Forest Ecology and Management 425 (2018) 75–84

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Review and synthesis

Opening the silvicultural toolbox: A new framework for conserving biodiversity in Chilean timber plantations

Tyler N. McFadden*, Rodolfo Dirzo

Department of Biology, Stanford University, Stanford, CA 94305, United States

ARTICLE INFO

Keywords:
Forest management
Chile
Pinus radiata
Eucalyptus
Understory
Land-use change

ABSTRACT

Intensively managed timber plantations represent 7% of global forest cover and may partially compensate for deforestation-related biodiversity loss, yet are often criticized as 'green deserts' which support limited biodiversity. Growing concerns about the environmental impact of plantations in Chile have prompted numerous calls for a new forestry paradigm. Here, we systematically review the literature on biodiversity maintenance or loss in Chilean timber plantations and outline a new framework for biodiversity conservation therein, envisioning plantations as potential habitat that can be improved through informed management. Our review (N = 67 relevant publications) shows a strong taxonomic bias towards plants, mammals, birds, and invertebrates, as well as biases in the age and species composition of plantations studied. Most studies (78%) examined *Pinus radiata* plantations, 48% examined mature stands, and 46% did not specify stand age. Research to date is difficult to translate into conservation policy, since most studies simply compare biodiversity within versus outside of plantations, and do not evaluate alternative management options. To better inform conservation, we identify six critical stages of plantation development during which management decisions may greatly influence biodiversity outcomes. Within each stage we discuss the effects of specific management practices on Chilean biodiversity, highlighting opportunities and key knowledge gaps. Strategies which promote structural complexity, understory cover, and landscape connectivity should help convert plantations into a less hostile matrix that provides adequate habitat for substantial native biodiversity. Given the global proliferation of plantations and their consequences for biodiversity, similar studies are needed in multiple regions of the world.

1. Introduction

Despite recent reductions in the rate of global forest loss, deforestation and land-use change persist as primary drivers of current and future biodiversity change (Dirzo et al., 2014; Pereira et al., 2010). Highly productive timber plantations have the potential to reduce pressure on natural forests and provide secondary habitat for biodiversity where natural forests are scarce, yet they may also replace natural forests and are often criticized as 'biological deserts' that support little biodiversity (Brockerhoff et al., 2008; Paquette and Messier, 2010). Timber plantations are increasing in area by 2.5 M ha annually and now represent 7% of global forest cover (Keenan et al., 2015). Identifying strategies to effectively manage plantations for maintaining biodiversity is therefore a critical challenge to sustainable forest management and biodiversity conservation.

Chile contains 2.95 M ha of plantation forests, making it one of the top 10 countries in the world in terms of area dedicated to timber plantations (FAO, 2015). Plantation forestry was first promoted in the early 1900s to stabilize soils in degraded agricultural areas, and later rapidly expanded in the 1970s and 1980s during the military government of Augusto Pinochet. In addition to implementing neoliberal economic reforms, Pinochet enacted the Decree Law 701 of 1974 (D.L. 701), which subsidized 75% of the costs of plantation establishment and remained in effect through 2012 (Niklitschek, 2007). The Chilean forestry sector now provides about 300,000 jobs, and represents the country's second largest export industry, generating US$5.9 billion in 2011 (Salas et al., 2016).

The Valdivian Rainforest Ecoregion (35–48° S) in southern Chile is recognized as a global biodiversity hot spot due to its rich diversity, high levels of endemism, and extensive habitat loss (Myers et al., 2000). Indeed, the rapid expansion of exotic timber plantations in this ecoregion during the last four decades has prompted concerns about the impacts of plantations on native biodiversity and ecosystem function (Reyes and Nelson, 2014). Ninety-five percent of Chile's timber production comes from intensively managed monoculture plantations of exotic species such as Monterey pine (*Pinus radiata*, hereafter 'pine

* Corresponding author.
E-mail address: tyler.neal.mcfadden@gmail.com (T.N. McFadden).

https://doi.org/10.1016/j.foreco.2018.05.028
Received 26 March 2018; Received in revised form 11 May 2018; Accepted 12 May 2018

plantations') and *Eucalyptus* spp. (INFOR, 2016). Furthermore, nearly a quarter of all new plantations from 1986 to 2011 were established on lands that were native forests before 1986 (Heilmayr et al., 2016). Numerous studies highlight the deleterious effects of plantations on Chilean biodiversity (Estades et al., 2012), clean water provisioning (Fierro et al., 2016; Lara et al., 2009), fire risk (Úbeda and Sarricolea, 2016), and rural communities (Andersson et al., 2016). In the austral summer of 2016–2017, Chile experienced its worst wildfire season in history, burning 600,000 ha and launching the debate over plantations into the national spotlight (Kozak, 2017). Several scientists wrote prominent editorials in national newspapers arguing for a new forest management paradigm (e.g. González et al., 2017), while international newspapers ran stories tying the fires to the neoliberal economic policies of Chile's former dictator Pinochet (Kozak, 2017). The mayor of Valparaíso, Chile's third largest city, went so far as to call for the removal of all *Eucalyptus* plantations within the metropolitan area (see Ahora Noticias, 2017).

The Chilean forestry sector is at a crossroads. Plantation managers are under increasing public pressure to balance timber production and environmental stewardship (CONAF, 2017). While 52% of Chilean plantations are now certified under the Forest Stewardship Council's sustainability certification scheme, these environmental standards are largely implemented in the areas surrounding plantations (in the form of conservation reserves), and the plantations themselves continue to be managed using intensive methods (Salas et al., 2016). Despite a substantial body of research documenting the negative effects of plantations on Chilean biodiversity (e.g. Estades et al., 2012), less is known about the role of innovative forest management practices in mitigating or exacerbating these impacts. Some recent studies indicate that appropriately managed plantations may provide important habitat for native biodiversity, serve as a 'softer' matrix than alternative anthropogenic land uses (e.g. pasture), and may even be critical to the conservation of some threatened species (Acosta-Jamett et al., 2003; Estades et al., 2012; Heinrichs et al., 2016). While many studies examine plantation-associated changes in biodiversity, documentation of these changes alone provides limited guidance to landowners or policy makers who may wish to manage plantations for increased biodiversity. Here, we review the literature of biodiversity maintenance in Chilean plantations and complement it with insights derived from studies in plantations from other parts of the world, leading us to outline a new framework for managing timber plantations for biodiversity in Chile, but with potential relevance for plantations elsewhere.

This review synthesizes the results of 67 studies of biodiversity in Chilean timber plantations, with the aim of identifying strategies that managers can utilize to conserve biodiversity in working plantations. We begin by conducting a systematic review to identify key trends and knowledge gaps in the field. We then summarize the literature on the effects of plantations on Chilean biodiversity, which we analyze in the context of critical silvicultural decisions made at six stages of plantation management. We discuss the state of the art regarding the effects of specific management practices on biodiversity in Chile and throughout the world, and identify areas where more research is needed to inform sustainable plantation management. In doing so, we lay out a new framework for the conservation of biodiversity in Chilean timber plantations, in which plantations are viewed as potential habitat that can be improved through informed management. Given the global proliferation of plantations and the consequences for biodiversity thereof, our study is of broad significance (Fitzherbert et al., 2008; Paquette and Messier, 2010).

2. Systematic review: Biodiversity in Chilean timber plantations

We conducted a systematic search of the peer-reviewed literature in Web of Science on April 4, 2017, using the search terms "plantation *OR* pine *OR* eucalyptus" ***AND*** "Chile*" ***AND*** "biodiversity *OR* wildlife *OR* animal *OR* invertebrate *OR* insect *OR* vertebrate *OR* bird *OR* mammal *OR* reptile *OR* amphibian *OR* plant *OR* tree *OR* fungus". Our search returned a list of 504 results, which we refined using inclusion criteria presented in Table 1. The resulting database includes 67 studies (Table A1) published from 1987 to 2017, with 72% being published in the last decade (Fig. 1).

Table 1
Criteria governing inclusion of literature for the systematic database, and data collected from each study.

Criteria	Publication characteristics	Data collected
Inclusion	• Empirical studies conducted in Chilean Regions V, VI, VII, VIII, IIX, X, or XIV[a], **and** • Peer-reviewed primary research, **and** • Examine effects of timber plantations on Chilean biodiversity, **or** • Document biodiversity in Chilean plantations	1. Chilean region in which study was conducted 2. Taxa studied 3. Species of tree planted 4. Stage of stand development[b] 5. Control (reference) habitats (if any)
Exclusion	• Examine plantations only as driver of land-use and land cover change, **or** • Only examine effects of management treatments on pests or planted trees	

[a] These seven regions contain > 98% of Chilean timber plantations (INFOR, 2016).
[b] Stand development stages: mature (> 8 yrs), young (3–8 yrs), new (< 3 yrs), clear cut (harvested but not yet replanted), mature abandoned (abandoned plantation with trees > 8 yrs), thinned (stand recently thinned), unspecified (no information provided), and multiple pooled (authors grouped multiple stages together).

At least one study took place in each of the seven Chilean regions included in our analysis, but the studies were unevenly distributed geographically (Fig. 2). Eighty-four percent of studies (56 of 67) occurred in the Maule or Biobío Regions, which combined contain 64% of Chile's timber plantations (INFOR, 2016). Relatively few studies occurred in the Araucanía Region, which is Chile's third largest timber producing region and also the epicenter of conflicts between the timber industry and the Mapuche People (Reyes and Nelson, 2014). Eleven studies simultaneously examined two or more regions.

Plants were the most commonly studied taxa, followed by mammals, birds, and invertebrates (Fig. 3). Very few studies examined other vertebrate taxa, microbes, or fungi. Most notably, no studies examined amphibians, although south-central Chile supports a high diversity of forest-associated frogs, many of which are threatened and/or endemic to the region (Vidal and Díaz-Páez, 2012). Most studies focused on

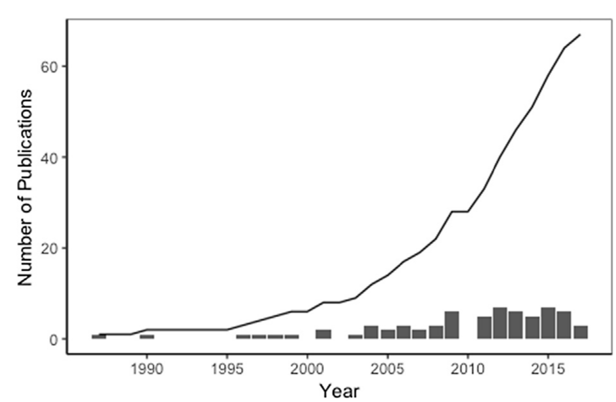

Fig. 1. Time course of publications (n = 67) examining the effects of timber plantations on Chilean biodiversity (Regions V-X, and XIV). Vertical bars represent the number of publications per year. Line shows the cumulative number of publications since 1987.

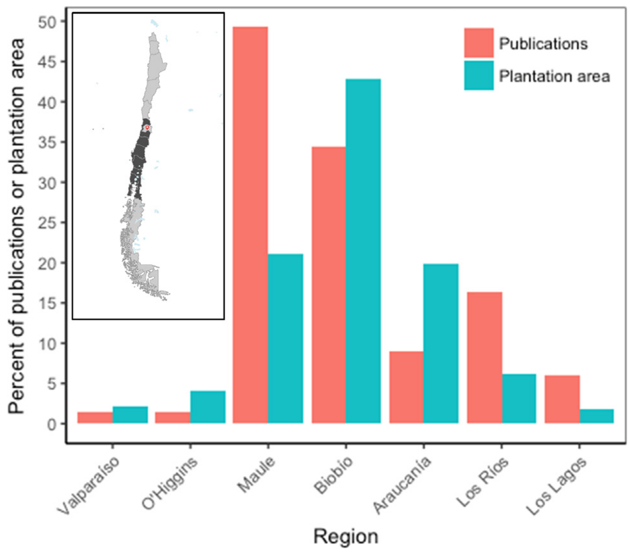

Fig. 2. Percent of publications and plantation area by Chilean region, ordered from north to south. Red bars sum to > 100% because some publications examined multiple regions. Blue bars total < 100% because some plantations occur in other regions. These seven regions represent > 98% of Chilean timber plantations. Plantation area data are from INFOR (2016). Publications and regional plantation area are highly correlated (Spearman's rank correlation, $S = 10.593$, $p = 0.0269$). *Inset:* The seven Chilean regions studied here are shown in dark grey. Red marker indicates the capital city Santiago.

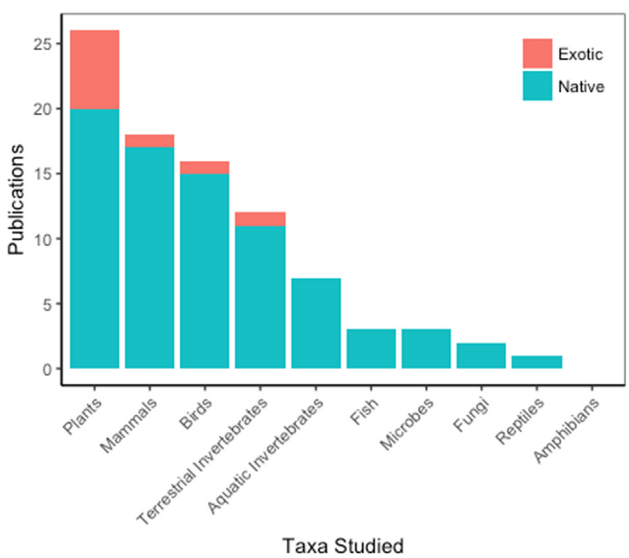

Fig. 3. Number of publications by taxa examining biodiversity (including native and exotic species) in Chilean timber plantations.

native biota, while six studies examined the effects of plantations on the proliferation of exotic species. Since different taxa respond uniquely to plantations (e.g. Barlow et al., 2007), these strong taxonomic biases may hinder the development of holistic management strategies.

In terms of relevance for forest management policy, the most informative studies are those comparing biodiversity across plantations that differ in tree species composition and/or stage of stand development. Only 29 studies (43%) compared biodiversity across plantations that varied in their habitat or management characteristics (e.g. stand age, plantation species, understory cover, etc.). Instead, most studies compared biodiversity found in plantations with that of native forest (either continuous or fragmented), and a quarter of studies used no control habitat at all. More broadly, the publications identified in our search show strong biases in terms of the types and ages of plantations selected for study (Fig. 4). Forty-eight percent examined mature plantations and 46% either failed to specify the stand age, or pooled multiple stages of stand development, thereby reducing their ability to inform specific management policies. The large majority of publications (78%) focus on pine plantations, which represent 59% of Chilean plantations. Only 18% of the studies examined *Eucalyptus* spp., although these represent 35% of Chilean plantations (INFOR, 2016). This mismatch is especially concerning, given the recent and continuing expansion of *Eucalyptus* plantations, particularly in the more southerly regions of Araucanía, Los Ríos, and Los Lagos (INFOR, 2016).

3. Biodiversity and the silvicultural toolbox

While silvicultural tools are traditionally applied to increase yields and improve timber quality, these techniques are increasingly used to manage forests for biodiversity and ecosystem services (Hartley, 2002; Lindenmayer et al., 2006; Demarais et al., 2017). Managers make decisions at six key stages of plantation management which can result in the development of vastly different stand conditions and ultimately affect the plantation's capacity to support biodiversity (Table 2; McComb, 2001). Following this framework, we draw on the information derived from our review to discuss the current state of knowledge concerning the effects of silvicultural decisions on biodiversity in Chilean timber plantations. We supplement our literature search with other relevant publications which our search did not return (i.e. book chapters, dissertations, studies of Chilean biodiversity in native forests), and we also draw on information from other countries when Chile-specific data are not available.

3.1. Stage 1: Spatial and temporal planning

The spatial and temporal distribution of habitat fundamentally influences the diversity, abundance, and identity of species that can exist in an area. In the context of plantation management, both the properties of an individual stand and the landscape context in which it occurs determine the outcomes for biodiversity (Lindenmayer and Franklin, 2002). Managers typically consider properties such as the size and shape of the harvest, harvest rotation length, site-level properties such as slope, aspect, elevation, and edaphic conditions, and the distance to other features such as native forests, riparian areas, and other harvest areas (Carnus et al., 2006). A substantial body of research explores the landscape-level effects of plantations on Chilean biodiversity, both within plantations, and within native forests adjacent to or surrounded by plantations.

The rapid expansion of plantations has left native forests severely fragmented throughout south-central Chile. Echeverria et al. (2006) documented a 67% decline in native forest from 1975 to 2000 in the coast range of the Maule and Biobío regions, largely due to conversion to plantations. In 1975, 44% of native forest area was concentrated in patch sizes greater than 20,000 ha, yet by 2000, 69% of native forest patches were less than 100 ha, and only 3% of patches were greater than 1000 ha. Small forest patches generally support reduced wildlife populations and experience increased edge effects and reduced connectivity (Fahrig, 2003). For example, continuous native forests in the Maule Region supported greater richness of small mammals than either forest fragments or pine plantations (Saavedra and Simonetti, 2005). Alternatively, some species benefit from forest fragmentation. Reptiles, for example, exhibited the greatest abundance and richness at forest and plantation edges (Uribe and Estades, 2014). Fragmentation may also affect species interactions, either by differentially impacting multiple interacting species, or by reducing interaction rates (Fig. 5).

Plantation-dominated landscapes represent a shifting-mosaic of habitats, ranging from unplanted clear-cuts to mature plantations (Demarais et al., 2017). The ability of this mosaic to support biodiversity depends on the size of harvest units, the length of rotation intervals, and the connectivity between habitat patches (Acuña and

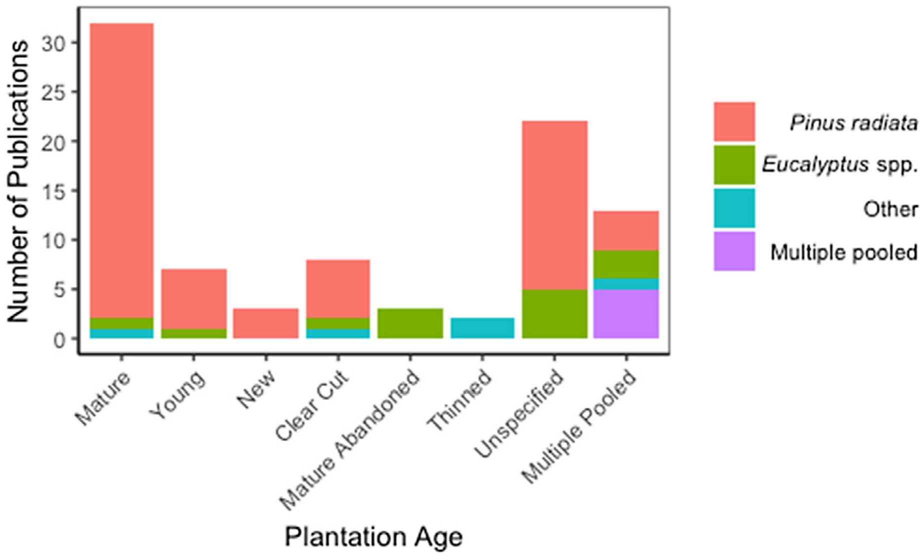

Fig. 4. Number of publications examining biodiversity in Chilean timber plantations, separated by plantation age and species. Plantations were classed into stand development categories using the following criteria: mature (> 8 yrs), young (3–8 yrs), new (< 3 yrs), clear cut (harvested but not yet replanted), mature abandoned (abandoned plantation with trees > 8 yrs), thinned (stand recently thinned), unspecified (no information provided), and multiple pooled (authors grouped multiple stages together).

Table 2
Six stages of plantation management and relevant management considerations that will influence stand conditions and biodiversity conservation. Table adapted from McComb (2001).

Management stage	Spatial and temporal planning	Legacy retention	Site preparation	Regeneration	Vegetation management	Thinning and pruning
Management considerations	Landscape context Size Shape Slope/aspect Rotation length	Leave trees Snags Shrubs Logs Riparian buffers	Burn Herbicide Ground scarification	Species Density Size Survival Fertilization	Manual Chemical Duration/Intensity of management	Density Spacing – Uniform – Variable

Estades, 2011; Wimberly, 2006). Graph theoretic or circuit-based approaches to modeling landscape connectivity across multiple habitats may be particularly useful in understanding biological connectivity in plantation-dominated landscapes. Lander et al. (2011) used one such circuit-based approach to model reproduction of the endangered tree *Gomortega keule* (Gomortegaceae) and found that pollination probability was lowest across clear-cuts, and varied up to 7-fold depending on the composition of the landscape mosaic. Alternatively, mature plantations may serve as suitable (albeit temporary) habitat for many species. For example, Meynard et al. (2014) found no differences in bat species richness or abundance between native forest and *Eucalyptus* plantations. Similarly, Bustamante-Sánchez et al. (2004) observed similar richness and abundance of dung beetles in continuous native forests and pine plantations. Mature plantations may also represent a relatively “soft” barrier to wildlife movements compared to other anthropogenic land uses, given their structural similarities to forests (Tomasevic and Estades, 2008). In contrast, clear-cuts are likely to form a more definite barrier to animal movement and have been shown to exhibit reduced bat activity and reduced abundance of an understory bird, relative to native forests and mature plantations (Rodríguez-San Pedro and Simonetti, 2015; Ramirez-Collio et al., 2017). Managers may be able to increase connectivity by altering the size and distribution of harvest units, though this approach has received little attention in the literature (Pawson et al., 2006).

Fig. 5. Fragmentation of native forests by plantations may disrupt species interactions. *Left*: *Lapageria rosea* (Philesiaceae) experiences reduced pollination success in fragmented native forests due to reduced abundance of its primary pollinators (the hummingbird *Sephanoides sephanoides* [pictured] and the bumblebee *Bombus dahlbomii*; Valdivia et al., 2006). Photo: Juan Andrés Varas Braun. *Right*: Avian frugivory of *Aristotelia chilensis* (Elaeocarpaceae) was 2.4 times higher in continuous native forest than in forests fragmented by pine plantations (Valdivia and Simonetti, 2006). Furthermore, seeds from forest fragments germinated at less than half the rate of those from continuous forests, suggesting a lack of dispersal may be contributing to inbreeding depression in this species. Photo: Morrana, CC-BY 4.0 license, Wikimedia Commons.

The historic 2016–2017 wildfire season prompted calls for more fire breaks within timber plantations to limit the spread of wildfires. Depending on how they are implemented, fire breaks could provide the dual benefit of increasing biological connectivity within fragmented landscapes, or contribute to further habitat fragmentation. Fire breaks within a Monterrey pine plantation in Argentina did not support higher richness or abundance of small mammals compared to the plantations, suggesting that their role as a wildlife corridor was limited in this case (Lantschner et al., 2011). Another study found that two important birds [the seed disperser White-crested elaenia (*Elaenia albiceps*), and the pollinator Green-backed firecrown (*Sephanoides sephanoides*)] experienced reduced functional connectivity through an open matrix between native forest patches as compared to a matrix consisting of shrubs with interspersed trees (Magrach et al., 2012). Because fire breaks by design have little vegetation cover, they are unlikely to facilitate connectivity for forest-associated wildlife. In contrast, Rubio and Simonetti (2011) observed the highest reptile richness and abundance (including that of one species of conservation concern: *Liolaemus lemniscatus*) at the edges of pine plantations, followed by edges of native forest fragments surrounded by clear cuts and roads. Clear cuts and forest edges may therefore play a role in the conservation of these and other edge-associated species.

Less is known about how plantations may affect Chilean aquatic biodiversity, though studies from other countries indicate that plantations can reduce runoff and alter stream flow regimes (Farley et al., 2005; Scott and Prinsloo, 2008). In Chile's Los Ríos and Los Lagos Regions, for example, Lara et al. (2009) estimated a mean increase in total summer stream flow of 14.1% for every 10% increase in native forest cover within a watershed. Similar negative effects of plantations on summer water flows have also been demonstrated within large ($>$ 10,000 ha) watersheds (Little et al., 2009). Given flow regimes are a major determinant of physical habitat in streams, and that aquatic species are generally adapted to specific flow regimes (Bunn and Arthington, 2002), these changes may have substantial implications for aquatic biodiversity in plantation-dominated watersheds.

3.2. Stage 2: Legacy retention

During a harvest, managers may retain certain structural components of the previous stand. These legacy elements, including standing trees or snags, downed logs, woody debris, shrub cover, and streamside riparian buffers, can provide structural heterogeneity that greatly increases the types of habitat features present within a stand (Demarais et al., 2017; Gustafsson et al., 2010). In selecting what types of legacy elements to retain, managers might want to consider the habitat preferences of forest-associated biodiversity in native forests and attempt to create similar conditions in managed stands (Perera et al., 2004).

Díaz et al. (2005) examined forest bird abundance and richness in relation to forest structure and composition in old-growth, mid-successional, and early successional native forests. Both species richness and abundance were greatest in old-growth forests and were associated with large emergent trees, snags, logs, and bamboo cover. These features provide important foraging and nesting substrate for many birds, particularly trunk and branch insectivores, and cavity nesters, both of which groups are less abundant in plantations than in native forests (Vergara and Simonetti, 2004). Plantation managers may be able to emulate these properties of old-growth forests and thereby increase the habitat suitability for forest birds by leaving legacy structures such as large standing trees and snags, downed logs, and remnant shrub/bamboo cover.

Streamside buffer zones of native forest vegetation can help maintain stream flows and improve water quality, and are a common management tool worldwide (e.g. Lee et al., 2004). In Chile, Fierro et al. (2016) compared water quality and macroinvertebrate assemblages between streams with native riparian forest (in the form of a riparian buffer) and streams with exotic (*Eucalyptus* spp.) riparian vegetation (no buffer). They found that the exotic vegetation sites had higher concentrations of dissolved and suspended solids, nitrates, and sulfates, as well as reduced richness and abundance of macroinvertebrates relative to the native vegetation site. In another study, Little et al. (2015) measured a 1.4% increase in run-off relative to precipitation for every meter of increase in native buffer zone width within *Eucalyptus* plantations. Additionally, native buffer zones led to reduced concentrations of total nitrogen (TN), dissolved inorganic nitrogen (DIN), and sediments. Buffer widths of 17–22 m for TN and DIN and $\geq$ 36 m for sediments reduced concentrations to levels comparable with reference native forest watersheds.

Streamside buffers may have the added benefit of increasing landscape level connectivity for mobile animals (Lees and Peres, 2008). Estades and Temple (1999) found a positive relationship between the abundance of cavity-nesting birds and the proximity of riparian strips, and hypothesized but could not confirm that this was due to increased connectivity via riparian corridors. Studies tracking animal movement have found little evidence in Chile to support or refute this hypothesis, but these studies were limited in scope and only considered one generalist bird, the Austral thrush, *Turdus falcklandii* (Vergara et al., 2013; Pérez-Hernández et al., 2015).

3.3. Stage 3: Site preparation

Prior to replanting, managers may prepare the site using methods such as mechanical scarification, burning, and herbicide application. Depending on their intensity, site preparation methods may remove legacy structures and inhibit shrub development, or induce the sprouting of new vegetation (McComb, 2001). The choice of site preparation methods will influence the trajectory of plant community development and the species a plantation can support (Demarais et al., 2017).

Site preparation methods which disturb (e.g. soil scarification) or compact the soil may impact burrowing or ground-dwelling species, both indirectly through habitat modification, and directly through mortality events (Demarais et al., 2017). Taxa that may be particularly vulnerable include ground-dwelling frogs (*Eupsophus* spp., *Alsodes nodosus, Rhinoderma darwinii*, several of which are threatened), burrowing mammals, and ground-nesting birds (e.g. species of the Rhinocryptidae family). To our knowledge, no studies have evaluated this phenomenon in Chile. Escobar et al. (2015) documented greater than 50% mortality of one forest specialist mouse (*Abrothrix longipillis*) due to being crushed during harvest operations. The authors observed that instead of fleeing the area, *A. longipillis* hid in burrows or under forest litter in response to disturbance, suggesting that this species would also be vulnerable to mortality from soil scarification.

Chilean clear-cuts and newly established plantations generally maintain little native vegetation because vegetation is intensively cleared either mechanically or using controlled burns (Kogan et al., 2002). Newly established stands typically exhibit a prevalence of exotic species (Frank and Finckh, 1997). Plant species richness and abundance generally increase subsequently as the stand develops (Estades and Escobar, 2005).

Both shrub-associated and understory birds may persist in early-successional habitat where adequate structure and cover are provided, suggesting that new plantations and clear-cuts could support substantial biodiversity if managed appropriately. Des Mur's Wiretail (*Sylviorthorhynchus desmursii*) and Magellanic Tapaculo (*Scytalopus magellanicus*), two understory birds, utilize log piles, scattered bamboo thickets, and shrub patches in native early successional forests, while shrub-associated species such as the Southern House Wren (*Troglodytes aedon*) and Plain-mantled Tit-spinetail (*Leptasthenura aegithaloides*) are found in shrub patches and piles of woody debris (Díaz et al., 2005). Similarly, the understory bird Chestnut-throated Huet-Huet (*Pteroptochos castaneus*) is more likely to enter clear cuts that have abundant shrub cover, especially when adjacent forests or plantations also have abundant understory vegetation (Ramirez-Collio et al., 2017). Site preparation methods which retain legacy elements and promote the development of early seral vegetation will likely minimize the negative impacts of clear-cuts on forest biodiversity.

3.4. Stage 4: Regeneration

Managers influence the structure and composition of a developing plantation through their selection of which tree species to plant and at what densities (O'Callaghan et al., 2017). Managers may also fertilize newly planted seedlings, which may affect both terrestrial plant growth and nutrient loading in nearby streams (Hartley, 2002). Foresters often plant at very high densities to encourage rapid vertical growth. Increasing seedling spacing, however, can increase target tree growth rates (Hébert et al., 2016), allowing for greater light penetration and supporting understory regeneration. To our knowledge, no published studies address the effects of planted seedling density on Chilean biodiversity, though stem density and canopy cover are two major determinants of understory growth in plantations (Carnus et al., 2006).

Chilean plantations are typically grown as monocultures of Monterey pine or *Eucalyptus* spp. Many foresters and biologists have called for a re-examination of this practice, arguing that plantations of native species can better conserve biodiversity and ecosystem services (Reyes and Nelson, 2014, Salas et al., 2016). A thorough examination of forestry with native species is outside the scope of the current study, but Salas et al. (2016; and references therein) suggest that plantations of native species may be economically feasible and could provide improved habitat for native biodiversity. The conservation benefits of using native tree species, or mixtures of native and non-native tress have been thoroughly discussed in the international literature (e.g. Hartley, 2002). However, local studies often show equivocal results, and indicate that biodiversity may benefit more from the increased structural complexity that native or mixed species plantations confer, rather than from the species composition *per se* (Oxbrough et al., 2012; Sweeney et al., 2010). Most studies examining biodiversity in Chilean exotic timber plantations focus on pine plantations, though *Eucalyptus* plantations represent 35% of Chilean plantations (INFOR, 2016). Since *Eucalyptus* plantations are generally managed for pulpwood, and therefore rarely thinned, they likely affect biodiversity very differently than pine plantations, which generally undergo multiple thinning treatments and may support a well-developed understory (Estades et al., 2012). Estades and Escobar (2005) noted that the dense and unthinned pine plantations of the 1960s (mostly used for erosion control and pulp production) supported very few plants and animals, and likely contributed to the popular image of plantations as "green deserts."

3.5. Stage 5: Vegetation management

Managers frequently use herbicides and/or mechanical removal of vegetation to reduce plant competition with the target trees (Kogan et al., 2002). Vegetation management directly influences plant diversity and greatly affects the availability of food and cover for wildlife (Brockerhoff et al., 2008; Carnus et al., 2006; Demarais et al., 2017). Chilean plantations often develop understory vegetation that is compositionally similar to that of secondary shrublands, with common species including *Aristotelia chilensis, Peumus boldus, Cryptocarya alba,* and *Rubus* spp. (Ramírez et al., 1984, Simonetti et al., 2013). Compared to native forests, the plantation understory generally contains higher richness and abundance of exotic species (Becerra and Simonetti, 2013; Gómez et al., 2009; Heinrichs and Pauchard, 2015), as well as greater herbaceous cover and less shrub cover (Heinrichs et al., 2016).

Understory cover is a strong predictor of avian species richness and abundance in mature pine plantations (Estades and Temple, 1999; Vergara and Simonetti, 2004). Plantations with well-developed understories may even support some forest specialist birds (Fig. 6). For instance, understory cover was the best predictor of presence and

Fig. 6. Plantations which provide adequate habitat structure may support rich wildlife communities, including strict forest specialists such as the Black-throated Huet-huet (*Pteroptchos tarnii*, Rhinocryptidae). Understory cover consisting of native shrubs and bamboo (*Chusquea* spp.) provides important habitat for this and other understory birds (Díaz et al., 2005). Photo credit: Fernando Rosselot.

abundance of three understory, ground-nesting Rhinocryptid birds (Vergara and Simonetti, 2006). However, the abundance of generalist small mammals (the primary predators of Rhinocryptid nests) also increases with understory cover (Saavedra and Simonetti, 2005). Consequently, Rhinoctryptid nest predation in pine plantations is double that of continuous native forest, suggesting that plantations may represent an ecological trap for these forest specialist birds (Vergara and Simonetti, 2003).

This positive association with understory cover is consistent among other taxa. In one manipulative study, medium-sized forest mammals (kod kod [*Leopardus guigna*], culpeo fox [*Lycalopex culpaeus*], hog-nosed skunk [*Conepatus chinga*], and Southern pudu deer [*Pudu puda*]), were detected 2.5 times less frequently in pine plantations following the removal of understory vegetation (Simonetti et al., 2013). Even the arboreal forest specialist marsupial *Dromiciops gliroides* may use plantations with complex understory vegetation. This keystone seed disperser is generally considered a strict forest specialist, but exhibits similar activity patterns in both native forest and abandoned *Eucalyptus* plantations, although nests were exclusively found in native forest (Salazar and Fontúrbel, 2016). Among terrestrial invertebrates, Cerda et al. (2015) found that *Ceroglossus chilensis* (an endemic and flightless ground beetle) was 5 times more abundant and had higher survival rates in pine plantations with dense understory vegetation, compared to pine plantations with little understory vegetation (> 50% vs. < 30% shrub cover). Understory cover may also influence the persistence of species interactions, with one study measuring higher avian insectivory in structurally complex pine plantations (Poch and Simonetti, 2013). Increased insectivory occurred concurrently with reduced herbivory on the shrub *Aristotelia chilensis*, suggesting that plantation structural complexity mediates a trophic cascade from vertebrate insectivores to understory plants.

3.6. Stage 6: Thinning and pruning

Managers often thin and prune plantations at least once to promote rapid tree growth and the production of high quality, knot-free lumber (Salas et al., 2016). Mid-successional forests, whether planted or natural, typically exhibit low horizontal and vertical heterogeneity and are very dense, shading out understory vegetation and providing limited habitat for forest wildlife (Demarais et al., 2017; Díaz et al., 2005). Thinning can be a valuable tool for creating habitat complexity for forest wildlife (Cahall et al., 2013) and increasing light penetration to support understory growth (McComb, 2001), but may also represent a disturbance for some species (Escobar et al., 2015).

Only two studies in our review specifically examined the effects of thinning on biodiversity in Chile, yet both indicate that increased light penetration facilitates understory establishment. Frank and Finckh (1997) observed similar plant species richness in native forest and recently thinned Douglas fir (*Pseudotsuga menziesii*) plantations, while observing reduced plant richness in un-thinned Douglas fir plantations. Old-growth native forests are characterized by frequent treefall gaps which support the generation of native bamboo thickets (*Chusquea* spp.) and provide habitat for forest specialist birds and mammals (Díaz et al., 2005; Fajardo and de Graaf, 2004; Fontúrbel et al., 2009). In general, thinning and pruning techniques that increase horizontal heterogeneity and create gaps, such as variable density thinning, may create additional niche space for plants and animals, increase light penetration to the understory, and allow for the maintenance of dense understory (Aukema and Carey, 2008; Lindenmayer and Hobbs, 2004).

4. Principles for supporting biodiversity conservation in plantations

Based on our review, we have compiled a list of guiding principles that are likely to support the conservation of forest-associated biodiversity in Chilean timber plantations. These strategies may not be appropriate for all species, and may need to be applied differently depending on the type of plantation. This is not an exhaustive list, but rather a compilation of strategies that are supported by empirical studies in Chile, or that can be inferred to be relevant given information discussed from other countries.

- *Landscape context.* The conservation value of a plantation will depend on the habitat that it replaces and its proximity to native habitats. Plantations adjacent to native forest are of greater value since they can serve as supplementary habitat for species in native forest patches. Plantations that displace native forest will be overwhelmingly detrimental to conservation outcomes, while those which replace degraded agricultural or pasture lands will likely be beneficial. Conversion of shrublands and early-successional habitats should be avoided since these habitats may mature relatively quickly into secondary forests, which themselves have significant conservation value (Chazdon, 2014).
- *Remnant forests*. Conversion of remnant native forests to plantations should be avoided, since many species may not persist in plantations. Larger patches of native vegetation provide greater resources, experience less edge effects, and will be more likely to support viable populations.
- *Connectivity*. Managers should maintain physical links between remnant forest patches to facilitate the dispersal and movement of genes (e.g., seed dispersal or pollen movement via biotic vectors) and individuals. Loss of connectivity reduces the effective habitat area of remnant patches, and can result in the disruption of species interactions and gene flow.
- *Riparian buffers.* Intact riparian vegetation supports the conservation of aquatic biodiversity by reducing sedimentation, maintaining water quality, and stabilizing stream flow. Riparian buffers also provide important habitat for terrestrial species and may serve as wildlife corridors. Riparian buffers that are wide and consist of native vegetation will provide the greatest conservation benefits.
- *Legacy structures.* Legacy structures such as snags, logs, debris piles, and large emergent trees provide important foraging and reproductive habitat for many species. These features increase stand-level heterogeneity and provide niche space for many species, especially forest specialists. Legacy structures may take decades to develop, and should be preserved whenever possible.
- *Understory vegetation.* Understory cover is consistently identified as one of the most important predictors of species richness and abundance among Chilean mammals, birds, terrestrial invertebrates, and plants. Managers can support the development of understory vegetation by retaining shrub and bamboo patches during harvest, employing site preparation methods that encourage regrowth, planting seedlings at lower densities, minimizing the application of herbicides, and maintaining an open canopy through thinning and pruning.
- *Stand structure.* Heterogeneous stands provide a greater variety of niches and better emulate the conditions found in native forest stands. Efforts should be made to increase vertical heterogeneity through the cultivation of multiple layers of vegetation, and horizontal heterogeneity using variable thinning techniques.
- *Species-specific responses.* Each species responds uniquely to plantations, depending on its behavior, life-history traits, and species-specific habitat requirements. The effects of plantations on biodiversity may therefore appear idiosyncratic, even among closely related species. These differential responses may force managers to make difficult decisions regarding trade-offs between the conservation of multiple species. For example, soil scarification is a site preparation method that can maintain and promote shrub cover, but may also compact the soil and negatively impact burrowing animals. The maintenance of stand and landscape heterogeneity can help compensate for potential trade-offs by providing a wide range of potential habitats.

5. Knowledge gaps and future research

There is a large and growing body of literature examining the effects of plantations on biodiversity in Chile. Despite this immense body of research, a lack of specificity regarding the types and characteristics of plantations studied hinders the application of this research to solving Chile's most pressing forest management challenges. Of the 67 publications identified in our systematic literature review, 31 (46.3%) either did not specify what stage of plantation they examined, or pooled multiple stages together. Similarly, less than half of the studies examined the effects of alternative stand conditions or management regimes on biodiversity. Instead, most studies made simple comparisons between biodiversity in plantations versus other habitat types, despite the widespread recognition that forest structure and composition greatly influence the diversity and abundance of forest-associated species (Hartley, 2002, Lindenmayer et al., 2006).

Studies which examine specific habitat elements can help to explain the seemingly incongruent responses that even closely related species show to plantation establishment, as well as elucidate the underlying drivers of species responses. For example, in a study comparing habitat use by four carnivores in pine plantations and native forests, Zúñiga et al. (2009) found suggestive evidence for *Leopardus guigna* preferring forests over plantations. However, since the study only compared plantations and native forest, and not any specific habitat variables, they had no data to explain the potential association between *L. guigna* and native forest. In contrast, Moreira-Arce et al. (2016) studied habitat use in response to fine-grain habitat structure in both plantations and native forest. They found that *L. guigna* increased in abundance with understory cover regardless of habitat type and only showed a small preference for native forest *per se*. To facilitate translation of research into policy, future studies should evaluate the effects of specific silvicultural treatments on both forest structure and composition, and biodiversity outcomes.

To better inform plantation management for biodiversity, future studies should address six key knowledge gaps:

(1) More comparative studies of *Eucalyptus* and pine plantations are needed to understand their differential impacts on biodiversity.
(2) Very few studies examine biodiversity in clear-cuts or young plantations, although clear-cuts likely elicit the most dramatic effects on forest species, and are the subject of much societal conflict.
(3) Almost no information exists on the effects of site preparation and

seedling planting decisions on biodiversity within Chilean plantations.

(4) Strong taxonomic biases make it difficult to draw general conclusions about the effects of plantations on Chilean biodiversity. Fish, reptiles, amphibians, and fungi are particularly underrepresented in the literature.
(5) Despite several studies examining species interactions, few studies address the ecosystem-wide implications of plantation-mediated changes in ecological processes, such as pollination, seed dispersal, disease transmission, herbivory, nutrient cycling, etc.
(6) Policymakers and conservation practitioners would benefit from the identification of critical thresholds (i.e. tipping points), such as the minimum amount of understory cover, legacy elements, or native forest cover required to maintain biodiversity in plantation landscapes.

6. Conclusions

Chile has experienced growing societal and environmental conflicts associated with plantation forestry in recent years, leading to numerous calls for a new forest management paradigm (Conget and Ávila, 2010; Reyes and Nelson, 2014; Salas et al., 2016). While previous authors advocated for a transition to plantations of native trees, species composition is only one aspect of plantation management that affects biodiversity outcomes. We argue instead for a comprehensive re-examination of current management practices and their role in biodiversity conservation.

Although plantations typically support fewer species than native forests, a growing body of research in Chile and throughout the world demonstrates that well managed plantations may support substantial biodiversity (Brockerhoff et al., 2008; Estades et al., 2012; Lindenmayer and Hobbs, 2004; Miller et al., 2009; O'Callaghan et al., 2017). Furthermore, there is mounting evidence that protected areas in and of themselves will be unable to reverse the current global biodiversity crisis, and that conservation within production landscapes is essential (Laurance et al., 2012; Lindenmayer and Franklin, 2002; Martínez-Ramos et al., 2016). Chile's remaining native forests are already severely fragmented, and existing protected areas alone are unlikely to preserve this region's unique biota (Smith-Ramírez, 2004). Applying silvicultural tools to meet conservation outcomes in plantations (i.e. opening the silvicultural toolbox) is a critical step towards conserving Chile's biodiversity.

Acknowledgements

Javier Simonetti and two anonymous reviewers provided helpful comments on the manuscript. Funding was provided by a Stanford Graduate Fellowship and NSF GRFP (both to TNM).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.05.028.

References

Acosta-Jamett, G., Simonetti, J.A., Bustamante, R.O., Dunstone, N., 2003. Metapopulation approach to assess survival of Oncifelis guigna in fragmented forests of central Chile: a theoretical model. Mastozoología Neotrop. 10, 217–229.
Acuña, M.P., Estades, C.F., 2011. Plantation clearcut size and the persistence of early-successional wildlife populations. Biol. Conserv. 144, 1577–1584. http://dx.doi.org/10.1016/j.biocon.2011.02.003.
Andersson, K., Lawrence, D., Zavaleta, J., Guariguata, M.R., 2016. More trees, more poverty? The socioeconomic effects of tree plantations in Chile, 2001–2011. Environ. Manage. 57, 123–136. http://dx.doi.org/10.1007/s00267-015-0594-x.
Ahora Noticias, 2017. Alcalde Sharp propone eliminar Eucaliptos de Valparaíso para evitar incendios. Ahora Noticias. 3 January 2017. < > (accessed 18 December 2017).
Aukema, J.E., Carey, A.B., 2008. Effects of Variable-Density Thinning on Understory Diversity and Heterogeneity in Young Douglas-fir Forests.
Barlow, J., Gardner, T.A., Araujo, I.S., Avila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C., Peres, C.A., 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc. Natl. Acad. Sci. 104, 18555–18560. http://dx.doi.org/10.1073/pnas.0703333104.
Becerra, P.I., Simonetti, J.A., 2013. Patterns of exotic species richness of different taxonomic groups in a fragmented landscape of central Chile. Bosque (Valdivia) 34, 11–12. http://dx.doi.org/10.4067/S0717-92002013000100006.
Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv. 17, 925–951. http://dx.doi.org/10.1007/s10531-008-9380-x.
Bunn, S.E., Arthington, A.H., 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environ. Manage. 30, 492–507. http://dx.doi.org/10.1007/s00267-002-2737-0.
Bustamante-Sánchez, M.A., Grez, A.A., Simonetti, J.A., 2004. Dung decomposition and associated beetles in a fragmented temperate forest. Rev. Chil. Hist. Nat. 77, 107–120. http://dx.doi.org/10.4067/S0716-078X2004000100009.
Cahall, R.E., Hayes, J.P., Betts, M.G., 2013. Will they come? Long-term response by forest birds to experimental thinning supports the "Field of Dreams" hypothesis. For. Ecol. Manage. 304, 137–149. http://dx.doi.org/10.1016/j.foreco.2013.04.042.
Carnus, J.-M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K., Walters, B., 2006. Planted forests and biodiversity. J. For. 104, 65–77.
Cerda, Y., Grez, A.A., Simonetti, J.A., 2015. The role of the understory on the abundance, movement and survival of Ceroglossus chilensis in pine plantations: an experimental test. J. Insect Conserv. 19, 119–127. http://dx.doi.org/10.1007/s10841-015-9752-y.
Chazdon, R.L., 2014. Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation. University of Chicago Press.
CONAF, 2017. Política Forestal 2015–2035: Protocol de Plantaciones Forestales.
Conget, C.F., Ávila, M.N., 2010. Hacia un nuevo Modelo Forestal en Chile. Rev. Bosque Nativ. 47, 25–35.
Demarais, S., Verschuyl, J.P., Roloff, G.J., Miller, D.A., Wigley, T.B., 2017. Tamm review: terrestrial vertebrate biodiversity and intensive forest management in the U.S. For. Ecol. Manage. 385, 308–330. http://dx.doi.org/10.1016/j.foreco.2016.10.006.
Díaz, I.A., Armesto, J.J., Reid, S., Sieving, K.E., Willson, M.F., 2005. Linking forest structure and composition: avian diversity in successional forests of Chiloé Island. Chile. Biol. Conserv. 123, 91–101.
Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the anthropocene. Science 345, 401–406. http://dx.doi.org/10.1126/science.1251817.
Echeverria, C., Coomes, D., Salas, J., Rey-Benayas, J.M., Lara, A., Newton, A., 2006. Rapid deforestation and fragmentation of Chilean Temperate Forests. Biol. Conserv. 130, 481–494. http://dx.doi.org/10.1016/j.biocon.2006.01.017.
Escobar, M.A.H., Uribe, S.V., Chiappe, R., Estades, C.F., Schlatter, K., Trenkamp, L., 2015. Effect of clearcutting operations on the survival rate of a small mammal. PLoS One 10, e0118883. http://dx.doi.org/10.1371/journal.pone.0118883.
Estades, C.F., Escobar, M.A.H., 2005. Los ecosistemas de las plantaciones de pino de la Cordillera de la Costa. In: Smith-Ramírez, C., Armesto, J.J., Valdovinos, C. (Eds.), Historia, Biodiversidad Y Ecologia de Los Bosques de La Cordillera de La Costa. Editorial Universitaria, pp. 600–616.
Estades, C.F., Grez, A.A., Simonetti, J.A., 2012. Biodiversity in Monterrey pine plantations. In: Simonetti, J.A., Grez, A.A., Estades, C.F. (Eds.), Biodiversity Conservation in Agroforestry Landscapes: Challenges and Opportunities. Editorial Universitaria, pp. 77–98.
Estades, C.F., Temple, S.A., 1999. Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine. Source Ecol. Appl. 9, 573–585.
Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515. http://dx.doi.org/10.1146/annurev.ecolsys.34.011802.132419.
Fajardo, A., de Graaf, R., 2004. Tree dynamics in canopy gaps in old-growth forests of Nothofagus pumilio in Southern Chile. Plant Ecol. (formerly Veg. 173, 95–105). 10.1023/B:VEGE.0000026333.54741.97.
FAO, 2015. Global Forest Resources Assessment 2015. Rome.
Farley, K.A., Jobbágy, E.G., Jackson, R.B., 2005. Effects of afforestation on water yield: a global synthesis with implications for policy. Glob. Chang. Biol. 11, 1565–1576. http://dx.doi.org/10.1111/j.1365-2486.2005.01011.x.
Fierro, P., Quilodrán, L., Bertrán, C., Arismendi, I., Tapia, J., Peña-Cortés, F., Hauenstein, E., Arriagada, R., Fernández, E., Vargas-Chacoff, L., 2016. Rainbow Trout diets and macroinvertebrates assemblages responses from watersheds dominated by native and exotic plantations. Ecol. Ind. 60, 655–667. http://dx.doi.org/10.1016/j.ecolind.2015.08.018.
Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P.F., Phalan, B., 2008. How will oil palm expansion affect biodiversity? Trends Ecol. Evol. 23, 538–545. http://dx.doi.org/10.1016/J.TREE.2008.06.012.
Fontúrbel, F.E., Silva-Rodríguez, E.A., Cárdenas, N.H., Jiménez, J.E., 2009. Spatial ecology of monito del monte (Dromiciops gliroides) in a fragmented landscape of southern Chile. Mamm. Biol. 75, 1–9. http://dx.doi.org/10.1016/j.mambio.2009.08.004.
Frank, D., Finckh, M., 1997. Impactos de las plantaciones de pino oregón sobre la vegetación y el suelo en la zona centro-sur de Chile Impact of Douglas-fir plantations on vegetation and soil m south-central Chile. Rev. Chil. Hist. Nat. 70, 191–211.
González, M.E., Lara, A., Gómez, S., 2017. Plantaciones de eucaliptos, pinos y aromos en Valparaíso: una sociedad pirófila de responsabilidad (i)limitada. El Mostrador, 7 January 2017. < http://www.elmostrador.cl/noticias/opinion/2017/01/07/

plantaciones-de-eucaliptos-pinos-y-aromos-en-valparaiso-una-sociedad-pirofila-de-responsabilidad-ilimitada/ > (accessed 18 December 2017).
Gómez, P., Hahn, S., San Martín, J., 2009. Estructura y composición florística de un matorral bajo plantaciones de Pinus radiata D Don en Chile central. Gayana. Botánica 66, 256–268. http://dx.doi.org/10.4067/S0717-66432009000200010.
Gustafsson, L., Kouki, J., Sverdrup-Thygeson, A., 2010. Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences. Scand. J. For. Res. 25, 295–308. http://dx.doi.org/10.1080/02827581.2010.497495.
Hartley, M.J., 2002. Rationale and methods for conserving biodiversity in plantation forests. For. Ecol. Manage. 155, 81–95. http://dx.doi.org/10.1016/S0378-1127(01)00549-7.
Hébert, F., Krause, C., Plourde, P.-Y., Achim, A., Prégent, G., Ménétrier, J., 2016. Effect of tree spacing on tree level volume growth, morphology, and wood properties in a 25-year-old Pinus banksiana plantation in the boreal forest of Quebec. Forests 7, 276. http://dx.doi.org/10.3390/f7110276.
Heilmayr, R., Echeverría, C., Fuentes, R., Lambin, E.F., 2016. A plantation-dominated forest transition in Chile. Appl. Geogr. 75, 71–82. http://dx.doi.org/10.1016/j.apgeog.2016.07.014.
Heinrichs, S., Pauchard, A., 2015. Struggling to maintain native plant diversity in a peri-urban reserve surrounded by a highly anthropogenic matrix. Biodivers. Conserv. 10.1007/s10531-015-0964-y.
Heinrichs, S., Stiehl, C., Müller-Using, B., 2016. Can native plant species be preserved in an anthropogenic forest landscape dominated by aliens? A case study from Mediterranean Chile. Ann. For. Res. 59, 1. http://dx.doi.org/10.15287/afr.2016.498.
INFOR, 2016. Anuario Forestal 2016: Chilean Statistical Yearbook of Forestry.
Keenan, R.J., Reams, G.A., Achard, F., De Freitas, J.V., Grainger, A., Lindquist, E., 2015. Dynamics of global forest area: results from the FAO Global Forest Resources. Assessment. http://dx.doi.org/10.1016/j.foreco.2015.06.014.
Kogan, M., Figueroa, R., Gilabert, H., 2002. Weed control intensity effects on young radiata pine growth. Crop Prot. 21, 253–257.
Kozak, P., 2017. Did Pinochet-era deregulation cause Chile's worst-ever wildfires? The Guardian. 3 March 2017. < wildfires-forestry-industry-plantations > (accessed 18 December 2017).
Lander, T.A., Bebber, D.P., Choy, C.T.L., Harris, S.A., Boshier, D.H., 2011. The Circe principle explains how resource-rich land can waylay pollinators in fragmented landscapes. Curr. Biol. http://dx.doi.org/10.1016/j.cub.2011.06.045.
Lantschner, M.V., Rusch, V., Hayes, J.P., 2011. Influences of pine plantations on small mammal assemblages of the Patagonian forest-steppe ecotone. Mammalia 75, 249–255. http://dx.doi.org/10.1515/MAMM.2011.031.
Lara, A., Little, C., Urrutia, R., McPhee, J., Álvarez-Garretón, C., Oyarzún, C., Soto, D., Donoso, P., Nahuelhual, L., Pino, M., Arismendi, I., 2009. Assessment of ecosystem services as an opportunity for the conservation and management of native forests in Chile. For. Ecol. Manage. 258, 415–424. http://dx.doi.org/10.1016/j.foreco.2009.01.004.
Laurance, W.F., et al., 2012. Averting biodiversity collapse in tropical forest protected areas. Nature 489, 290–294. http://dx.doi.org/10.1038/nature11318.
Lee, P., Smyth, C., Boutin, S., 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. J. Environ. Manage. 70, 165–180. http://dx.doi.org/10.1016/j.jenvman.2003.11.009.
Lees, A.C., Peres, C.A., 2008. Conservation value of remnant riparian forest corridors of varying quality for amazonian birds and mammals. Conserv. Biol. 22, 439–449. http://dx.doi.org/10.1111/j.1523-1739.2007.00870.x.
Lindenmayer, D., Franklin, J.F., 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press.
Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006a. General management principles and a checklist of strategies to guide forest biodiversity conservation. doi:10.1016/j.biocon.2006.02.019.
Lindenmayer, D.B., Hobbs, R.J., 2004. Fauna conservation in Australian plantation forests – a review. Biol. Conserv. 119, 151–168. http://dx.doi.org/10.1016/j.biocon.2003.10.028.
Little, C., Cuevas, J.G., Lara, A., Pino, M., Schoenholtz, S., 2015. Buffer effects of streamside native forests on water provision in watersheds dominated by exotic forest plantations. Ecohydrology 8, 1205–1217. http://dx.doi.org/10.1002/eco.1575.
Little, C., Lara, A., McPhee, J., Urrutia, R., 2009. Revealing the impact of forest exotic plantations on water yield in large scale watersheds in South-Central Chile. J. Hydrol. 374, 162–170. http://dx.doi.org/10.1016/j.jhydrol.2009.06.011.
Magrach, A., Larrinaga, A.R., Santamaría, L., 2012. Effects of matrix characteristics and interpatch distance on functional connectivity in fragmented temperate rainforests. Conserv. Biol. 26, 238–247. http://dx.doi.org/10.1111/j.1523-1739.2011.01818.x.
Martínez-Ramos, M., Ortiz-Rodríguez, I.A., Piñero, D., Dirzo, R., Sarukhán, J., 2016. Anthropogenic disturbances jeopardize biodiversity conservation within tropical rainforest reserves. Proc. Natl. Acad. Sci. USA 113, 5323–5328. http://dx.doi.org/10.1073/pnas.1602893113.
McComb, W.C., 2001. Management of within-stand features in forested habitats. In: Johnson, D.H., O'Neill, T.A. (Eds.), Wildlife Habitat Relationships in Oregon and Washington. OSU Press, Covallis, Oregon.
Meynard, C.N., Soto-Gamboa, M., Heady, P.A., Frick, W.F., 2014. Bats of the Chilean temperate rainforest: patterns of landscape use in a mosaic of native forests, eucalyptus plantations and grasslands within a South American biodiversity hotspot. Biodivers. Conserv. 23, 1949–1963. http://dx.doi.org/10.1007/s10531-014-0697-3.
Miller, D.A., Wigley, T.B., Miller, K.V., 2009. Managed forests and conservation of terrestrial biodiversity in the Southern United States. J. For. 107, 197–203.
Moreira-Arce, D., Vergara, P.M., Boutin, S., Carrasco, G., Briones, R., Soto, G.E., Jiménez, J.E., 2016. Mesocarnivores respond to fine-grain habitat structure in a mosaic landscape comprised by commercial forest plantations in southern Chile. For. Ecol. Manage. 369, 135–143. http://dx.doi.org/10.1016/j.foreco.2016.03.024.
Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403.
Niklitschek, M.E., 2007. Trade liberalization and land use changes: explaining the expansion of afforested land in Chile. For. Sci. 53, 385–394.
O'Callaghan, C.J., Irwin, S., Byrne, K.A., O'Halloran, J., 2017. The role of planted forests in the provision of habitat: an Irish perspective. Biodivers. Conserv. 26, 3103–3124. 10.1007/s10531-016-1125-7.
Oxbrough, A., French, V., Irwin, S., Kelly, T.C., Smiddy, P., O 'halloran, J., 2012. Can mixed species stands enhance arthropod diversity in plantation forests? For. Ecol. Manage. 270, 11–18. 10.1016/j.foreco.2012.01.006.
Paquette, A., Messier, C., 2010. The role of plantations in managing the world's forests in the Anthropocene. Front. Ecol. Environ. 8, 27–34. http://dx.doi.org/10.1890/080116.
Pawson, S.M., Brockerhoff, E.G., Norton, D.A., Didham, R.K., 2006. Clear-fell harvest impacts on biodiversity: past research and the search for harvest size thresholds. Can. J. For. Res. 36, 1035–1046. http://dx.doi.org/10.1139/X05-304.
Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. Scenarios for global biodiversity in the 21st century. Science 330, 1496–1501. http://dx.doi.org/10.1126/science.1196624.
Perera, A.H., Buse, L.J., Weber, M.G., 2004. Emulating Natural Forest Landscape Disturbances: Concepts and Applications. Columbia University Press, New York.
Pérez-Hernández, C.G., Vergara, P.M., Saura, S., Hernández, J., 2015. Do corridors promote connectivity for bird-dispersed trees? The case of Persea lingue in Chilean fragmented landscapes. Landsc. Ecol. 30, 77–90. http://dx.doi.org/10.1007/s10980-014-0111-2.
Poch, T.J., Simonetti, J.A., 2013. Insectivory in Pinus radiata plantations with different degree of structural complexity. For. Ecol. Manage. 304, 132–136. http://dx.doi.org/10.1016/j.foreco.2013.04.044.
Ramirez-Collio, K., Vergara, P.M., Simonetti, J.A., 2017. Converting clear cutting into a less hostile habitat: the importance of understory for the abundance and movement of the Chestnut-throated Huet-Huet (Pteroptochos castaneus: Rhinocryptidae). For. Ecol. Manage. 384, 279–286. http://dx.doi.org/10.1016/j.foreco.2016.11.005.
Ramirez-Collio, K., Vergara, P.M., Simonetti, J.A., 2017. Converting clear cutting into a less hostile habitat: the importance of understory for the abundance and movement of the Chestnut-throated Huet-Huet (Pteroptochos castaneus: Rhinocryptidae). For. Ecol. Manage. 384, 279–286. http://dx.doi.org/10.1016/j.foreco.2016.11.005.
Ramírez, C., Figueroa, H., Carrillo, R., Contreras, D., 1984. Estudio fitosociológico de los estratos inferiores en un bosque de pino. Valdivia, Chile.
Reyes, R., Nelson, H., 2014. A tale of two forests: why forests and forest conflicts are both growing in Chile. Int. For. Rev. 16, 379–388. http://dx.doi.org/10.1505/146554814813484121.
Rodríguez-San Pedro, A., Simonetti, J.A., 2015. The relative influence of forest loss and fragmentation on insectivorous bats: does the type of matrix matter? Landsc. Ecol. 10.1007/s10980-015-0213-5.
Rubio, A.V., Simonetti, J.A., 2011. Lizard assemblages in a fragmented landscape of central Chile. Eur. J. Wildl. Res. 57, 195–199. http://dx.doi.org/10.1007/s10344-010-0434-5.
Saavedra, B., Simonetti, J.A., 2005. Small mammals of Maulino forest remnants, a vanishing ecosystem of south-central Chile. Mammalia 69, 3–4.
Salas, C., Donoso, P.J., Vargas, R., Arriagada, C.A., Pedraza, R., Soto, D.P., 2016. The forest sector in Chile: an overview and current challenges. J. For. 114, 562–571. http://dx.doi.org/10.5849/jof.14-062.
Salazar, D.A., Fontúrbel, F.E., 2016. Beyond habitat structure: landscape heterogeneity explains the monito del monte (Dromiciops gliroides) occurrence and behavior at habitats dominated by exotic trees. Integr. Zool. 11, 413–421. http://dx.doi.org/10.1111/1749-4877.12198.
Scott, D.F., Prinsloo, F.W., 2008. Longer-term effects of pine and eucalypt plantations on streamflow. Water Resour. Res. 44. http://dx.doi.org/10.1029/2007WR006781.
Simonetti, J.A., Grez, A.A., Estades, C.F., 2013. Providing habitat for native mammals through understory enhancement in forestry plantations. Conserv. Biol. 27, 1117–1121. http://dx.doi.org/10.1111/cobi.12129.
Smith-Ramírez, C., 2004. The Chilean coastal range: a vanishing center of biodiversity and endemism in South American temperate rainforest. Biodivers. Conserv. 13, 373–393.
Sweeney, O.F.M., Wilson, M.W., Irwin, S., Kelly, T.C., O 'halloran, J., 2010. The influence of a native tree species mix component on bird communities in non-native coniferous plantations in Ireland. Bird Study 57, 483–494.
Tomasevic, J.A., Estades, C.F., 2008. Effects of the structure of pine plantations on their "softness" as barriers for ground-dwelling forest birds in south-central Chile. For. Ecol. Manage. 255, 810–816. http://dx.doi.org/10.1016/j.foreco.2007.09.073.
Úbeda, X., Sarricolea, P., 2016. Wildfires in Chile: a review. Glob. Planet. Change 146, 152–161. http://dx.doi.org/10.1016/j.gloplacha.2016.10.004.
Uribe, S.V., Estades, C.F., 2014. Reptiles in Monterey pine plantations of the Coastal Range of Central Chile. Rev. Chil. Hist. Nat. 87, 25. http://dx.doi.org/10.1016/S0378-1127(01)00692-2.
Valdivia, C.E., Simonetti, J.A., 2006. Decreased frugivory and seed germination rate do not reduce seedling recruitment rates of Aristotelia chilensis in a fragmented forest. 10.1007/s10531-006-9007-z.
Valdivia, C.E., Simonetti, J.A., Henr Quez, C.A., 2006. Depressed pollination of Lapageria rosea Ruiz et Pav. (Philesiaceae) in the fragmented temperate rainforest of southern South America. Biodivers. Conserv. 16, 1845–1856. http://dx.doi.org/10.1007/s10531-004-6683-4.
Vergara, P.M., Pérez-Hernández, C.G., Hahn, I.J., Jiménez, J.E., 2013. Matrix

composition and corridor function for austral thrushes in a fragmented temperate forest. Landsc. Ecol. 28, 121–133. http://dx.doi.org/10.1007/s10980-012-9821-5.
Vergara, P.M., Simonetti, J.A., 2006. Abundance and movement of understory birds in a maulino forest fragmented by pine plantations. Biodivers. Conserv. 15, 3937–3947. http://dx.doi.org/10.1007/s10531-005-2355-2.
Vergara, P.M., Simonetti, J.A., 2004. Avian responses to fragmentation of the Maulino Forest in central Chile. Oryx 38, 383–388. http://dx.doi.org/10.1017/S0030605304000742.
Vergara, P.M., Simonetti, J.A., 2003. Forest fragmentation and rhinocryptid nest predation in central Chile. Acta Oecol. 24, 285–288. http://dx.doi.org/10.1016/j.actao.2003.09.006.
Vidal, M., Díaz-Páez, H., 2012. Biogeography of Chilean Herpetofauna: biodiversity hotspot and extinction risk. In: Stevens, L. (Ed.), Global Advances in Biogeography. InTech. 10.5772/31255.
Wimberly, M.C., 2006. Species dynamics in disturbed landscapes: when does a shifting habitat mosaic enhance connectivity? Landsc. Ecol. 21, 35–46. http://dx.doi.org/10.1007/s10980-005-7757-8.
Zúñiga, A., Muñoz-Pedreros, A., Fierro, A., 2009. Uso de habitat de cuatro carnívoros terrestres en el sur de Chile. Gayana (Concepción) 73, 200–210. http://dx.doi.org/10.4067/S0717-65382009000200004.