

Ecology and Ethics 3

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# From Biocultural Homogenization to Biocultural Conservation

 Springer

# Ecology and Ethics

## Volume 3

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# Foreword

The challenging issue of global biocultural homogenization is comprehensively presented and discussed in this important book – and its arrival is none too soon! Biocultural homogenization, as defined by Rozzi et al. in the first chapter of the book, “entails the interwoven losses of native biological and cultural diversity at local, regional, and global scales.” This issue of biocultural homogenization is neither widely understood nor is its importance adequately appreciated even while it is occurring at an accelerating rate. This book will be an important aid in increasing recognition of the issue and its importance.

Homogenization is one outcome of an ever-increasing emphasis on the goal of economic efficiency, albeit it is a goal that is generally very narrowly defined. This goal of efficiency drives societies to move toward approaches focused upon production of singular outcomes, such as of food or fiber, without regard to the consequences to nature or to local cultures. Furthermore, these days the efforts toward economically efficient production of commodities are organized so as to primarily benefit global capital markets. This leads to such outcomes as the replacement (indeed, destruction) of family farms by corporate enterprises, all in the guise of economic efficiency. Of course, in turn this leads to practices which frequently have very negative effects on native biological diversity and local cultures.

This homogenization in pursuit of efficiency represents incredible threats to native biological and cultural diversity, if we truly care about such things. Homogenization is about simplification and standardization in many forms whereas nature and culture are about complexity and diversity. Approaches that incorporate complexity and diversity are not as efficient in the pursuit of many singular goals, such as production of food and fiber. However, approaches that conserve complexity and diversity are approaches that achieve multiple rather than singular objectives with their activities, reduce risks from both natural and social upheavals, and increase future societal options.

I would venture that there are powerful, fundamentally maleficent forces that specifically do not value diversity and do not wish to see it conserved. Do global capital markets really see value in diversity, other than a diversity of portfolios? Do global corporations see value in local solutions, local markets? Is there a wide

appreciation that the pursuit of efficiency, of homogenization, can lead to dysfunctional outcomes for global societies? For example, is there real concern in the United States for improving the opportunities and conditions of the diversity represented by rural America? I worry a great deal about the answers to such questions as these.

Forests are the ecosystems that I am most familiar with, and they offer great examples of some of the challenges that are faced as we attempt to deal with the issue of biocultural homogenization. There has been a global movement toward the creation and management of plantations of exotic tree species in pursuit of efficient production of wood fiber, much of this in the southern hemisphere. In the last several decades, this movement has been driven by global capital markets that invest in wood production as yet another means of seeking high returns on capital. The emphasis on capital return has put an economic cap on the already highly agronomic approaches associated with plantation forestry. The collective consequences have been what I call fiber farms, which involve practices that ignore other services and goods that are provided by forest ecosystems as well as the stability of local communities and viability of other forest landownerships. The only environmental constraints on such practices are those that are imposed by legal authorities present in the regions where such plantations are grown. Usually the harvested wood goes to the global market that is willing to pay the most for it and not to a local wood processing facility, which might result in greater economic benefits for local communities. Forest landowners who wish to manage for a diversity of values are challenged because they must find markets and compete in a global wood products economy dominated by the fiber farms.

This highly simplified, homogenized approach to wood production finds support in many quarters, including a globalized economy and history, and there are many similarities here between forestry and agriculture and fisheries. I have already talked about how a capital-dominated global economy favors homogenization and the marginalization of other forest values, except where governmental authorities insist otherwise. The dominant focus of the forestry profession on wood production as the most important use of forestland has been largely congruent with the emphasis on homogenization and efficiency in pursuit of a singular outcome.<sup>1</sup> Local communities and governments are advised that the homogenized approach is in their best economic interest and sometimes told that this is the only real way to do sustainable forestry. (The same is presented regarding corporate agriculture and fish farms.) Forestry as a profession has failed to even conceive, let alone demonstrate to society, credible alternatives to intensive plantation management based on clearcutting and even-aged management.<sup>2</sup> The foresters have been abetted by the community of academic conservation biologists who argue that native biodiversity can only be conserved in preserves – areas that are set aside from human societies (as if such a

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<sup>1</sup>Franklin, J. F., K. N. Johnson, and D. L. Johnson 2018. *Ecological forest management*. 646 p. Long Grove, IL, USA: Waveland Press.

<sup>2</sup>Bennett, Brett. 2015. *Plantations and protected areas. A global history of forest management*. 201 p. Cambridge, MA, USA: MIT Press.

thing was possible in the twenty-first century!). Biodiversity will not be preserved primarily by separating it from humankind but, rather, must be a part of conserved bioculture.

This book is an important contribution to the dialogue and hard work that is ultimately required to conserve as much as we can of diverse bioculture. The future of native biodiversity and local human societies are linked and face the same array of challenges. Many ideas, concepts, and examples are laid down in this volume that can move this important work forward. We are talking here about nothing less than the future of humankind – is it to be a homogenized future or one that nurtures diversity and the richness and resilience that it brings?

Let us all get on with it!

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# Acknowledgments

This volume conveys the work of many researchers, students, and people from different regions of the world. We are grateful to our institutions in Chile and in the USA, which have supported our editorial activities. At the Institute of Ecology and Biodiversity (IEB) and the University of Magallanes (UMAG) in Chile, we are especially thankful for the support of Andrés Mansilla, UMAG VP for Research and Graduate Studies. At the University of North Texas (UNT), the Center for Environmental Philosophy (CEP) provided support; we especially thank its director Eugene Hargrove for his constant advice. At Springer, we appreciate the encouragement and editorial guidance offered by Valeria Rinaudo, Ineke Ravesloot, and Jill Ritchie; this is the third volume of the *Ecology and Ethics* book series.

Part of the impulse for developing this book came from the field graduate course “Trends in Ecology of Plant Invasions” coordinated by Aníbal Pauchard and Ramiro Bustamante of the Laboratorio Invasiones Biológicas (LIB-IEB) located in the Chilean Cordillera of the Andes Mountains, April 2014. The course involved also the participation of three of other editors of this volume: Martín Nuñez, Daniel Simberloff, and Ricardo Rozzi. Some of the co-authors of chapters in this volume were students at that course. We are especially thankful to Brian O’Connor for his valuable editions to several manuscripts of chapters. Rozzi acknowledges the financial support of the National Commission for Scientific and Technological Research (CONICYT, Chile) grants PFB-23 and *Apoyo a Centros Científicos y Tecnológicos de Excelencia con Financiamiento* (Basal CONICYT AFB170008) awarded to IEB in Chile. This book is a contribution to the Sub-Antarctic Biocultural Conservation Program coordinated by UNT in the USA and IEB and UMAG in Chile.

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# Chapter 15

## Non-native Pines Are Homogenizing the Ecosystems of South America



**Rafael A. García, Jorgelina Franzese, Nahuel Policelli, Yamila Sasal, Rafael D. Zenni, Martin A. Nuñez, Kimberley Taylor, and Aníbal Pauchard**

**Abstract** A large area previously dominated by native ecosystems in South America is now covered by monocultures of non-native tree species, mainly of the genus *Pinus*. Currently, pine plantations and the invasions that have been generated from these are causing a homogenization process at the landscape, stand, and even micro-site scales. The continuous and extensive areas covered by pine plantations have replaced the native ecosystem heterogeneity in many landscapes of South America. Within these plantations, the diversity of plants and animals is lower than

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that of the nearest remnant native ecosystems. These plantations can also act as a barrier to the movement of species across the landscape. In addition, in most places where pine plantations have been established, invasions have occurred into the surrounding ecosystems. Overall, pine invasions are more evident in open ecosystems (e.g., grasslands, steppes, and degraded native forest), but they can also occur in denser vegetation (e.g., temperate forests). Native species loss as a consequence of pine invasions has been recorded in tropical, mediterranean, and temperate ecosystems. Increased pine abundance and the resultant native species loss bring changes to all levels of organization within the ecosystem, from soil microorganisms to invertebrates, plants, and vertebrates. These changes reduce the ecosystem's spatial heterogeneity and thus cause biotic homogenization. These biodiversity losses can affect the stability of ecosystems by decreasing their resilience to environmental change and disturbances. To mitigate the impacts caused by pines, it is important to implement comprehensive landscape planning, understanding that pine plantations coexist and interact with other land uses in a complex ecological and social setting.

**Keywords** Homogenization · *Pinaceae* · Invasive trees · Plant invasions · Impacts

## 15.1 Introduction

Pine plantations are growing in South America, and their direct and indirect effects on biodiversity remain uncertain. Currently, 68% of the tree plantation area added annually in the Southern Hemisphere (estimated in 750,000 ha year<sup>-1</sup>) occurs in South America (Food and Agriculture Organization 2010). On this continent, almost all tree plantations are based on introduced species, and conifers, particularly *Pinus* spp., are one of the most common choices (Food and Agriculture Organization 2010). The accelerated growth of forest plantations in South America raises concerns about the risks and the potential impacts of pine plantations on biodiversity and ecosystem services, especially in those areas of high conservation value (Armesto et al. 2010). Much of the research on the biotic consequences of pine plantations has been conducted at landscape or even larger scales (e.g., Echeverría et al. 2006), where plantations have been blamed for landscape homogenization and replacement of native forests (Rozzi et al. 1994), as well as for changes in hydrological regimes (e.g., Farley et al. 2005; Little et al. 2008). However, biotic impacts at smaller scales have been less studied, with local reduction of understory plant diversity as one of the most reported problems (Paritsis and Aizen 2008; Simonetti et al. 2013; Heinrichs and Pauchard 2015).

In addition to the direct impacts of pine plantations, conifers have long been recognized as one of the most invasive plant taxon (e.g., Richardson et al. 1994; Rejmánek and Richardson 1996; Ledgard 2001; Buckley et al. 2005; Essl et al. 2011; Gundale et al. 2014; Nuñez et al. 2017). Pine invasive potential emerges par-

tially from their widespread ornamental use and mainly from their extensive use for forest plantations (Richardson 2006; Simberloff et al. 2010; Essl et al. 2010). In addition, this taxon has biological attributes that increase its invasive potential such as high reproductive rate, fast growth, and long-distance dispersal (Rejmánek and Richardson 1996). Conifer invasions can have severe impacts on ecosystem processes causing changes in water and fire regimes and reductions in local diversity (Simberloff et al. 2010). South America has been increasingly affected by conifer invasions, especially in the case of *Pinus* spp. (Pauchard et al. 2015), due to the high invasibility of the ecosystems and the novelty of the *Pinaceae* south of the equator (Lusk 2008). Nevertheless, it is only recently that researchers have started to pay close attention to pine invasions in South America and their effects on local biota (see Richardson et al. 2008).

Although the impacts of invasive pines are highly variable and depend upon the habitats they invade (Pauchard et al. 2015; Nuñez et al. 2017), biotic homogenization is one of the most noticeable and consistent impacts across latitudes and continents. Two mechanisms largely explain the process of homogenization caused by pine invasions.

1. An increase in the similarity between different invaded ecosystems caused by the dominance of a single non-native species (i.e., *Pinus* spp.), which usually has very different functional traits than the native plant communities (Pauchard et al. 2016).
2. Homogenization occurs as pine cover and biomass increase, and competition for resources causes a decrease in the abundance and diversity of the native species (Franzese et al. 2017; Taylor et al. 2016).

This process can develop quickly (in less than a year) in burned habitats invaded by pines, but in less-disturbed ecosystems, it can take multiple years or decades from the beginning of the invasion until the impacts on the native biota become evident (Franzese and Raffaele 2017). Pine invasions can have legacy impacts on plant communities, even after they are removed, resulting in increases in other exotic species (Dickie et al. 2014). Furthermore, there is growing evidence that plant community homogenization is usually preceded by a biotic homogenization of animal and fungal communities, either through increases in new invasive species or simplification of the native ecosystem (Simberloff and Von Holle 1999; Nuñez et al. 2013; Dickie et al. 2017).

The impacts of pine plantations and invasions in South America, and the consequent biotic homogenization, are expected to increase because of continuing expansion of the afforested areas (Food and Agriculture Organization 2010), as well as increases in invasion drivers, such as fire (Franzese and Raffaele 2017), habitat degradation (Echeverría et al. 2007), and grazing (Loidy et al. 2010; de Villalobos et al. 2011). In this context, the aim of this chapter is to review the evidence of biotic homogenization caused by pine plantations and pine invasions on plant and fungal communities of South America to better understand the causes and consequences of this ongoing conservation problem.

## 15.2 Pine Plantations Dual Effect: Homogenization and Invasion

Forest plantations, especially pine plantations, generate a series of economic, social, and environmental goods and services (Sutton 1995; Gerrand et al. 2003; Vihervaara et al. 2012). On the other hand, the lack of management or inadequate management in plantations causes negative impacts that may be more noticeable to society than the supposed benefits they generate (Spellerberg 1996; Aber et al. 2000; Hartmann et al. 2010; Salas et al. 2016). Although pine invasions and pine plantations are two different phenomena, it is important to understand the ecological, social, and economic links between them, especially when addressing biotic homogenization. Commercial plantations are the most important promoter of pine invasions, particularly in South America, and also a fundamental component of the process of biotic homogenization, with strong implications at landscape and local scales.

### 15.2.1 Landscape Homogenization

The landscape is a mosaic of different biophysical elements (natural and/or anthropic), and the distribution of species within the landscape is determined by the diversity and spatial distribution of resources in the landscape (Debinski et al. 2001; Hartmann et al. 2010). A simplification of the landscape will, therefore, have a direct effect on the composition of animal and plant communities, as well the ecosystem services they provide (Carnus et al. 2006; Hartmann et al. 2010). Thus, the transformation of natural forest habitats into productive and homogenous systems, as a consequence of the establishment of large-scale plantations of non-native tree species, is one of the most direct threats to biodiversity conservation (Potton 1994; Larsson and Danell 2001).

In South America, a massive expansion of commercial pine plantations has occurred in tropical, mediterranean, temperate, and alpine ecosystems (Cubbage et al. 2007; Pauchard et al. 2015). This expansion has been particularly remarkable in the Coastal Range in central Chile, where native vegetation is composed of deciduous forest, with dominance by different *Nothofagus* species (i.e., *Nothofagus glauca* (Phil.) Krasser, *N. obliqua* (Mirb.) Oerst., and *N. alessandrii* Espinosa). This forest has been continuously degraded and replaced by extensive area of timber plantation (mostly *Pinus radiata* D. Don) (Bustamante and Castor 1998; Smith-Ramirez 2004; Echeverría et al. 2006). In this area, 41.5% of new plantations in the 1975–1990 period and 22.8% in the 1990–2007 period were established by clearing secondary native forests, which confirms that plantation expansion in Chile has been a direct cause of deforestation and biodiversity loss (Nahuelhual et al. 2012). Nevertheless, in recent years (2001–2011 period), the rate of forest conversion has decreased due to tighter regulations, which suggests that pressure on remaining native forests is beginning to ease (Heilmayr et al. 2016).

### 15.2.2 Local Biodiversity Homogenization

In addition to an increase in homogenization at the landscape scale, within pine plantations, the diversity of species is usually much lower than in adjacent natural or seminatural habitats. The change of land use (direct or indirect) from forests or other native ecosystems to commercial plantations necessarily implies a simplification of the structure and composition of species (Potton 1994; Spellerberg 1996; Freedman et al. 1996; Gjerde and Saetersdal 1997; Hartley 2002; Braun et al. 2017).

In the central zone and Chilean Patagonia, Braun et al. (2017) found a strong negative impact of extensive plantation forestry on plant biodiversity. The extensive areas of pine plantations have negative impacts on  $\alpha$  (local),  $\beta$  (species turnover), and  $\gamma$  (landscape) biodiversity, where plant communities are predominantly native and endemic in natural forests and predominantly non-native in plantations (Braun et al. 2017). Furthermore, these pine crops do not serve as an alternative habitat for native species, leaving many species threatened by extinction (Braun et al. 2017).

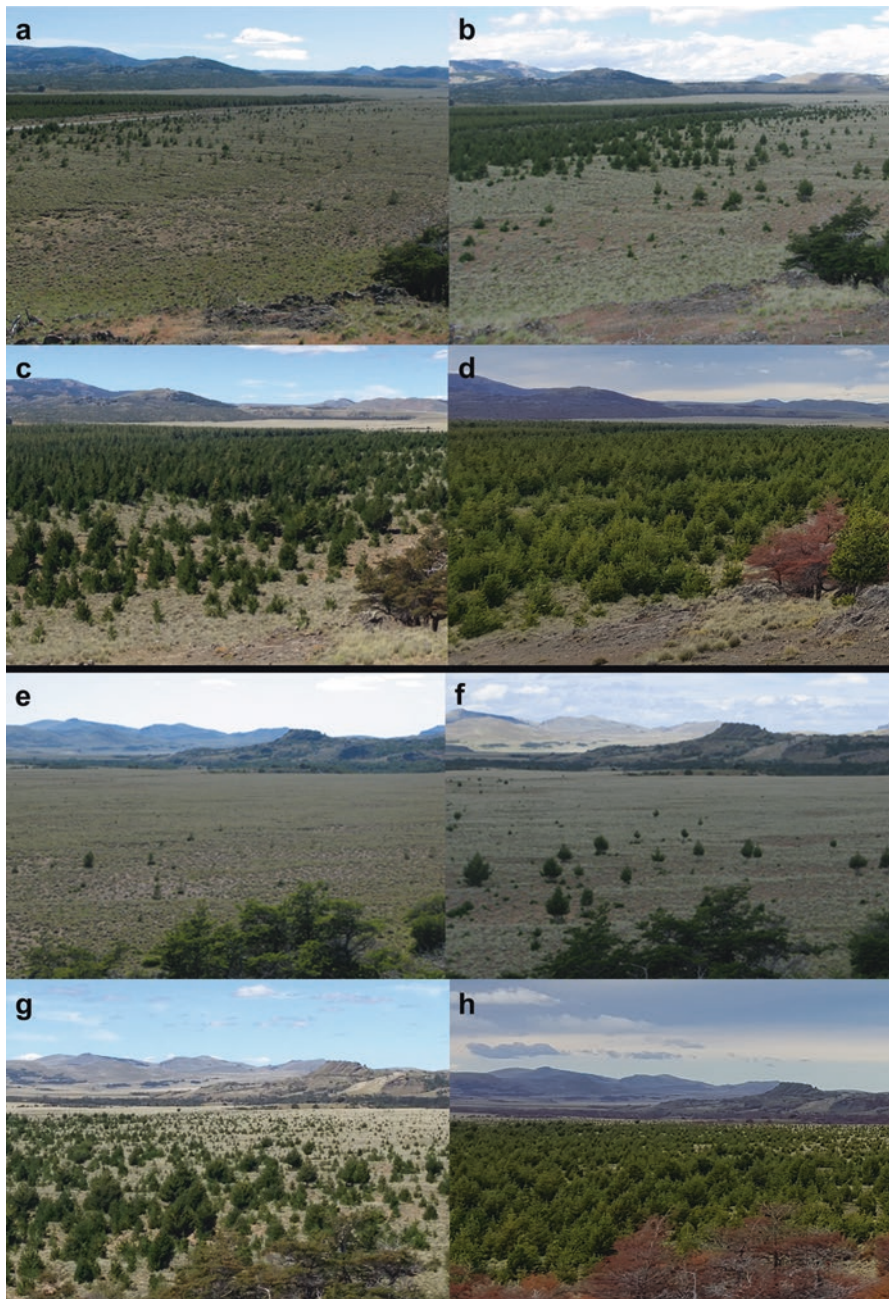
A study carried out in Patagonia, which compares the structure and composition of *Nothofagus dombeyi* forests and small pine forest plantations (<5 ha), shows that even at the stand level the same pattern of habitat structure homogenization is observed (Paritsis and Aizen 2008). The largest impact was detected on understory plants, followed by the beetle and bird assemblages, with a reduction in evenness in plants and beetles, an increase of non-native plants and birds, and a loss of rare and specialist species in all three assemblages (Paritsis and Aizen 2008). Additionally, pine plantations with little or minimally developed understories contained fewer species of medium-sized mammals than plantations with more understory vegetation (Simonetti et al. 2013). When understory plants are present in commercial plantations, they can enhance the quality of plantations as habitat for native fauna (mammals, birds, and insects) and even for some vulnerable species (Briones and Jerez 2007; Tomasevic and Estades 2008; Nájera and Simonetti 2010; Simonetti et al. 2013). In more tropical areas, the effects of pine plantations depend largely on the intensity and frequency of management actions. For instance, *P. elliottii* plantations under low-intensity management were shown to have similar understory species richness and diversity as native woody Cerrado formations in Brazil (Abreu et al. 2011), but more intense management techniques (e.g., shorter rotation, higher herbicide applications) would likely reduce local biodiversity. Thus, choosing the right management options may help to increase or at least reduce the losses of local biodiversity. For example, a management scheme that allows the establishment of well-developed understories (e.g., intensive pruning and thinning) would not only minimize the impact on plant diversity by providing substitute habitats for native species but also mitigate the effects on wildlife (Simonetti et al. 2013).

### 15.2.3 *Plantations as the Main Source of Pine Invasions*

The different species of pines cultivated in South America have a variable level of invasiveness (Pauchard et al. 2015), but overall it is higher than other tree taxa. High invasive potential and high propagule pressure transform the pine plantations into the main source of invasions into native ecosystems. In fact, forest plantations release a large amount of seeds each year into the landscape, which increases the likelihood of invasion by a mass effect (Richardson and Brown 1986; Kruger et al. 1989; Richardson and Higgins 1998). This high propagule pressure overwhelms microsite-scale interactions and independently explains invasion success (Pauchard et al. 2016). Depending on the species of pine planted (invasiveness) and the characteristics of the invaded ecosystem (invasibility), invasion from the plantations can follow two basic patterns: continuous invasion and mosaic invasion.

Continuous invasion is frequent in open, less competitive ecosystems, as is the case of *Pinus contorta* Douglas ex Loudon in the Patagonian steppe (e.g., Langdon et al. 2010; Pauchard et al. 2016). The initial population growth is usually characterized by a dispersal kernel, where dense regeneration is located next to the seed source (short distance dispersal), while medium- and long-distance dispersal generates scattered outlier pines (Higgins and Richardson 1999; Richardson 2001; Ledgard 2003; Langdon et al. 2010). In this first stage, intraspecific competition is low, and therefore wildings can establish at any distance from the seed source within the first “invasion wave.” After some of the pines reach maturity, propagules originate from the original source, the invasion front, and the outlier trees. Once the second wave of invasion has started, the opportunities for successful control are greatly reduced, increasing the overall impacts of the invasion in the landscape (Fig. 15.1).

Mosaic invasion occurs in forests or other competitive vegetation (i.e., shrubs or grassland) with relatively stable dense vegetation cover but some spatial heterogeneity that includes suitable habitat for the invader. In this case, the invasion process is slower due to the low light availability and absence of bare soil for seedling establishment. This process is frequent in remnants of Maulino Forest in the Coastal Range of central Chile (Bustamante and Simonetti 2005). Today this forest covers only a few percent of the original area, persisting as small remnants. These remnants are surrounded by extensive *P. radiata* plantations (Bustamante and Castor 1998). Although seeds of pines can arrive in the interior of well-developed forest fragments (Bustamante and Simonetti 2005), this shaded habitat generates abiotic conditions which impose constraints to germination and establishment that reduce seedling recruitment (Bustamante et al. 2003). The permeability of these forests to the invasion not only depends on the maintenance (or degradation) of the canopy layer but also on the size of the fragments. The fragment size seems to be a good indicator of susceptibility to being invaded by pines: small fragments are more susceptible to invasion while large fragments are more resistant (Gómez et al. 2011).



**Fig. 15.1** Example of a continuous invasion of pines into grassland environments in Patagonian steppe, in Coyhaique Alto, Aysen Region, Chile. Top panel: *invasion core* of *P. contorta* from 2007 (a) to 2011 (b), 2015 (c), and 2017 (d). Bottom panel: *invasion front* from 2007 (e) to 2011 (f), 2015 (g), and 2017 (h). The high dispersal capacity and rapid growth and development of pines can generate invasion processes with a high impact on the invaded community. In short periods of time (less than 10 years), complete ecosystem transformations can occur. The change from a steppe to a monospecific pine forest results in important changes in microclimatic conditions and availability of resources, reduction in the richness and abundance of native plants, modification of the soil biota, and alteration of the trophic networks of the invaded ecosystems

### 15.3 Pine Invasions and the Aboveground Biotic Homogenization

Most of the invasion impact studies in South American habitats are focused on the aboveground components of the biota (e.g., Urrutia et al. 2013; Cobar-Carranza et al. 2014; Franzese et al. 2017), with few of them focused on the belowground components (e.g., Chapela et al. 2001; Dickie et al. 2011; de Oliveira et al. 2014). This section describes work quantifying the direct impacts on aboveground biodiversity caused by pine invasions in different South American ecosystems.

Three pine species are currently recognized as invasive in the tropical ecosystems in South America: *Pinus elliottii*, *P. caribaea*, and *P. oocarpa* (Braga et al. 2014; Zenni 2015). The tropical invasive range of pines includes the Brazilian central savanna (Cerrado) and open and degraded areas of the Atlantic Forest Biome (Zenni and Ziller 2011; Zenni 2015). Pine plantations in tropical regions are usually associated with declines in species richness and abundance in native plant regeneration (Valduga et al. 2016).

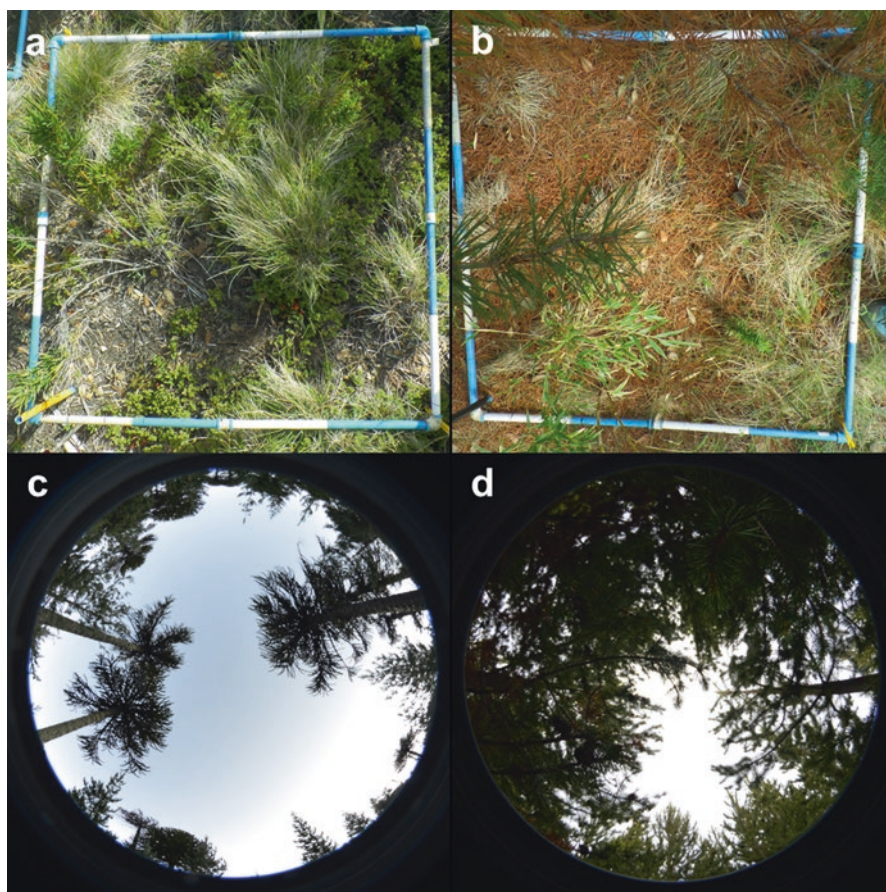
In open habitats, such as grassland Cerrado and Cerrado *sensu stricto*, pine invasions can result in massive decreases in native species richness and abundance. One study comparing invaded and non-invaded grassland savanna found a tenfold decrease in plant density (non-invaded site = 12,656 plants ha<sup>-1</sup>; invaded site = 1210 plants ha<sup>-1</sup>) and a twofold decrease in species richness in the pine-invaded site ( $H' = 2.82$ ) in comparison to a non-invaded reference site ( $H' = 1.53$ ). Furthermore, the pine invasion completely excluded the herbaceous layer (Abreu and Durigan 2011).

Most pines used in forestry have evolved in more temperate or colder environments, and, therefore, the southern part of South America could be more suitable for pine invasions. In fact, much of the Andean temperate forests of Argentina and Chile are characterized by a tree layer that is relatively permeable to light (e.g., open *Araucaria araucana* forest, deciduous forest of *Nothofagus* species); for this reason, the probability of being invaded by pines is greater than in more closed forests (Peña et al. 2008; Simberloff et al. 2010). However, currently closed forests with evergreen species are also being invaded by pines, mainly by *Pseudotsuga menziesii* (Sarasola et al. 2006; Pauchard et al. 2008).

Plant diversity in open temperate forests is negatively affected by *P. contorta* invasions. Richness and cover of plants beneath pine canopies decreased with increasing pine size (i.e., height and canopy area) (Franzese et al. 2017). This decrease did not affect all species equally, generating changes in the relative cover of different life-forms between invaded and non-invaded areas (Urrutia et al. 2013). These impacts began in the early stages of the invasion, before canopy closure, when the pines had a height of less than 10 m (Franzese et al. 2017). With increasing pine canopy closure in the invaded area, the diversity of species declined considerably as a result of the decreased light availability under the tree crowns (Rodríguez-Calcerrada et al. 2011; Taylor et al. 2016). This evidence suggests that some impacts



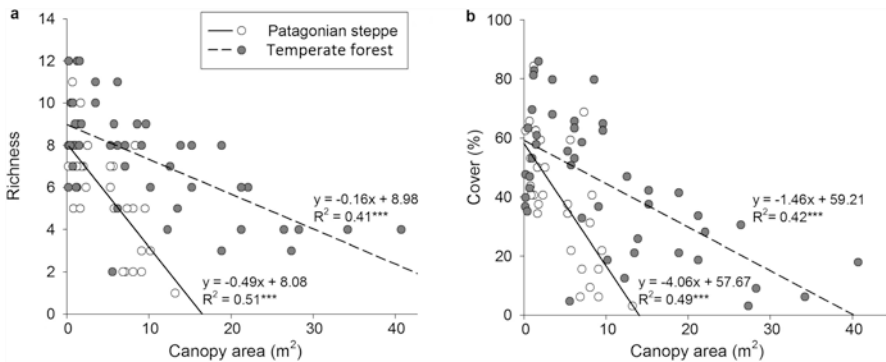
go beyond the reduction of plant diversity and are related to a change in the ecosystem functioning. In this modified ecosystem, pines not only compete for resources but also modify resource availability by altering microenvironmental conditions. Invaded sectors have a dense and deep layer of needles (Taylor et al. 2016), less light availability (Fig. 15.2), and more moderate temperatures (García unpublished data). The moderation of extreme conditions in these high-mountain forests could facilitate the arrival of new species that previously were excluded due to the harsh environment, thus promoting the homogenization of these unique ecosystems currently dominated by species adapted to these relatively harsh conditions.



**Fig. 15.2** Araucaria forests in the Andes of south-central Chile with low (a, c) and high pine invasion (b, d). At the ground level, the accumulation of pine needles decreases the amount of bare soil limiting the germination and establishment of native plants. Ground view (1 m<sup>2</sup> plot) (top panel: a, b). Hemispheric canopy view (bottom panel: c, d). The pine invasions generate a more closed canopy with less light availability

Temperate steppes in Patagonia can be extremely susceptible to pine invasion in comparison to forested habitats (Franzese et al. 2017). In a steppe of the southern Chilean Patagonia invaded by *P. contorta*, a significant reduction in plant richness and cover of the invaded community was registered even at early pine invasion stages (i.e., pines of low height and small canopy areas) (Franzese et al. 2017). As pine canopy cover increased, there was a strong decline in native plant richness and cover (Taylor et al. 2016). The abrupt modification of the habitat conditions produced by pine invasion, along with the addition of novel functional traits, could be acting as an ecological filter on plant biodiversity of steppe ecosystems (Bravo-Monasterio et al. 2016). The differential level of impact among distinct habitat types (forest and treeless ecosystems) could be related to how adapted the invaded community is to tree cover. This highlights the importance of context-dependency as a key factor in determining the overall impact of pines on diverse natural plant communities (Fig. 15.3).

Although conifer invasions are regarded as a serious threat to biodiversity, information on their impacts beyond plant communities is very limited. In fact, little is known about changes in invertebrate assemblages. Replacement of open native treeless vegetation with dense, closed, even-aged forests is by far the most striking impact of pine invasions (Richardson et al. 1994; Richardson and Higgins 1998). These changes in vegetation composition and structure result in new abiotic conditions that could have cascading effects on invertebrates. Many invertebrates depend on particular plant species or structures for food or reproduction sites. Losses of these plants, or structural and/or compositional changes to the natural vegetation communities, may be especially detrimental for invertebrates.



**Fig. 15.3** Plant species richness and abundance under invading pine trees decreases significantly as pine canopy area increases. Species richness (a) and cover (b) in two different habitats, temperate forest (dark dots) and Patagonian steppe (white dots). The magnitude of this decrease will depend on the degree to which the native species are adapted to conditions similar to those created by the pines (e.g., level of shade tolerance). The impact of the pines is most pronounced in those ecosystems where shrub and grass life-forms are dominant (e.g., steppes). (Figure modified from Franzese et al. 2017)

In *Araucaria angustifolia* moist forest of Brazil, the average richness and abundance of land planarians were lower in areas invaded by pine than in uninvaded forests. This reduction was a consequence of the alterations in microhabitat caused by the accumulation of pine litter (de Oliveira et al. 2014). Pawson et al. (2010) examined the impact of non-native conifer density on native invertebrate assemblages in *Pinus nigra* invasions in New Zealand. They found that the effects of non-native conifer invasion on grassland invertebrate assemblages were strongly dependent on conifer density after 14 years of invasion. The relative abundance of major classes and orders of invertebrates was largely unaffected by conifer invasion at densities below 800 trees per hectare but differed in higher-density conifer stands (canopy cover >50%). At the species level, beetle species composition was highly sensitive to conifer invasion at densities as low as 400 trees ha<sup>-1</sup>. Changes in beetle species composition were correlated with reduced soil moisture, increased canopy cover, and increasing trap distance from the nearest seminatural grassland. The effects of conifer invasions on invertebrates may have strong ecological consequences because invertebrates influence ecosystems as important links in the food web but also as pollinators, decomposers, and predators of pest insects (Losey and Vaughan 2006).

## 15.4 Biotic Homogenization Belowground

The potential replacement of native belowground biota by non-native invasive microorganisms is probably one of the most unexplored aspects of *Pinaceae* invasions. *Pinaceae* trees are only able to invade if their belowground mutualists are present in the invaded range (Nuñez et al. 2009; Hayward et al. 2015a); therefore they co-invade with a group of species of ectomycorrhizal fungi (EMF) (Dickie et al. 2010). Once introduced, ectomycorrhizal fungi can disperse via water, wind, mammals, soil movement, and intentional or accidental human transport (Nuñez et al. 2013; Dickie et al. 2016).

Since pines were introduced to South America for forestry purposes, there have also been large-scale introductions of non-native ectomycorrhizal fungi (Rivera et al. 2015; Hayward et al. 2015b), which may cause severe ecological impacts. Ectomycorrhizal fungi invasion produces loss of soil carbon, movement of phosphorus into labile pools, and a shift toward fast nutrient cycling and bacterial-dominated decomposition (Chapela et al. 2001; Dickie et al. 2011). These changes in the soil can in turn facilitate invasion by plant species that are adapted to high-nutrient soils (Dickie et al. 2014). The spread and invasion of non-native fungi can also have cultural and social impacts, as it affects the perception of the native habitat by local people with a subsequent loss of sense of place (Dickie et al. 2016). Economically, the introduction of new species can positively impact timber production, and the use of novel edible fungi may emerge with commercial interest. However, many introduced species can also be toxic to humans that accidentally consume their fruiting bodies (Nuñez and Dickie 2014).

In the invaded range, non-native ectomycorrhizal fungi interact with native biota. Some non-native ectomycorrhizal fungi, for example, can form novel associations with native plants. Some cosmopolitan ectomycorrhizal fungi species that associate with *Pinus spp.* can also be found associated with native *Nothofagus spp.* (Dickie et al. 2010). Moreover, some non-native ectomycorrhizal fungi, such as *Amanita muscaria*, have been found to be spreading into native forests associated with native tree species (Orlovich and Cairney 2004; Dickie and Johnston 2008). The mechanisms underlying this process, together with the impact of these novel associations, are still uncertain. In any case, beta diversity of the belowground communities decreases, as the arrival of these species of cosmopolitan ectomycorrhizal fungi associated with pines increases similarity between different communities. There is also evidence that native ectomycorrhizal fungi generally do not associate with pine species (Dickie et al. 2010; Gundale et al. 2016). Intrinsic ectomycorrhizal fungi species traits define their invasion success and probably are involved in the interaction with native biota. Some non-native ectomycorrhizal fungi, for example, perform better in the invasion front due to high spore resistance, long-distance dispersal, and high spore production. Although these groups of ectomycorrhizal fungi allow pines to establish, they are then outcompeted by late-successional non-native species (Peay et al. 2010). If and how these sets of non-native species interact with each other and with native ectomycorrhizal fungi are still not clear. We also have limited information about whether non-native fungi replace native ectomycorrhizal fungi, but this is clearly a possibility (Nuñez and Dickie 2014), which would have a direct impact on plant species composition. Given the above information, there is sufficient evidence to suggest that the spatial complexity of ectomycorrhizal fungal communities has implications for forest succession, expansion, and invasion dynamics (Dickie and Reich 2005).

Undoubtedly, there is a clear need to shed light onto the mechanisms by which simplification of the belowground community could occur. More work is needed to fully understand how non-native ectomycorrhizal fungi could influence the rate of species spread and the resistance of the community to future invasions, in addition to altering a much wider range of ecosystem processes such as soil respiration and soil carbon stocks.

## 15.5 Conclusions

Due to the wide latitudinal and climatic gradient present in South America, there is a great variety of ecosystems and species, with high endemism and very limited distributions. The addition of large areas planted with non-native conifer species represents an important driver of biodiversity loss in these areas. Currently more than ten million hectares are covered by a small subset of non-native tree species, mainly of the *Pinaceae* family. Additionally, an undetermined area is being invaded by pines, generating a homogenization process at landscape, stand, and even micro-site scales, causing ecosystem consequences across trophic levels.

The planted and invading pines are perceived by society, in most cases, as transforming agents of the landscape. The extensive and homogeneous areas planted with pines are seen as antagonistic to the diverse and increasingly threatened native ecosystems. Currently across South America, it is possible to attribute homogenization at the landscape scale to the expansion of commercial plantations. However, land use change is a much more complicated process dominated by constant degradation and deforestation of native forest (e.g., agricultural expansion, fires, forest substitution, firewood extraction) generally resulting in a final state of plantations; however, plantations are not always the initial drivers of this change (Echeverría et al. 2006; Nahuelhual et al. 2012). Thus, comprehensive landscape planning is required to maintain landscape heterogeneity and conserve the remaining patches of native ecosystems.

Pine invasions initiate largely from pine plantations. Therefore, recognizing that pine plantations provides a series of goods and services (such as wood, fiber, and fuel), there is now a pressing need to develop practices oriented toward avoiding negative externalities, such as invasion of native ecosystems. Non-native conifer plantations are an undeniable source of propagules that cause invasion in natural ecosystems, even in protected areas, with all the problems for biodiversity conservation that follow from these invasions. Most of the cultivated pine species have the potential to become invasive (Pauchard et al. 2015; Nuñez et al. 2017), but we should avoid planting those with the highest invasive potential (Rejmánek and Richardson 1996) or with international evidence of becoming invasive. Appropriate management strategies need to be developed inside and outside pine plantations in order to prevent or reduce impacts on local biodiversity (Pauchard et al. 2015; Braun et al. 2017; Nuñez et al. 2017). Less dense plantations with a well-developed understory are key to increasing diversity within plantations, as well as allowing species to disperse across the landscape. On the other hand, the establishment of pines outside the plantations should be avoided by controlling wildings, especially in riparian zones and open ecosystems.

Homogenization generated from pine invasion in natural areas is a gradual process, which can take years or decades, but it is inevitable if timely control measures are not taken. In the early stages of pine invasion, there is a reduction in the abundance of some native plant species associated with increased of canopy cover (Urrutia et al. 2013; Franzese et al. 2017) and a restructuring of the soil fungal communities initiated by the arrival of ectomycorrhizal fungi associated with the pines (Nuñez and Dickie 2014). In later invasion stages, changes occur in plant community composition resulting from the inevitable loss of native species (Abreu and Durigan 2011; Bravo-Monasterio et al. 2016). This homogenization, as a result of the loss of native species and the increase in pine abundance, brings changes to all levels of organization within the ecosystem, which can be permanent, giving rise to a novel habitat. Furthermore, this biodiversity loss can affect the stability of ecosystems by decreasing the ability of communities to respond to environmental change and disturbances (Gámez-Virués et al. 2005).

One of the current challenges in biodiversity conservation lies in how to deal with the synergy of factors that promote ecosystem homogenization. Wildfires and

invasions could generate a positive feedback (Brooks et al. 2004; Mandle et al. 2011), speeding up the process of biodiversity homogenization in degraded ecosystems. Positive feedbacks between fire and invasion of pines adapted to fire (i.e., serotinous pines; e.g., Taylor et al. 2017) can be a major cause of unidirectional changes in natural ecosystems (Simberloff et al. 2010; Veblen et al. 2011), especially in those which have not evolved under a high fire frequency (Brooks et al. 2004). The main effect of invasive pines on fire risk in natural forests is related to higher flammability and fuel continuity, although over time it is expected that the amount of fine fuel could also increase (Cobar-Carranza et al. 2014). In steppe systems, invasive pines contribute to greatly elevated fuel loads in invaded areas (Taylor et al. 2017). In mediterranean and temperate ecosystems, the number and severity of wildfires are expected to increase in the future due to the current scenario of climate change, coupled with an increase in human activity, and the large concentration of pine plantations (Peña and Valenzuela 2008; McWethy et al. 2018). In the summer of 2017, more than 100,000 ha of native forest burned just within Chile, in sectors dominated by pine plantations (CONAF 2017) or with evidence of pine invasion (Bustamante and Simonetti 2005; Gómez et al. 2011). If a timely restoration and control of post-fire pine regeneration are not performed in these zones, it is expected that vegetation composition will be drastically modified and dominated by pines. This highlights the importance of analyzing the traits of the pine species that are proposed for introduction into natural areas and discouraging the use of those species whose abundances would likely be promoted by disturbances such as fire (Franzese and Raffaele 2017).

To mitigate future impacts caused by pines, and other tree plantations, it is important to develop a comprehensive landscape plan, understanding that pine plantations coexist and interact with other land uses, productive and non-productive, and, therefore, the management of these plantations must be implemented in accordance with the social and ecological context in which they are located. Along the same lines, the reduction of large areas planted with a single objective and management strategy is crucial to reduce landscape homogenization and other negative impacts associated with intensive and extensive management of tree monocultures.

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