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Invasion, Evenness, and Species Diversity in Human-Dominated Ecosystems

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1. Introduction

Biological invasions have become a major ecological problem globally (Vitousek et al., 1997; Mooney & Hobbs, 2000) for several non-mutually exclusive reasons. From the perspective of economics, many invasive alien species have become pests, sometimes causing severe damages to crops (Mack et al., 2000; Pimenel et al., 2000). From the ecological point of view, invasive species can inflict drastic changes in the invaded community altering its structure and function (Simberloff, 1997; Mooney & Cleland, 2001), and leading to biodiversity loss (Herbold & Moyle, 1986; Clavero & García-Berthou, 2005). The battle against invasions of alien species requires a great deal of efforts and resources, and yet is not always successful (Kaiser, 1999; Zavaleta et al., 2001). Whereas complete eradication of successfully established invasive species is in most cases impossible, controlling their population growth may decrease economical damages, and prevent biodiversity loss in the invaded community. Furthermore, successful eradication of one alien species may result in a worse alternative stable state (Beisner et al., 2003), where another, potentially more harmful invasive species dominates the community (e.g., Zavaleta et al., 2001). Therefore, fighting invasions should be done carefully and wisely, while taking into account multiple biotic and abiotic factors and outcomes. More importantly, such actions should emerge from a deep understanding of the evolutionary and ecological mechanisms that operate at different biological hierarchies to allow invasions, i.e., starting from the individual traits characterizing the invasive species (genetic background, morphology, physiology, behavior and life history), through its population parameters (demography, fluctuations, growth rate), and up to patterns and processes characterizing the invaded community (composition, structure, and age).

The demography of many invasive species has been well documented, and their damages were explored in details (Pimentel et al., 2000). However, the ways such species enter new ecosystems and communities, and their exact effect on community structure and biodiversity are not yet fully understood (Gurevitch & Padilla, 2004). Our goal is to review the evolutionary and ecological mechanisms of bio-invasions at the species (e.g., Facon et al., 2006) and community levels (e.g., Shea & Chesson, 2002), and present some of the general effects and outcomes of invasions at both levels. We discuss various mechanisms by which invasive species manage to establish viable populations and even dominate new ecosystems, how their unique biological traits allow rapid population growth, and the extent to which their interactions with native species trigger changes in community structure and function (i.e., community resilience).

Biological invasions are controlled by several factors. Invasive species must have good dispersal abilities, or otherwise they can only immigrate to remote places with the help of humans (Facon et al., 2006). Once the invader has found its way to the new environment, it must be reasonably adapted to the local conditions. If not, changes must occur within a short time, either in the species or in the environment (Facon et al., 2006). Rapid evolutionary changes have been shown to occur in invertebrates and plants shortly after immigration to the new environment (reviewed by Whitney & Gabler, 2008). Next, the invader's population must rapidly increase in size, reaching a critical threshold above which drift and disturbances are less likely to drive the invader into extinction (reviewed by Sakai et al., 2001). Once the invader is successfully established, it has the potential to modify community structure and function. For example, even if no changes in species composition occur, the relative abundance of the different species making up the community may change, resulting in few and highly abundant species dominating many low abundance species (Shochat et al., 2010). Below we discuss the potential negative effect of such reduction in evenness on community resilience.

2. The population/species level

2.1 Evolutionary mechanisms promoting invasion

Facon et al. (2006) discussed three potential scenarios for species to invade remote new environments. In the simple case, the only restriction is the species dispersal abilities, whereas the new environment is perfectly suitable for the species. If the species manages to arrive to the new environment (normally with the help of humans) it will establish successfully within a short time (assuming that it can overcome the negative interactions with the local species). The other two cases are more complex and interesting, because they deal with nearby species that either go through genetic or plastic changes (e.g., Maron et al., 2004), or take advantage of changes in the new environment (e.g., Seabloom et al., 2003).

In the second scenario the invader takes advantage of changes in the new environment. Such scenarios are probably common in nature, where some species may even manage to invade new environments within short temporal opportunities, such as disturbances in the new habitat. In such cases, the species may enter the environment during a periodical disturbance, quickly establish a self-sustained population, small as it may be, and remain in the new environment even if conditions return to the initial ones. For example, Seabloom et al. (2003) suggested that in California replacement of perennial grasses by invasive annual grasses across vast areas occurred as a result of disturbance that reduced water and nitrogen levels, and not because the perennial grasses were weak competitors. Such cases imply that proper management regimes may facilitate restoration of native biota in parts of the ecosystem.

Once established, the alien species may find a restricted niche, and remain rare and localized, or it may find perfect conditions, thrive, and even dominate the local community. Yet, even for such successful invasions, timing is also an important factor, because environmental factors change in both time and space. For several successful invasions of species that became abundant throughout countries and continents, it took more than one introduction and several failure cases before the population has established (e.g., Pimm, 1991; Veltman et al., 1996).

Both the first and the second scenarios suggest that a key trait for any invasive species is a high genetic variation (Mooney & Cleland, 2001). On the one hand, genetic variation serves as the raw material upon which natural selection can operate (Endler, 1986). On the other hand, genetic variation is positively correlated with population fitness (Reed & Frankham, 2003). The combined effect of both increases the survival probability of the species in the new environment (Facon et al., 2006). It is likely that selection will favor those individuals better adapted to the new environment. Assuming that their fitness advantage is large, their adaptive genes will rapidly increase in frequency, and despite the loss of genetic diversity, the invader's population will become highly adapted to the environment and successfully establish.

In the third scenario the species, that is originally not adapted to the new environment, has to change genetically or epigenetically [i.e., heritable changes in gene expression and function that cannot be explained by changes in DNA sequence (Richards, 2006)] in order to invade successfully. Environmentally induced epigenetic changes, usually occurring over a relatively short period of time, are often inherited by future generations (Richards, 2006). As such, they may increase the evolutionary potential of invasive species in response to challenges and stressors in novel environments (Bossdorf et al., 2008). Although epigenetic processes may play an important role in biological invasions, to date they have not been explored in that context. Future research on invasive species may benefit from including this aspect as a potential mechanism facilitating the establishment of alien species in novel environments.

2.2 Ecological mechanisms promoting invasion

Although species must be reasonably adapted to the new environment on the first place, lack of adaptations is not necessarily the most parsimonious explanation for invasion failure (Pimm, 1991). In other words, caution should be taken before arguing that an introduced species failed to establish in a new environment because it lacks physiological or genetic adaptation necessary to survive and reproduce in this environment (Pimm, 1991). For example, if adaptations are important, one would expect that prior experience of a habitat would increase invasion success. However, no support for this prediction was found by Moulton & Pimm (1986) when analyzing bird species that were introduced to Hawaii. Specifically, invasion success of birds originating from tropical habitats was not higher than that of birds originating from temperate habitats. Similarly, Crawley (1987) could not find evidence for the idea that “climate matching” between the habitat of origin and new habitat improves the invasion success of insects.

Both studies, however, found that widespread species were more successful invaders than species with small geographical range. The most intuitive explanation for this pattern is that widespread species experience a wide range of environmental conditions and thus have an advantage over restricted species, which are less likely to find suitable conditions in the new environment (Pimm, 1991). Clearly, there are many other possible explanations for this pattern such as that widespread species better cope with competitors and predators than the more geographically restricted species (Pimm, 1991).

A key feature for a successful invasion is an efficient utilization of food resources (i.e., competitive ability), which in turn can increase both individual and population growth rate (Sakai et al., 2001). For example, in plants, Grotkopp et al. (2002) found that the seedling relative growth rate of invasive pine species was higher than in non-invasive species. In addition to this characteristic, the studied pines were characterized by short generation time and low seed mass. Yet, high population growth rate alone is not necessarily sufficient for successful invasions, since in many cases increased growth rate is also associated with increased fluctuations in population size. In such cases species may reach high population density within a short time, but also decrease soon after to low population densities that may drive the population into extinction (Pimm, 1991).

Efficient utilization of resources may also relate to behavioral aspects. In central Arizona synanthropic bird species, including several exotic ones, were found to be more efficient foragers than native species (Shochat et al., 2004a). Yet, under certain conditions, species that have such a potential to become invasive may remain in low profile in wild habitats, where harsh conditions favor native species. Agricultural and urban developments may remove some key hurdles (e.g. specific predators) or add essential components to the environments (e.g. water, breeding sites or specific food resources) that allow 'dormant invasive species' to change their mode and become invasive.

For example, extremely dry deserts favor rodent species that do not drink, but gain water from food resources, including dry seeds. Such seeds are not available to birds as they are not digestive without water. However, agricultural development in such arid zones, that adds water holes and irrigation systems to the ecosystem, not only allows the establishment of seed-eating birds, but totally removes the restriction on their fast individual and population growth rates. This extreme change in the rules of the evolutionary game creates a new environment in which very few resources remain for the nocturnal rodents in the end of the day (Shochat et al., 2004a).

3. The community level

The relationship between species diversity of the local community and the probability of successful invasions has been widely discussed in the ecological literature (e.g., Elton, 1958; Kennedy et al., 2002). Both theory (Case, 1990) and small scale experimental studies (McGrady-Steed et al., 1997; Tilman, 1997; Levine & D'Antonio, 1999; Naeem et al. 2000; Kennedy et al. 2002) indicate that diverse communities better resist invasions [but see Planty-Tabacchi et al., (1996) and Stohlgren et al., (1999) for the opposite pattern detected at the regional scale]. In a field experiment, Kennedy et al. (2002) showed that species diversity in small grassland plots enhanced invasion resistance by increasing crowding and species richness in the local plant neighborhood. Both the number of invaders and success of invading plants were reduced. These results strongly suggest that local biodiversity represents an important line of defense against the spread of invaders.

In less diverse communities, invasive species may change community organization and break assembly rules. In California, invasion of the argentine ant (*Linepithema humile*) led to disassembly of local ant community. Where the Argentine ant was present, ant communities appeared random and weakly aggregated in species co-occurrence (Sanders et al. 2003).

How extreme can the impact of invasion on the local community be? Although alien species have been argued to drive local extinctions either indirectly through exploitation competition (Byers, 2000), or directly either via interference competition (Human & Gordon, 1996; Lach, 2005) or hybridization (Rhymer & Simberloff, 1996), the overall view of extinction as a result of invasions has been long criticized and is still under debate. In a review of ten studies covering 850 plant and animal introductions, Simberloff (1981) argued that invasive species rarely influence the invaded communities. This view has been criticized by Herbold & Moyle (1986) who questioned Simberloff's methodology and also argued that substantial density reductions can be as important as local extinctions. Davis (2003) suggested that in cases where invasion leads to biodiversity loss, it is more likely to be driven by habitat loss or predation rather than by competition. Gurevitch & Padilla (2004) also questioned the idea that invasive species are an important driver of native species extinctions. Their view has been criticized by Clavero and García-Berthou (2005) who provided a list of case studies supportive of extinction following bio-invasions [e.g., European birds (Birdlife International, 2000) and North American fish (Miller et al., 1989)].

Bio-invasions may also be facilitated if food webs are arranged in compartments (distinct food chains in which species interact more frequently among themselves than with species pertaining to other food chains) (Pimm, 1991). Such communities are easier to invade, because alien species can locate themselves among two or more food chains, relying on resources from several chains (Fig. 1). May (1982) suggested that food webs are organized in

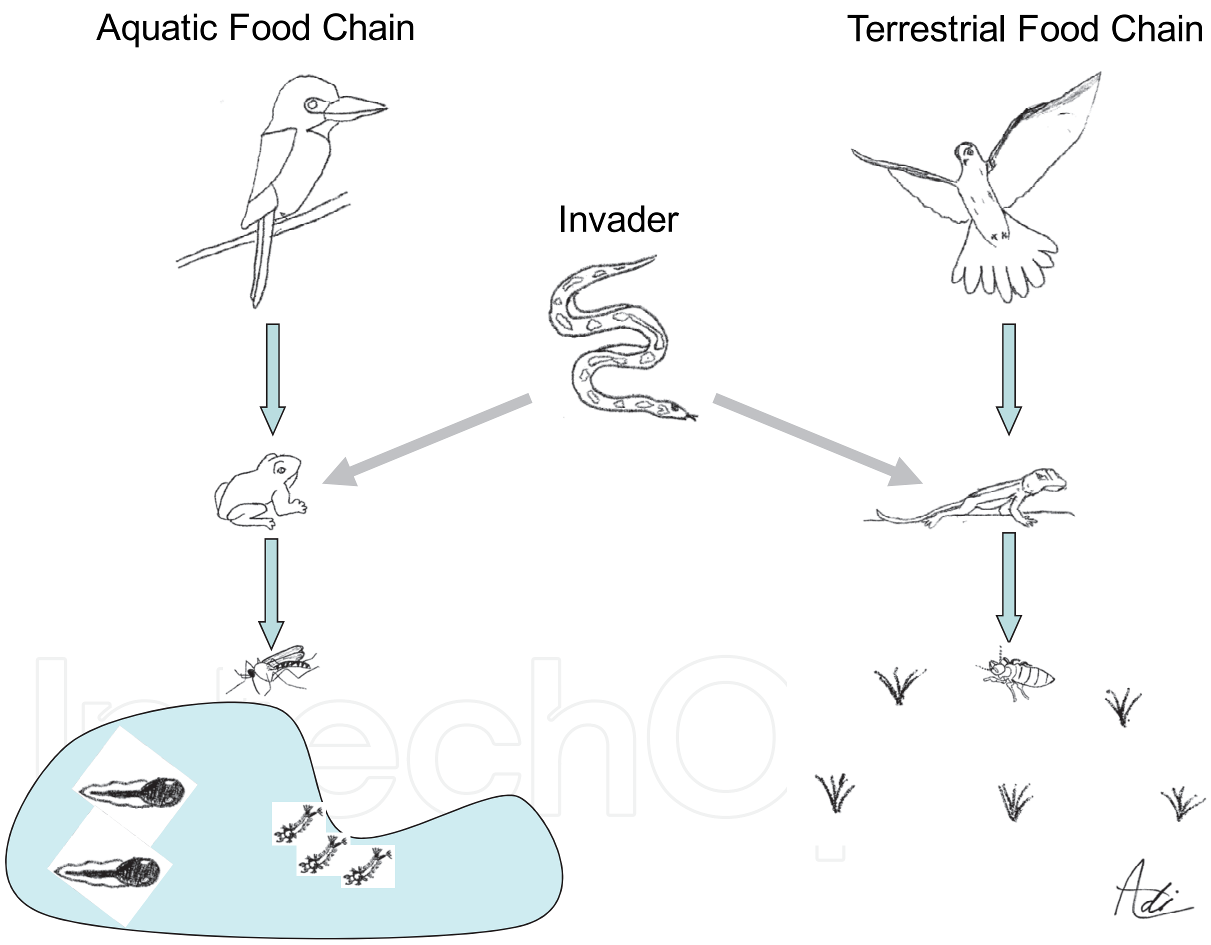


Fig. 1. Consequences of compartmentalization in food webs on biological invasions. An example showing a food web comprising of two distinct food chains occurring across two major habitat boundaries (aquatic and terrestrial) in which species only interact within chains. Such an organization can facilitate the invasion of the snake, which can consume prey from both chains. In the alternative scenario, the snake enters only one of the chains and thus suffers strong competition and possibly high predation pressure from the top predators.

compartments, but Pimm & Lawton (1980) could not find an empirical support for such organization. Recent studies (Krause et al., 2003; Stouffer & Bascompte, 2011), however, provide new evidence that food webs are indeed compartmented. Furthermore, Stouffer & Bascompte (2011) demonstrated how compartments in food webs directly buffer extinctions, while also increasing the persistence of species making up the community. Thus, if compartmented communities are indeed easier to invade, invasive species can indirectly lead to extinction, by disordering the food-web structure within the community.

In the case of hybridization the picture is much clearer, since the process of introgression should ultimately lead to elimination of native species ancestry, and eventually to its complete replacement by the invasive species (Hedrick, 2005). Examples include introgression by the introduced American Ruddy Duck (*Oxyura jamaicensis*) into the European White headed Duck (*Oxyura leucocephala*) (Green & Hughes, 2001), and introgression by domesticated Mallards (*Anas Platyrhynchos*) into the Florida Mottled Duck (*Anas fulvigula*) (Mazourek and Gray, 1994). In some cases hybridization may result in the formation of new species, either by speciation through recombination or allopolyploidy (Coyne & Orr, 2004).

In summary, since extinctions happen across evolutionary time scales, and because invasions involve many other changes in the environment, it is difficult to link extinctions and invasions. Altogether, it is agreed that the various negative effects of invasive species on community structure and biodiversity can lead, in extreme cases, to local extinctions. Below we discuss possible mechanisms that may lead to such scenarios.

3.1 The influence of invasion on community patterns and biodiversity

Elton (1958) suggested that disturbed communities are more susceptible to invasion because they comprised of mainly inferior species. This view has been revisited by Simberloff (1986) who associated disturbed communities with young and human-produced environments. Thus, the association of human-managed habitats with disturbances on one hand, and with invasive species on the other hands, implies that disturbances and invasions should be positively correlated. Furthermore, animal and plant communities in human-managed habitats are relatively new and therefore may not be fully saturated in terms of species richness. Notably, even in recently assembled, species-rich communities, the community resistance to invasion increases with its ecological age, as well as with the increase in the number of interspecific interactions (i.e., community connectedness, Post & Pimm, 1983; Pimm, 1991).

From the newer, global change perspective, the alteration of wildlands into agricultural and urban ecosystems by humans includes not only structural changes, but also involves changes in productivity, microclimate, and many other ecological variables that combine to change community structure (Shochat et al., 2004b, 2006). Yet, changes in productivity per se (bottom-up control) might be the major driver shaping plant and animal communities, with changes in predation (top-down control) acting as a secondary, yet important driver. In other words, whereas physical changes in the structure of environment are responsible for changes in community composition, changes in community structure, evenness, and the overall loss of diversity in human-managed ecosystems may be more related to changes in energy flow and resources, which in turn affect competitive interactions (Shochat et al., 2010).

Shochat et al. (2010) showed how changes related to land transformation lead to rapid population growth of a few species that become invasive. On the species rank distribution axis, such species move leftwards (i.e., they become the most abundant species). A case study on spiders in central Arizona demonstrated how dramatic such changes can be: wolf spiders that account for 7-8% of the whole spider community in desert and xeric yards, became the most abundant family in mesic yards and agricultural sites, accounting for up to 80% of the whole community (Shochat et al., 2004b, 2010). Although wolf spiders are not alien and reach these novel moist habitats from nearby arid ones, they can be treated as invasive species, as they respond to human-induced changes in productivity in the environment. Spider diversity in arid lands and xeric urban yards in Arizona is higher than in agricultural fields and mesic urban yards (Shochat et al., 2004b, 2010). Where invasive species become much more abundant than the dominant species in the original community, the overall outcome is that urban and agrarian ecosystem communities turn from fairly even to uneven communities monopolized by a few abundant species.

Evenness has been argued to enhance community resistance to total density changes (King & Pimm, 1983), an important indicator of community stability. Recent empirical studies illustrate that such stability is also linked to community resistance to invaders (Wilsey & Polley, 2002; Tracy & Sanderson, 2004). Experimentally reducing evenness of grassland species resulted in increased invasion of dicot plants, as well as in elevated levels of spittle-bug infestation (Wilsey & Polley, 2002). Similarly, Tracy & Sanderson (2004) found that maintaining pasture community productivity and evenness can effectively reduce weed invasion. Other findings, however, were less supportive of this view (e.g., Emery & Gross, 2007; Mattingly et al., 2007). Mattingly et al. (2007) found that evenness increased community productivity, but had no effect on resistance to invasion. Moreover, Emery & Gross (2007) showed that resistance to invasion was driven by the identity of the dominant species rather than by the reduction in evenness. In summary, although not always the major factor decreasing invasibility, evenness appears to play an important role in community stability and resistance.

Following the above findings on community evenness, Shochat et al. (2010) suggested a mechanism for the loss of diversity, based on foraging efficiency. They found that in the desert, species body mass was negatively correlated with foraging efficiency. That is, the most dominant species were the least efficient foragers. Such a pattern concurs with the "temporal partitioning" mechanism of species coexistence, where subordinate species may be able to find sufficient amount of food resources after dominant species quit foraging (Kotler & Brown, 1988; Ziv et al., 1993). In the urban environment, however, body size was positively correlated with foraging efficiency. Some of the larger, very efficient foragers, such as the Inca Dove (*Scardafella inca*), were completely absent from desert and xeric habitats in central Arizona, but thrived in mesic environments such as parks, lawns and agricultural fields. These species dominated artificial food patches, and obviously depleted food resources to extremely low levels, meaning that subordinate species are not likely to coexist with dove species through "temporal partitioning" (Shochat et al., 2010). Such uneven communities, where the "temporal partitioning" mechanism of coexistence collapses, must lose species, because most resources are now consumed by the few dominant species, leaving very little for the many others. Furthermore, when the populations of native species dramatically decrease, their genetic variation also decreases. Both these processes increase the probability of random extinction (i.e., drift and disturbance) (Lande, 1988).

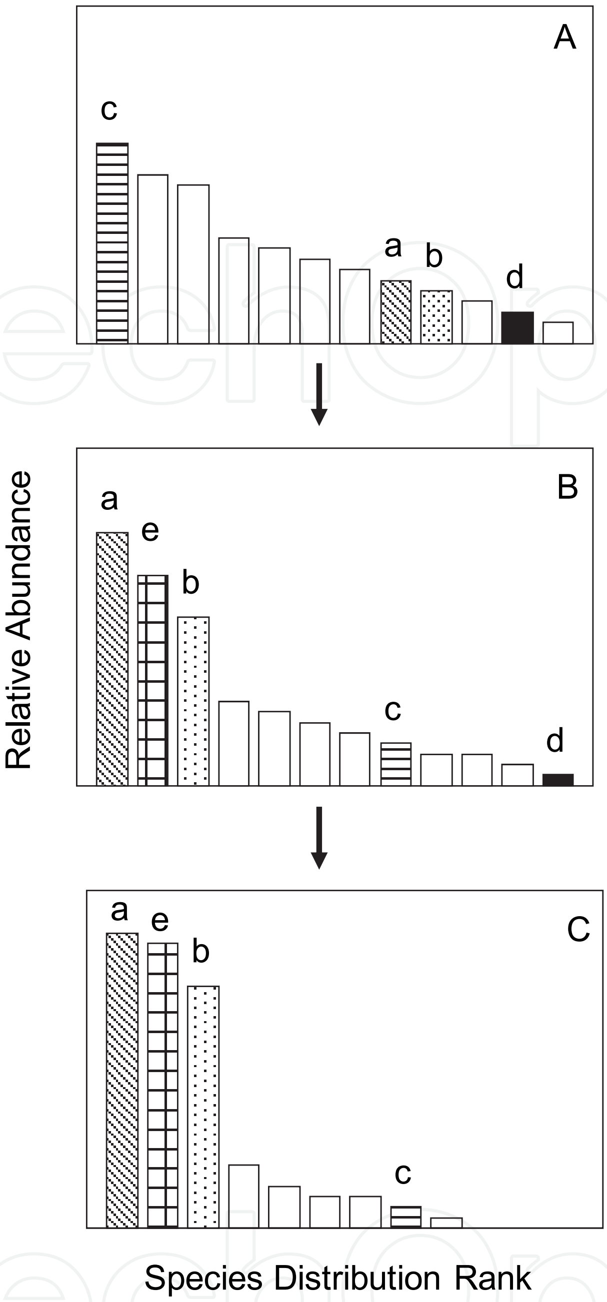


Fig. 2. Changes in community structure following anthropogenic disturbances. (A) Wildland communities are relatively even, with the most dominant species (three in this case) accounting for relatively low proportion of the whole community. Such equilibrium in wild ecosystems with low resource predictability is maintained in the long-term by high variation in productivity (temperature, rainfall, food and water resources), high predation pressure, and relatively low food abundance. (B) Human activities often dampen environmental variability by increasing overall available water and food, buffering seasonal and annual variations in resource abundance, and removing key predators. In such relatively constant and predictable environments, where key hurdles are removed, a few either dormant or alien species may rapidly spread. This includes species a and *b* that were originally ‘minor players’ in the community, and species *e*, as an example for an alien species that did not exist in the original community. The wildland community ‘major players’ (such as species *c*)

move right on the species distribution rank axis. The profile of the whole community becomes significantly less even. (C) The invasive species eventually reach their maximum population size, accounting for a relatively high proportion of the whole community, leaving much less space and resources for many of the local subordinate species. The subordinate species populations are now small, and some, like species *d*, vanish. This extinction can be the result of competition, loss of genetic variability, or stochastic events. The figure was adopted from Shochat et al. (2010).

The loss of diversity in human-managed ecosystems may therefore be the result of competition with some invasive species, though this competition may not necessarily be direct and short, but rather a long process with several stages (Fig. 2). Furthermore, it is important to note that not all invasive species may have a negative effect on local native species, and that some manage to invade by occupying vacant niches, or by "affecting many native species slightly and evenly". The goal of conservation ecologists is to learn to distinguish between invasive species that have a potential to cause severe ecological and economical damages and those that find empty niches and cause negligible damages, and to find ways to reduce, as much as possible, the negative influence of the first group's more harmful invasive species.

To understand possible ways for management of rich communities with minimized negative impact of invasive species, Shochat et al. (2010) studied the competition between an alien, aggressive species, the House Sparrow (*Passer domesticus*), and a native species, the Lesser Goldfinch (*Carduelis psaltria*). Feeders were designed to exclude sparrows, and the abundance and behavior of the goldfinch were compared between two situations: the presence of sparrow proof, and the presence of sparrow friendly feeders in urban yards. When sparrows had access to the feeders and dominated them, the number of aggressive encounters increased on the short term (1-2 hours), until the goldfinches avoided the sparrow-friendly feeders. On a longer term, Goldfinch abundance in the yards decreased, and in extreme cases reached "local extinction". In contrast, the use of "sparrow proof" feeders forced the sparrows to forage on the ground, among doves and pigeons. This turned the sparrows subordinate, as they suffered aggressive encounters from the larger birds, especially Mourning Doves (*Zenaida macroura*). At the same time, the use of sparrow proof feeders allowed the return of goldfinches to the yards within a fairly short period (1-2 weeks), and their numbers peaked under this treatment. When both feeder types were offered, Goldfinches avoided as much as possible the sparrow friendly feeders. A third granivorous passerine species, the House Finch (*Carpodacus mexicanus*), neither appeared to be suffering aggressive interactions from the similar-sized alien House Sparrow, nor to hassle the smaller Lesser Goldfinch.

These results illustrate the different extent of negative effects of alien species on native species, and how community structure and organization change depending on realized niche dimension of the alien species. Some species may be hardly affected, while other species suffer greatly from invasions. From the pure ecological perspective, this experiment shows that although some subordinate species manage to persist regionally, locally they experience a strong interference competition from the invasive species, and are thus forced to turn to alternative activities. From the applicable perspective, preventing the access of invasive species to resource patches by simple, yet clever, manipulations can largely reduce the pressure on the subordinate species. A classic example is the manipulation of nest boxes to include hole-diameter which is too small for the invasive European Starling (*Sturnus* *vulgaris*) in North America, that allows smaller, native cavity nesting species, to persist and breed successfully, with no obvious effect on starling densities (Newton, 1994). Creating such new niche opportunities for subordinate species can facilitate their rapid population growth as a result of immigration. This is important, because it suggests that the battle against harmful invasive species, whose goal is to sustain high diversity in human managed ecosystems, does not necessarily require great budget and effort, neither should it aim to eradicate such species. Rather, understanding the ecology and evolution of species may allow us to turn the advantages of invasive species to disadvantages, by re-opening niche opportunities for subordinate, native species.

4. Conclusions

For half a century ecologists have studied biological invasions by focusing either on the invasive species, or on characteristics of the invaded community (resources, natural enemies, or species richness) (Sakai et al., 2001; Shea & Chesson, 2002). Early studies attempted to generalize characteristics that facilitate invasions. Although some trends were identified, generalizations were limited and no clear patterns have emerged (Sakai et al., 2001). This approach has failed because the different modalities of biological invasions considered are ecosystem-specific and are also dependent on each other. Thus, understanding biological invasions requires adopting an integrated research approach, considering patterns and process that operate at different biological hierarchies jointly (Shea & Chesson, 2002). Among the many factors that should be considered, we suggest that future research should consider epigenetic processes. Such environmentally-induced epigenetic processes, often inherited by future generations, usually occur over relatively short time periods, increasing the evolutionary potential of invasive species in response to challenges in novel environments (Bossdorf et al., 2008).

Because the effects of bio-invasions on the local species pool may be complex and slow, loss of biodiversity may not always be evident over short ecological time scales. This has triggered a long-running debate among ecologists regarding the extent of the negative impact of invasive species on biodiversity (Pimm, 1991). Current views tend to agree about the remarkable negative influence of bio-invasions on both biodiversity and economy, even if no immediate loss of native species is detected (Vitousek et al., 1997; Mooney & Hobbs, 2000; Lockwood et al., 2007). We demonstrate that, for several reasons, changes in species abundance within invaded communities may be as crucial as extinctions. Small populations may suffer loss of genetic diversity, and become vulnerable to extinction by drift and disturbances. Furthermore, even if such small populations manage to persist, the reduction in genetic diversity dictates that their ability to adapt to future changes in the environment will be limited. Inflation in invasive species densities and reduction in local species abundance severely reduces the invaded community evenness, a process that may further facilitate invasions by reducing the community ability to resist invasions (Wilsey & Polley, 2002; Tracy & Sanderson, 2004).

Finally, because complete eradication of invasive species may be costly and in most cases impossible, more applicable solutions that allow re-opening niche opportunities for native species should be adopted. For example, manipulations of artificial nest sites (Newton, 1994) or feeders (Shochat et al., 2010) that exclude dominant invaders without affecting their densities yet allow restoring densities of subordinate local species.

5. References

Beisner, B.E., Haydon, D.T. & Cuddington, K. (2003). Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, Vol. 1, pp. 376-382

Birdlife International (2000). *Threatened Birds of the World*, Lynx Editions and BirdLife International, ISBN 8487334288, Cambridge, UK

Bossdorf O., Richards C.L. & Pigliucci, M. (2008) Epigenetics for ecologists. *Ecology Letters*, Vol. 11, pp. 106–115

Byers J.E. (2000). Competition Between Two Estuarine Snails: Implications For Invasions Of Exotic Species. *Ecology*, Vol. 81, pp. 1225–1239

Clavero, M. & García-Berthou, E. (2005). Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution*, Vol. 20, p. 110

Coyne, J.A. & Orr, H.A. (2004). *Speciation*. Sinauer Associates, Sunderland, MA

Davis, M.A. 2003. Biotic Globalization: Does Competition from Introduced Species Threaten Biodiversity? *BioScience*, Vol. 53, pp. 481-489

Elton, C.S. (1958). *The ecology of invasions by animals and plants*, ISBN 9780226206387, Methuen, London

Emery, S.M. & Gross K.L. (2007). Dominant species identity, not community evenness, regulates invasion in experimental grassland plant communities. *Ecology*, Vol. 88, pp. 954-964

Endler, J.A. (1986) *Natural selection in the wild*, ISBN 9780691083872, Princeton University Press, Princeton.

Facon, B., Genton, B.J., Shykoff, J., Jarne. P., Estoup, A. & David P. (2006). A general eco-evolutionary framework for understanding bioinvasions. *Trends in Ecology and Evolution*, Vol. 21, pp. 130-135

Green, A.J. & Hughes, B. (2001) *Oxyura leucocephala. White-headed duck*. BWP Update, Vol. 3, pp. 79–90

Gurevitch, J. & Padilla, D.K. (2004). Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution,* Vol. 19, pp. 470-474

Grotkopp, E., Rejmanek, M. & Rost, T.L. (2002). Toward a causal explanation of plant invasiveness: Seedling growth and life-history strategies of 29 pine (*Pinus*) species. *American Naturalist*, Vol. 159, pp. 396-419

Hedrick, P.W. 2005. *Genetics of populations* (3rd Edition), ISBN 9780763757373, Jones and Bartlett Publishers, Sudbury MA.

Herbold, B. & Moyle, P.B. (1986). Introduced Species and Vacant Niches. *American Naturalist*, Vol. 128, pp.751-760

Human, K.G. & Gordon, D.M. (1996). Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia*, Vol. 105, pp. 405-412

Kaiser, J. (1999). Stemming the Tide of Invading Species. *Science*, Vol. 285, pp. 1836-1841

Kotler, B.P. & Brown, J.S. (1988). Environmental heterogeneity and the coexistence of desert rodents. *Annual review of ecology and systematics*, Vol. 19, pp. 281-307

King, A.W. & Pimm, S.L. (1983). Complexity and stability: a reconciliation of theoretical and experimental results. *American Naturalist*, Vol. 122, pp. 229-239

Krause, A.E., Frank, K.A., Mason, D.M., Ulanowicz R.E. &Taylor W.W. (2003). Compartments revealed in food-web structure. *Nature*, Vol. 426, pp. 282-285.

Lach, L. (2005). Interference and exploitation competition of three nectar-thieving invasive ant species. *Insect Sociaux,* Vol. 52, pp. 257-262.

Lande, R. (1988). Genetics and demography in biological conservation. *Science*, Vol. 241, pp. 1455-1460

Lockwood, J.L., Hoopes, M.F. & Marchetti M.P. (2007). *Invasion Ecology*, ISBN 9781405114189, Blackwell Publishing, Malden MA.

Mack, R.N., Simberloff D., Lonsdale W.M., Evans H., Clout M. and Bazzaz F.A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, Vol. 10, pp. 689–710

Maron, J.L., Vil, M., Bommarco, R., Elmendorf, S. & Beardsley, P. (2004). Rapid evolution of an invasive plant. *Ecological Monographs*, Vol. 74, pp. 261-280

Mattingly, W.B., Hewlate, R., & Reynolds, H.L. (2007). Species evenness and invasion resistance of experimental grassland communities. *Oikos*, Vol. 116, pp. 1164-1170

May, R.M. (1972). Will a large complex system be stable? *Nature*, Vol. 238, pp. 413–414.

Mazourek, J.C. & Gray, P.N. (1994). The Florida duck or the Mallard. *Florida Wildlife*, Vol. 48, pp. 29-31

Miller, R.R. Williams MJ, Williams JE. (1989) Extinctions of North American fishes during the past century. *Fisheries*, Vol. 14, pp. 22–38

Mooney, H.A. & Hobbs, R.J. (2000) *Invasive Species in a Changing World*, ISBN 9781559637824, Island Press, Washington DC.

Mooney, H.A. & Cleland, E.E. (2001). The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences*, Vol. 98, pp. 5446–5451

Moulton, M.P. & Pimm, S.L. (1986) The extent of competition in shaping an introduced avifauna. In: *Community Ecology*, J. Diamond and T. Case, (Eds.), Harper & Row, ISBN 006041202X, New York.

Newton, I. (1994). The role of nest sites in limiting the numbers of hole-nesting birds: A review. *Biological Conservation*, Vol. 70, pp. 265-276

Planty-Tabacchi, A.M., Tabacchi, E., Naiman, R.J., Deferrari, C. & Decamps, H. (1996). Invasibility of species-rich communities in riparian zones. *Conservation Biology*, Vol. 10, pp. 598–607

Pimentel, D., Lach, L., Zuniga, R. & Morrison D. (2000). Environmental and economic costs of nonindigenous species in the United States. *BioScience*, Vol. 50, pp. 53-65

Pimm, S.L. (1991). *The balance of nature? Ecological issues in the conservation of species and communities.* University of Chicago Press, Chicago, Illinois, 434 p.

Pimm, S.L. & Lawton J.H. (1980). Are food webs compartmented? *Journal of Animal Ecology*, Vol. 49, pp.879-898

Post, W.M. & Pimm, S.L. (1983). Community assembly and food web stability. *Mathematical Biosciences*, Vol. 64, pp. 169-192

Reed, D.H. & Frankham, R. (2003). Correlation between fitness and genetic diversity. *Conservation Biology*, Vol. 17, pp. 230–237

Rhymer, J. & Simberloff, D. (1996). Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics*, Vol. 27, pp. 83-109

Richards, E.J. (2006). Inherited epigenetic variation – revisiting soft inheritance. *Nature Reviews Genetics*, Vol. 7, pp. 395–401

Sakai, A.K, Allendorf, F.W, Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N. & Weller S.G. (2001). The population biology of invasive species. *Annual Review of Ecology and Systematics*, Vol. 32, pp. 305-332

Seabloom, W.E., Harpole, S.W., Reichman, O.J. & Tilman, D. (2003). Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences*, Vol. 100, pp. 13384-13389

Shea, K. & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, Vol. 17, pp. 170-176.

Shochat, E., Lerman, SB, Katti, M & Lewis, D. (2004a). Linking optimal foraging behavior to bird community structure in an urban-desert landscape: field experiments with artificial food patches. *American Naturalist,* Vol. 164, pp. 232-243

Shochat, E., Stefanov, W.L., Whitehouse, M.E.A. & Faeth, S.H. (2004b). Urbanization and Spider Diversity: Influences of Human Modification of Habitat Structure and Productivity. *Ecological Applications*, Vol. 14, pp. 268-280

Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E. & Hope D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution*, Vol. 21, pp. 186-191

Shochat, E., Lerman, S.B., Anderies, J.M., Warren, P.S., Faeth, S.H. & Nilon, C.H. (2010). Invasion, Competition, and Biodiversity Loss in Urban Ecosystems. *BioScience*, Vol. 60, pp. 199-208

Simberloff, D. (1981). Community effects of introduced species. In: *Biotic crisis in ecological and evolutionary time*. H. Nitecki Ed. 53-81, Academic press, ISBN 0125196407, New York.

Simberloff, D. (1986). Introduced species: a biogeographic and systematic perspective. In: *Ecology of biological invasions of North America and Hawaii*. H.A. Mooney and J.A. Drake (Eds.), pp. 3-26 Springer-Verlag, NY.

Simberloff, D. (1997). The biology of invasions. In: *Strangers in Paradise: impact and management od nonindigenous species in Florida*. Simbeloff, D., Schmitz, D.C. & Brown, T.C. (Eds.), pp. 3-17, Island Press, ISBN-10: 038797153X, Washington DC.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. (1999) Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, Vol. 69, pp. 25–46.

Stouffer, D.B. & Bascompte, J. (2011). Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences,* Vol. 108, pp. 3648-3652

Tracy, B.F., & Sanderson, M.A. (2004). Forage productivity, species evenness and weed invasion in pasture communities. *Agriculture, Ecosystems and Environment*, Vol. 102, pp. 175–183

Veltman, C.J., Nee, S. & Crawley, M.J. (1996)Correlates of introduction success in exotic New Zealand birds. *American Naturalist*, Vol. 147, pp. 542-557

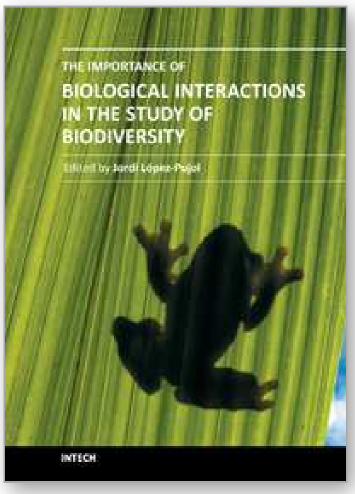
Vitousek, P.M., D'Antonio, C.M., Loop, L.D., Rejmánek, M. & Westbrooks, R. (1997). Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology*, Vol. 21, pp. 1-16

Whitney, K.D. & Gabler, C.A. (2008). Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. *Diversity and Distributions*, Vol. 14, pp. 569–580

Wilsey, B.J., & and Polley, H.W. (2002). Reductions in grassland species evenness increase dicot seedling invasion and spittle bug infestation. *Ecology Letters*, Vol. 5, pp. 676–684

Yoshida, T., Goka, K., Ishihama, F., Ishihara, M. & Kudo, S. (2007). Biological invasion as a natural experiment of the evolutionary processes: Introduction of the special feature. *Ecological Research*, Vol. 22, pp. 849-854

Zavaleta, E.S., Hobbs, R.J. & Mooney, H.A. (2001). Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* Vol 16, pp. 454-459



The Importance of Biological Interactions in the Study of Biodiversity

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The term biodiversity defines not only all the variety of life in the Earth but also their complex interactions. Under the current scenario of biodiversity loss, and in order to preserve it, it is essential to achieve a deep understanding on all the aspects related to the biological interactions, including their functioning and significance. This volume contains several contributions (nineteen in total) that illustrate the state of the art of the academic research in the field of biological interactions in its widest sense; that is, not only the interactions between living organisms are considered, but also those between living organisms and abiotic elements of the environment as well as those between living organisms and the humans.

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