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

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<u>Abstract</u>

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/).

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., Rodíguez 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

60   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.

64   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

68   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

72   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

76   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

80   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

84   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

88   likely when there are few ecological and behavioural similarities between natives and non-natives. In the UK, for example, the alien slender speedwell (*Veronia filiformis*) does not compete with native grassland plants

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(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-

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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 in urban and sub-urban environments, such that many species would likely become extirpated in urban

132   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 mauritianus* (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 fir 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 gymnorrhiza*) (Mortensen et al. 2008). More species-specific predators include the American mink (*Mustela vison*), which has reduced the population of

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

192   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,

196   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

200   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 introgesssive 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, d*e 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
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
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
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
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
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
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,
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*)
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 psammosere 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.

312   **Lag effects**

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).

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.

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