment! *J. Agr. Environ. Ethic.* 18: 595–607.
- 536 Simberloff, D. and von Holle, B. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions.* 1: 21-32.
- Taitt, M.J. 1981. The effect of extra food on small rodent populations: deermice (*Peromyscus maniculatus*). *J. Anim. Ecol.* 50:111–124.
- 540 Tompkins, D.M., Greenman, J.V., Robertson, P.A. and Hudson, P.J. 2000. The role of shared parasites in the exclusion of wildlife hosts: *Heterakis gallinarum* in the ring-necked pheasant and the grey partridge. *J. Anim. Ecol.* 69: 829-840.
- Torchin, M.E., Lafferty, K.D. and Kuris, A.M. 2002. Parasites and marine invasions. *Parasitology.* 124: 137-151.
- 544 Valéry, L., Fritz, H., Lefeuvre, J.C. and Simberloff, D. 2009. Ecosystem-level consequences of invasions by native species as a way to investigate relationships between evenness and ecosystem function. *Biol. Invasions.* 11: 609-617.
- 548 Vivrette, N.J. and Muller, C.H. 1977. Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum crystallinum*. *Ecol. Monogr.* 47: 301-318.
- Warner, R.E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor.* 70: 101-120.
- 552 Williams, C.K., Parer, I., Coman, B.J., Burley, J. and Braysher, M.L. 1995. *Managing Vertebrate Pests: Rabbits*. Australian Government, Canberra.
- Williamson, M. 1993. Invaders, weeds and the risk from genetically modified organisms. *Experientia.* 49: 219-224.
- 556 Williamson, M. And Fitter, A. 1996. The varying success of invaders. *Ecology.* 77: 1661-1666.
- Wonham, M.J., O'Connor, M. and Harley, C.D.G. 2005. Positive effects of a dominant invader on introduced and native mudflat species. *Marine Ecology Progress Series.* 289: 109-116.
- 560 Yoshida, T., Goka, K., Ishihama, F., Ishihara, M. and Shin-ichi, K. 2007. Biological invasion as a natural experiment of the evolutionary processes. *Ecol. Res.* 22: 849-854.
- Zavaleta, E.S., Hobbs, R.J. and Mooney, H.A. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.* 16: 454-459.

Figure Legends

564

Figure 1: The range of impacts alien species can have on native species.