Facing the broader dimensions of biological invasions
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Abstract
Invasive species are an excellent opportunity to think about the nature society desires, particularly in the face of global changes. Nature, and human views of nature, are rapidly evolving; our approach to biological invasions through biosecurity institutions and land management policies must evolve in tandem with these changes. We review three dimensions that are insufficiently addressed. *First*, biological invasions are culturally shaped and interpreted. Humans play a major role in the movement and nurturing of alien life, and aesthetics, perception, and emotion are deeply implicated in the and management of invasive species. What people fear or regret with invasive species are not their effects on nature per se, but their effects on a particular desired nature, and policymaking must reflect this. *Second*, biological invasions are not restricted to negative impacts. Invasions take place in landscapes where many natural conditions have been altered, so policy tools must recognize that invasive species are a functional, structural and compositional part of transformed ecosystems. In some cases, native species benefit from changes in resource availability caused by invasions or from protections provided by an invasive plant. *Finally*, invasive species can help ecosystems and people to adapt to global change by maintaining ecosystem processes such as productivity, carbon storage, and nutrient cycling in a context of climate change or land cover transformations. While recognition is growing among ecologists that novel, invaded ecosystems have value, and while the on-the-ground application of biosecurity policies has of necessity adjusted to local contexts and other agendas, invasion biology could aid policymaking by better addressing the three complexities inherent in the three dimensions highlighted above.

Keywords
Alien invasive species; Biological invasion; Biosecurity; Climate change; Culture; Land use changes; Positive impact; Weed policy

Introduction
The emergence of the term ‘biosecurity’ and its incorporation into legislation, policy instruments, and institutional structures in many countries over the past two decades signalled an intensified focus on invasive species. Threats as diverse as disease epidemics, food safety, agricultural pests, and environmental weeds are lumped together under ‘biosecurity’ with an associated sense of urgency (Bingham *et al*., 2008; Dobson *et al*., 2013; Barker, 2008).

Yet, managing and legislating for the control of biological invasions in the broader landscape is quite different than dealing with the specific, human health and economic threats of H1N1, foot and mouth disease, or fruit flies. The concept of biological invasions evokes a tension between what nature is and what nature ought to be. Yet nature is changing, and what nature ought to be is changing as well, in response to the evolution of human society and our views of nature. As such, the concept of biological invasions...
must be considered by policy makers as an unstable, evolving concept requiring place-based deliberations of values and interests as well as global-scale science.

Vigorous debate has engulfed the field of invasion biology since the 50th anniversary of the seminal work of Elton (1958), with tensions between those who consider that the spread of alien species is categorically undesirable, and others who think that invasive organisms should instead be assessed on their environmental effects (Davis, 2009). While the majority of arguments are restricted to the terrain of neutral scientific language, some suggest that invasion biologists need to more explicitly recognize the value systems that influence their work (Rozzi, 1999; Larson, 2005; Kueffer, 2013; Humair et al., 2014). Furthermore, it is increasingly pointed out that invasive species must be investigated in the context of rapid change, ecological novelty, and global transformations to climate and land cover (Larson et al., 2013; Thomas, 2011). From such perspectives, invasive species and the new ecosystems to which they contribute may potentially be considered as ‘good’.

The aim of this short review is to argue that to adapt to our changing world, and as such to promote more pertinent policies on biosecurity and environmental management of living species, we should reevaluate invasive species. We address three new facets of biological invasions: their cultural dimension, their potentially positive environmental effects, and the benefits they can provide in a context of global change (i.e. climate and land cover change), before concluding with some policy recommendations.

Recognizing the cultural dimension of biological invasions

Biological invasions are both biological phenomena (movements, distributions, and community dynamics of species) and cultural phenomena (how people – including scientists – in different places facilitate, are affected by, interpret, react to, label, and judge invasions and the landscape changes they induce or represent). This is quite different from saying that biological invasions have a cultural impact: this is to say that they are cultural. Reducing such hybrid phenomena to purely biological aspects is appealing for strictly focused research on species redistribution or ecological interactions, but useless for policy makers. Decisions on funding, management and research topics regarding invasive species are made by people, who as social beings, necessarily mobilize cultural references (Rozzi, 1999; Hall, 2003; Larson, 2005, Rotherham and Lambert, 2011). Cultural considerations – which are dynamic in themselves (Starfinger et al., 2003; Stromberg et al., 2009) – are inextricable from the science and management of invasions in at least three ways.

First, perceptions and aesthetics play a major role in the treatment of particular species. Some are highlighted as invaders primarily because they are ugly, annoying, noxious, or highly visible. For instance, the decision to manage purple loosestrife (Lythrum salicaria) in North America was mainly based on aesthetic considerations (Hager and McCoy, 1998), or Europe’s efforts to control ragweed (Ambrosia artemisifolia) are justified through both its strong allergic impact and its alien status (Fried, 2012). Other actions to control invasive plants are based on the perception that they cause extinctions, despite the fact that such extinctions do not appear to be occurring (Powell et al., 2013).

Conversely, other invaders are downplayed because they are attractive, useful, or scarcely noticed. Plans to kill feral mammals (e.g. camels in Australia, deer in New Caledonia, gray squirrels in Europe, mountain goats in America’s Olympic National Park), or to remove alien trees (e.g. eucalypts in the San Francisco bay area) encounter opposition from the public (Stokes, 2007). Australian Aborigines have been known to resist eradication programs of feral species, believing that the worth of a species lies in its ability to flourish in an environment, not in its claim to being an original inhabitant (Warren, 2007).
Second, different parts of the world have different ‘environmental imaginaries’, or cultural ways of understanding their interactions with the environment, shaped by history, politics, and geography (Peet and Watts, 1996). As a result, different discourses about invasive species are current in different places. South Americans, for instance, tend to be less concerned about biological invasions than people from Anglophone settler colonies (Speziale et al., 2012). Environmental imaginaries also influence the use of arbitrary thresholds like national borders and historical dates to separate natives from exotics (Head, 2012). Such thresholds can result in perceptions of national or regional ecological integrity that shape whether species are treated as exotic or not. One can also imagine alternative discourses that are compatible with incorporating new species (Kueffer and Kaiser-Bunbury, 2013), metaphors such as ‘melting pot’ landscapes (Kull et al., 2013) or ‘novel ecosystems’ (Hobbs et al., 2006; 2013).

Third, reliance on words and labels inevitably makes invasion biology cultural. The discursive impacts of categories like ‘invasive’ and ‘alien’ are profound, stirring up emotions via anxiogenic metaphors. Discourses on invasive species commonly use military, medical or xenophobic references that are not neutral and cannot be discounted as simply scientific terminology (Larson, 2011; Tassin and Kull, 2012). They represent values that are rarely explained, inspired by certain moral imperatives about what nature ought to be. Unsurprisingly, there are numerous stories about indigenous peoples who take offense of the way language about invasive species shifts attention away from the colonizing people who have brought much greater ecological impacts to their lands and lives (Larson, 2005).

Environmental managers and policy makers working in specific landscapes already recognize many of these cultural aspects, as their work necessarily confronts different interests and viewpoints on the ground (Atchison and Head, 2013). However, much higher scale policy and science confronts these cultural issues only with the suggestion that ‘awareness’ be increased, presuming that people will come around to the dominant scientific point of view (Rotherham and Lambert, 2011). What is necessary instead is recognition that other politics, interests, and agendas in each particular national and local context will re-shape the categories, debates, and policy possibilities (Forsyth 2005; Barker 2008; Fall 2013).

Recognizing the positive effects of biological invasions

Invasive species can endanger native species through predation, herbivory, disease transmission, hybridization and competition, and they can alter the functioning of ecosystems, affect human health, and result in great economic losses (Vitousek et al., 1997; Pimentel et al., 2000). These kinds of impacts have led scientists and managers to focus on the negative aspects of invader-driven catastrophes. Indeed, many studies on invasive species appear biased towards negative impacts (Pysek et al., 2008). Yet a holistic view of the ecological consequences of biological invasions would also include positive impacts. As biological invasions become ever more common in a world where many natural conditions have been altered, any assessment must recognize that invasive species are a functional, structural and compositional part of the invaded or restored ecosystems (Van Riel et al., 2000; Marris, 2009; Ewel and Putz, 2004). For instance, the potential benefits of plant invaders on native species have been largely under-appreciated (Lugo, 2004; Goodenough, 2010; Schlaepfer et al., 2010; Evine et al., 2012; Lugo et al., 2012; Rodewald, 2012). We briefly review some of these positive impacts here.

In numerous cases, native species benefit from an increase in resource availability after an invasion due to the diversification, enhancement, or replacement of food sources. Native phytophagous insects are increasingly colonising non-native plants, demonstrating...
rapid adaptations and becoming model systems for evolutionary biology (Jahner et al., 2011). Waterfowl communities along the mid-Atlantic coast of United States thrive due to the exotic aquatic plants *Hydrilla verticillata* and *Myriophyllum spicatum* (Rybicki and Landwehr 2007). In Africa, the invasive tree tobacco (*Nicotiana glauca*) greatly increases the local abundance of sunbirds compared with un-invaded areas (Geerts and Pauw, 2009).

Another kind of positive impact is when populations of an endangered species depend on invasive plants providing food sources (Schlaepfer et al., 2010). In subtropical Australia, the vulnerable rose-crowned fruit dove (*Ptilinopus regina*) eats winter fruit from invasive stands of camphor laurel (*Cinnamomum camphora*) and may have been rescued from extinction thanks to this resource (Neillan et al., 2005). Due to their phenology, plant invaders may also extend the seasonal availability of food resources. In the foothills of California’s Sierra Nevada, introduced horticultural plant species fruit throughout the year, while only one native species (i.e. *Heteromeles arbutifola*) offers native frugivorous birds a substantial amount of fleshy fruits in winter (Aslan and Rejmanek, 2010).

Invasive plants create habitat or protective structures that may be beneficial for some native plant or animal species, especially during critical phases of reproduction. In *Acacia koa* forests of Hawaii, the invasion of *Cinchonia pubescens* and *C. calisaya* provides a structural layer which facilitates the development of understory native species – their species richness is about 20 % higher in invaded plots than in non-invaded plots (Fischer et al., 2009). At Little Swanport Estuary, Tasmania, *Spartina anglica* invasion of mudflat habitat promotes a more species-rich and abundant macrobenthos (Hedge and Kriwoken, 2000). On islands like the Azores, Madeira, and Mauritius, some invasive plants provide a good micro-ecological environment for endemic snails (Van Riel et al., 2000). In Arizona, 49 bird species use the salt-cedar (*Tamarix spp.*) as breeding habitat, though the relative use of these trees and their quality as habitat vary substantially by geographic location and bird species (Sogge et al., 2008).

Moreover, some invasive species can control problematic native species. For instance, on Cape Cod, the invasive green crab (*Carcinus maenas*) indirectly contributes to restoring degraded salt marsh ecosystems by forcing out the destructive native herbivorous marsh crabs (*Sesarma reticulatum*). This crab’s population has exploded due to a dearth of predatory fish (a consequence of overfishing), resulting in the denudation of hundreds of hectares of marsh (Bertness and Coverdale, 2013).

Finally, plant invaders may act as physical barriers protecting young native species against predation. On sandy shores in the northern Adriatic Sea, the introduced green alga, *Codium fragile* ssp. *tomentosoides*, enhances the recruitment and survival of mussels by protecting them with a full canopy during the summer, the season during which the abundance and activity of predators is greatest (Bulleri et al., 2006). In forests of southeastern New York State, the Japanese barberry (*Berberis thunbergii*) offers greater refuge than native shrubs to verry (*Catharus fuscenscens*) from nest predators, probably because rodents rarely forage within barberry (Schmidt et al., 2005).

These kinds of positive effects on native populations resulting from invasive plants may be less numerous, or considered less important, than their negative effects. But before such judgments are made – mindful of the cultural aspects of invasions we evoked above – is it incumbent on the research community to investigate the full range of ways in which invasive species transform ecological relationships, and for policymakers to be open to such complexities. Policy tools evaluating species introductions, such as the much-copied Australian Weed Risk Assessment model (Kumschick and Richardson 2013), and more particularly the diversity of web-based lists of known invasive
species (Hulme and Weser 2011) can be inconsistent and biased towards negative aspects. This should be addressed.

**Recognizing the adaptive dimension of invasive species in global environmental changes**

Invasive species are typically seen as exacerbating the negative aspects of global environmental changes (Pyke et al., 2008; Walther et al., 2009). As global temperature warms, and as humans modify land covers at a large scale, it is presumed that native species will struggle while invaders will increasingly replace them, largely due to differential adaptations to diverse and changing conditions (Walther et al., 2009; Bradley et al., 2010). The amplification of biological invasions by global warming may lead to the erosion of genetic resources and attenuate the ecosystem services provided by the resulting ecological systems (Behning et al., 2002; Pejchar and Mooney, 2009). However, the reverse may also be true. The presence of some invasive species could instead be seen as a potential lever to increase the adaptability or resilience of ecosystems to climatic or land cover changes (Pyke et al., 2008).

For one, an invading species could replace resources squeezed out by changed climate or land transformations, ensuring the survival of a local species threatened by those changes. In Mayotte, the novel ecosystems resulting from shifting cultivation, involving several invasive fruiting species (e.g. *Mangifera indica*, *Syzygium sp.*), helps the native brown lemur *Eulemur fulvus* to survive in fragmented areas (Tonnabel et al., 2011). In the leeward lowlands of Reunion Island, where forests have been replaced by agricultural and urbanized areas, some invasive plant species (e.g. *Schinus terebenthifolius*, *Lantana camara*) have replaced native fruit resources used by certain native birds (e.g. *Zosterops borbonicus*); and the introduced and invasive vacoa (*Pandanus utilis*) has become the favorite habitat of the endangered gecko *Phelsuma inexpectata* (Bour et al., 1995; Tassin et al., 2006) On a longer time scale, palaeoecologists have long sought to document the dynamics of palaeo-invasions, such as those following the retreat of late Pleistocene ice sheets, that facilitated the new species assemblages in postglacial landscapes (Jackson and Overpeck, 2000; Gillson et al., 2008).

Second, invasive species may maintain or enhance the delivery of ecosystem services in conditions of climate or land cover change. Novel ecosystems resulting from plant invasions are increasingly recognized as maintaining critical ecosystem processes such as productivity, carbon storage, and nutrient cycling. For instance, in Hawaii, the productivity of novel forests increases as a result of increased N inputs in the N-limited environment, and may also be related to N and P turnover in these systems (Mascaro et al., 2012). Furthermore, invasive and introduced plants can strongly impact soil water content and landscape water balance, with both positive and negative impacts (Walker and Smith, 1997; Bruijnzeel, 2004; Brauman et al., 2007). In the context of rapid change, policies need to consider these complex and multi-faceted relationships.

Third, recent conservation biology research has investigated the need for ‘assisted colonization’ or translocation of species whose ranges are threatened by global change (Hoegh-Guldberg et al., 2008). Invasive species, particularly plants, may facilitate assisted colonization by enhancing resource availability, protecting new arrivals through shade or protective structures, or providing other ecosystem services, in ways similar to those we discussed earlier. Furthermore, invasive species can be seen as a form of ‘spontaneous colonization’, not requiring costly ‘assistance’. This may be particularly relevant in cases where the invader is, in its native area, threatened by climatic change or land transformations. Many examples exist of invasive species that are threatened in their home range but are highly successive elsewhere, e.g. the rabbit *Oryctolagus cuniculus* (Lees and Bell, 2008), the tammar
wallaby *Macropus eugenii* (Taylor and Cooper, 1999), the miconia *Miconia calvescens* (Meyer and Florence, 1996), the Monterey pine *Pinus radiata* (Moira et al., 2007) or the prickly pear *Opuntia stricta* (Foxcroft et al., 2004).

At a philosophical level, the displacement of climate zones and ecosystems due to global change throws into question the normative basis of invasion biology or the use of past ecological communities as a reference (Thomas, 2011). As climate changed during the Pleistocene and Holocene, many plants and animals had to be invasive to adapt and shifted their endemic range (Webber and Scott, 2012). For instance, several North American taxa (*Alnus, Quercus*) appeared in the Andes after Pliocene joining of North America and subsequent Pleistocene cooling (Hoooghiemstra and Sarmiento, 1991). Glaciated regions of North America were colonized by invasive species following late Wisconsinan ice retreat (Davis, 1976). With such a perspective in mind, it should be no surprise that they are doing the same in the Anthropocene. The question then becomes how land managers and policy makers plan for these processes, judging the positive and negative roles that invaders might play, and deciding between priorities such as the maintenance of ecosystem services or the preservation of native species (Lowler and Olden, 2011). Policies must recognize this long-term non-fixity in nature, the agency of plants and animals themselves, and the high potential for surprise and unexpected outcomes.

**Conclusion**

There is an urgent need for researchers and policy makers to give up a Manichean approach to biosecurity, particularly in terms of the multiple facets of biological invasions across landscapes and ecosystems. Whether an invasion is positive or negative depends on human perceptions of that particular situation. Or, in the words of Hamlet: “there is neither good or bad, but thinking makes it so”.

Biological invasions are an excellent opportunity to think about the landscapes that society wants. Land and its vegetation are our heritage to protect, and provide numerous functions to humanity. What humans dislike about invasive species is not their effects on nature *per se*, but their effects on a particular desired nature. The characteristics of that desired nature are highly contextual to different people and different landscapes, and are defended with reference to different ethical, ideological, and material perspectives. In restoration ecology, for example, there is a strong tradition of discussing the idealistic motivations behind management decisions (Clewell and Aronson, 2005).

Despite the relatively fixed discourse of invasion biology on the deleterious impacts of invasive species, policy makers working in specific landscapes have often adjusted to the complexities – cultural, ecological, and transformational – that we describe above. For instance, in New Zealand, Barker (2008, p. 1612) has shown how biosecurity practices ‘produce a complexity of semipermeable control boundaries that are flexible and sensitive to the shifting spatiotemporal geographies of indeterminate entities, and to changing and competing human values.’ In other words, actual policy processes and implementation are often more contingent than we might presume from the letter of the law. Invasion biology can help these policymaking contexts by better addressing the complexities. In a context of climate and land cover change, invasive species should not necessarily be considered as deleterious, bad or ecologically useless. Our living world is already a biodiversity melting pot, and global change is making it more and more mixed, and in that way, more and more complex. This is a fact, not an idea, and we have to face it in all its dimensions, without any blind spots.

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