

AN ABSTRACT OF THE THESIS OF

Daniel P. Soto for the degree of Doctor of Philosophy in Forest Ecosystems and Society presented on May 19, 2017.

Title: Recovery of High-graded *Nothofagus* Forests: Building Resilience Through Theory and Practice.

Abstract approved:

Klaus J. Puettmann

The increasing human demands on natural resources, in combination with uncertainties about ecosystem dynamics due to global change, has led the scientific community to conclude that new approaches in understanding of ecological systems are needed to tackle environmental issues in an efficient manner. One development that has received more attention globally is high-grading forests by removing only valuable trees with little attention paid to tree regeneration. In several forest regions, this practice has become widespread and can trigger the development of aggressive and recalcitrant understory vegetation. In these cases, successional progression stagnates or is “arrested” and many ecosystem processes typically associated with successional development stall as well or only act at reduced levels, leading to lower provision of desired ecosystem services.

In this dissertation, I present the results of three research studies based in high-graded *Nothofagus* forests in south-central Chile. In chapter 1, I developed a

conceptual framework by integrating ecological theories to provide a comprehensive understanding of ecosystem dynamics after disturbances and therefore for restoration practices focused on forests with arrested succession. Second, I evaluated the effectiveness of restoration activities (i.e., topsoil removal through scarification) to overcome and move the forest from the arrested succession condition toward a more standard or desirable (in terms of higher provision of ecosystem services) successional development. The last chapter evaluates how this restoration practice influences the seedling growth of different species, and thereby the potential successional development of these regenerating forests.

The integration of successional theory and properties of adaptive cycle phases and traps (i.e., potential, connectedness and resilience) with multiple equilibrium models offers an understanding of why ecosystems may remain in one basin of attraction or move into another basin. This knowledge provides a theoretical foundation for management practices aimed at pushing ecosystems over a threshold from an undesirable basin of attraction (i.e., arrested succession) to a more desirable basin, in which ecosystems transition to more diverse and productive forest ecosystems.

The field studies showed that ground disturbance was an effective management approach to overcome arrested succession, i.e., manipulating understory vegetation and to encourage tree regeneration, that is expected to facilitate the successional development of these forest ecosystems. This study provided insights into the relative importance of different biotic and abiotic environmental conditions

that lead to arrested succession after high-grading, and how ground disturbance alters these conditions and leads to successional development.

Growth of species established in the understory after ground disturbance were strongly related to light and nitrogen levels, suggesting that the interaction of these factors may influence successional trajectories. Thus, understanding the traits of undesirable and desirable vegetation in terms of their resources needs is key to designing restoration treatments. Such treatments can be specifically designed to alter resource levels to favor desirable species.

Collectively, these chapters contribute to the understanding of factors responsible for temperate rainforest ecosystems exhibiting arrested succession and how to overcome such conditions. Furthermore, the chapters provide more general insights into ecosystem dynamics that can be used to promote ecologically based management practices that are grounded in ecological theories in general.

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Recovery of high-graded *Nothofagus* forests: Building Resilience Through Theory
and Practice

by

Daniel P. Soto

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Daniel P. Soto, Author

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DEDICATION

To my parents, Carlos and Teresa.

To my sister, Yanela.

and



To my son, Gabriel... child in which I have high hopes for a better world with greater respect to our environment and its people.

RECOVERY OF HIGH-GRADED *NOTHOFAGUS* FORESTS: BUILDING RESILIENCE THROUGH THEORY AND PRACTICE

Chapter 1

General introduction

Forest successional dynamics can be unpredictable and complex due to variations in frequency and severity of disturbances, stochastic events, non-linear ecological interactions, and feedbacks (Suding et al., 2004). Ecological studies have documented how disturbances influence successional trajectories (Pickett et al., 2008 and citations therein). The outcomes of small- and large-scale disturbances can be anticipated in general terms of species composition and structure (Walker and del Moral, 2009). However, partial disturbances may be more unpredictable in terms of successional dynamics because of the influence of structural and compositional legacies (e.g., understory vegetation) that can lead to unexpected trajectories (Franklin and MacMahon, 2000; Suding et al., 2004; Walke and del Moral, 2009).

One partial disturbance that may not follow the typical succession trajectory is forest degradation (Lamb et al., 2005; Chazdon, 2008). Forest degradation (i.e., anthropogenic disturbance that induced arrested succession, sensu Ghazoul et al., 2015) has been documented as an important contributor of land degradation and global changes through emissions of carbon dioxide and dramatic losses of productivity and

biodiversity (Nepstad et al., 1999), mostly in developing countries (UNEP, 2007; FAO, 2010). Forests become degraded through different mechanisms, including species invasions, drainage of bog forests and peatlands, soil compaction, nutrient depletion, overgrazing or harvesting, such as high-grading (FAO, 2010). High-grading (sensu Nyland, 2005) can change a forest into a degraded state (Lamb and Gilmour, 2003; Chazdon, 2008). High-grading harvests only remove trees with superior timber attributes, with little attention paid to the remaining stand and tree regeneration (Lamb and Gilmour, 2003). Depending on the severity, this management can leave the forests in a condition that provides limited ecosystem services with a low diversity, and with low expected long-term economic returns (Lu and Buongiorno, 1993).

An outcome of high-grading can be the proliferation of dense thickets of understory vegetation, which prevent tree establishment and may arrest forest succession for extended periods of time (Royo and Carson, 2005 and citations therein). A forest with arrested succession due to the dominance of a “recalcitrant” understory vegetation is an example of a degraded forest, where many processes and functions that underlie the successional dynamics are dramatically reduced (Ghazoul et al., 2015). Concerns about ecological and economic implications of arrested succession have been increasing over the last decades (Royo and Carson, 2006; Ghazoul et al., 2015). Arrested succession condition could be seen as an opportunity to investigate restoration in the context of ecological theories to gain a better theoretical basis for this practice in terms of its impact on ecological processes. At the

same time, empirical studies of restoration may help refine ecological theories (Falk et al., 2006).

High-grading is a prominent regional issue in temperate rainforests of south-central Chile, where such partial overstory disturbances commonly result in dense thickets of native bamboo species (*Chusquea* spp.) in the understory (Fig. 1.1 B), that prevent establishment of trees (Veblen, 1982; González et al., 2002). Typically, bamboo can dominate a site 70-120 years until it flowers and dies. The death of bamboo creates a very short window for tree regeneration because bamboo can reestablish and grow (Veblen, 1982; González et al., 2002). A large area of degraded forest in southe-central Chile has been influenced by high-grading and bamboo growth (Donoso and Soto, 2010; Reyes et al., 2013; Zamorano-Elgueta et al., 2014; Soto et al., 2015). Thus, large area of degraded forests are characterized by damaged and low-vigor trees in the overstory and with a recalcitrant thicket of bamboo in the understory that limits regeneration of *Nothofagus* and other late-seral tree species (Fig. 1.1 C) (Reyes et al., 2013; Soto et al., 2015).

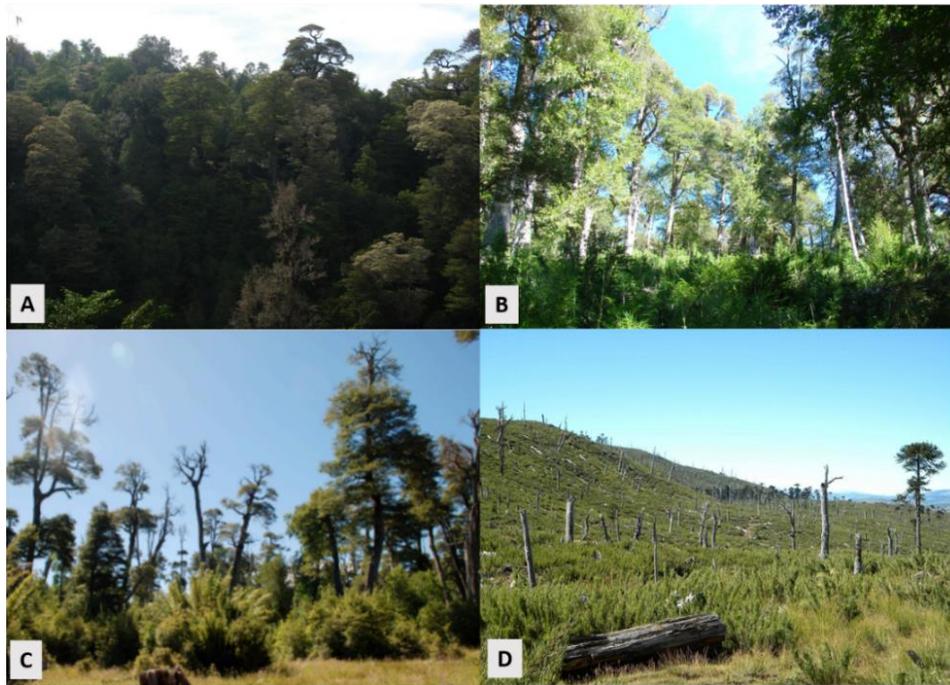


Fig. 1. Photos (A-C) depicting conditions of forest degradation due to high-grading in the temperate rainforests of south-central Chile. Photo A shows the pre-disturbed conditions (*Nothofagus*-dominated old-growth forest). Photo B shows the condition after partial overstory disturbance, e.g., gap creation and subsequent dominance of *Chusquea* spp. with a scattered presence of natural regeneration in understory. Photo C shows severe high-grading, where remnant trees show dieback and consolidated understory tickets of bamboo have established (note this condition is considered arrested succession in this study). Photo D shows an extreme condition where the system is deforested after severe and frequent high-grading operations, and additional disturbances such as cattle grazing and fire in *Araucaria*-*Nothofagus* dominated forests in South-Central Chile. Note the dominance of bamboo ca. 50 years since last disturbance (Photo credits: A-C, Daniel Soto and D, Rodrigo Mujica).

In response to concerns about such forest conditions, restorationists and forest managers have started to mimic natural disturbance patterns (i.e. large scale disturbances such as fire, landslides, massive treefalls) to encourage regeneration of early-seral tree species, i.e., species that initiate and encourage more “typical” succession patterns towards late-successional conditions. These managed disturbances that promote regeneration of early-seral regeneration are accomplished by reducing the competitive understory vegetation and exposing mineral soil (Reyes et al., 2013; Soto et al., 2015). Specifically, ground disturbance conducted with heavy machinery (i.e., bulldozer) has been used to remove the upper forest floor and create conditions that reduce bamboo cover, and promote regeneration of *Nothofagus* spp. (Reyes et al., 2013; Soto et al., 2014, 2015) (Fig. 1.2 B). This treatment has the goals of 1) controlling dense thickets of bamboo, removing the roots of bamboo (that could re-sprout) and the dense litter layer dominated by leaves of this species, 2) exposing the mineral soil to act as safe sites for germination and establishment for *Nothofagus* spp., and 3) create open areas for underplanting of desired tree species when seed source is lacking (Reyes et al., 2013). This practice leads to highly variable conditions, as the extent and patterns of the ground disturbance is determined by the spatial patterns of the residual trees, downed wood and snags (Soto et al., 2014) (Fig. 1.2 C). Despite widespread global application of ground disturbance as a regeneration management tool (Zaczek, 2002; Karlsson and Örlander, 2000; Hille and den Ouden, 2004; Yoshida et al., 2005; Löff et al., 2012), few studies in temperate rainforests in young forest soils

(i.e., Andisols and Inceptisols) have been conducted and all have been focussed on the success of underplanted seedlings (Reyes et al., 2013; Soto et al., 2014, 2015).



Fig. 2. Photos depicting (A-D) conditions for recovery of high graded *Nothofagus*-dominated forests in South-Central Chilean Andes. Photo A shows the pre-restoration treatment condition where a dense thicket of bamboo dominate the forest. Photo B shows the top-soil removal by heavy machinery as restoration tool. Photo C shows post-treatment conditions where bamboo was removed and mineral soil exposed. Photo D shows regeneration eight years since the restoration treatment was applied. Note left-bottom corner in D shows regeneration of desirable *Nothofagus* spp. in treated soil and upper-right corner a dense “wall” of bamboo in untreated soil (Photo credits: A, C Victor Gerding, B <http://forest.fsc.hokudai.ac.jp>, and D Daniel Soto).

The goal of this dissertation is to provide a better understanding of ecosystem dynamics in these forests, with specific focus on arrested succession. The dissertation starts with a development of a theoretical framework about ecosystem dynamics and its implications on restoration, focused on arrested succession (chapter 2). Second, I evaluate the effectiveness of a ground disturbance as a restoration treatment. Specifically, I assessed how such treatment removes undesirable vegetation that lead to arrested succession and how this treatment allows regeneration of desirable tree species that promote typical succession progression (chapter 3). Finally, I study how ground disturbance impacts the growth of selected species (with a range of traits) (chapter 4), with a special focus on restoration treatment impacts on resources as it relates to species traits. The knowledge about what biotic and abiotic variables should be altered is necessary for efficient application of restoration practices.

The high-graded *Nothofagus*-dominated forests in south-central Chile provided a worthy study object. The temperate rainforests of Chile are among 25 highest priority areas for the conservation of biodiversity in the world (Myers et al., 2000), due to their high level of endemism (ca. 50%) and to the dramatic reduction of their original area (ca. 70%) (Echeverria et al., 2006); this reduction in native forests has been considered similar to the reduction in area experienced by these forests during the last glaciation (Armesto et al., 1998). In addition, much of the remaining forests have been degraded due to lack of understanding of the forest functioning and/or narrow and short-term management goals (Lara et al., 2003). In these forests, the

forest degradation has been attributed mostly to high-grading, where the tree regeneration have been poorly reported in most of the forest assessed (Lara et al., 1996). This can be viewed as indicating a lack of resilience (in terms of maintaining tree cover and species composition, see photos in Figure 1), and it appears to be at least partially due to the expansion of native late-seral *Chusquea* spp. (bamboo species) in understories after harvestings (Fig. 1B-D, 2A).

This dissertation is divided in five chapters (including the present general introduction). Chapter two is a conceptual framework, where I integrate successional theory, adaptive cycle and ecological traps into multiple equilibrium models using the metaphor of basins of attraction. This framework can provide important insights into why ecosystems remain in stable states, and this knowledge can be used to implement efficient restoration practices to move ecosystems from an undesirable basin of attraction (e.g., arrested succession) to a basin that leads to more desirable ecosystem development.

Chapter three investigates the effectiveness of ground disturbance on: a) control of undesirable understory vegetation considered mainly responsible for arrested succession (e.g., bamboo) and b) promotion of safe sites for regeneration of key species for successional development. This study unveils what conditions are responsible for the high abundance of bamboo and which conditions promote tree regeneration. This information can guide practitioners seeking to used topsoil removal through scarification as a restoration practice (this work is under review in *Journal of Applied Ecology*, Soto and Puettmann 2017).

Chapter four quantifies plant growth as a function of resource levels (i.e. light + nitrogen + water + interaction of nitrogen and water) after partial disturbances (overstory and ground disturbances). I selected three distinct species in terms of resource use and their role in successional development. I used a modified version of the non-linear Michealis-Menten equation that incorporates effects of resources (single or interactions). This study provides information on how these different species respond to different levels of resource availabilities. In this context, efficient restoration treatments are based on information about species traits, specifically sensitivities to resources availabilities in conjunction with information about the impact of disturbances and restoration practices on resource levels (this work was published in *Forest Ecology and Management*, Soto et al., 2017).

The last chapter is the general conclusion of this dissertation. It provides a comprehensive integration of the knowledge gained with the aim of providing ecologists, restorationists and forest managers a new perspective to tackle important and complex environmental issues.

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Chapter 2

LINKING SUCCESSION AND MULTIPLE EQUILIBRIUM MODELS: INSIGHTS TO OVERCOME ARRESTED SUCCESSION IN FOREST RESTORATION

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Abstract

In forest restoration, successional theory provides important information about potential trajectories that forest communities may take after disturbances. Arrested succession, mostly due to a dominant recalcitrant understory vegetation layers that prevent successional development is less common than succession after large- and small-scale disturbances, but requires attentions as forest degradation is a prominent issue in many forest regions on the globe. We propose a unified framework that links successional theory with multiple equilibrium models. Using properties of the two phases of the adaptive cycle (for forests with successional progression) and ecological traps (for forests with arrested succession) provided important insights into designing restoration activities to overcome arrested succession and move the ecosystem over a threshold into desirable basin of attraction. Especially insightful are cycle and trap properties that define the shape of basins of attraction, e.g., connectedness (the rigidity of internal control) is influencing basin depths, and resilience (ability of the system to stay in basin of attraction) is influencing basin widths. In practical terms, our model suggests that restoration practices should be viewed as disturbances that modify connectedness (i.e. the rigidity of internal controls of ecosystems) and resilience (i.e. the ability of ecosystems to stay in the same basin of attraction after disturbances) through manipulation of species composition, enhancement or constraint of resources and provide proper microsite conditions, can deepen and widen a desirable basin of attraction or vice versa for undesirable one. We use restoration of degraded *Nothofagus*-dominated forests in the Andes of Chile as a real-world case study.

Introduction

Ecological systems are dynamic and rates of species turnover and successional direction are often strongly influenced by human activities and natural disturbances (Falk et al., 2006; Pickett et al., 2009). Human activities typically promote successional pathways that lead to desirable or undesirable states following disturbance (Suding et al., 2004). Outcomes of small- and large-scale disturbances can be anticipated in terms of species composition and structure in general terms (Walker and del Moral, 2009). However, specific successional dynamics may be unpredictable and complex due to spatial variation in disturbance intensity, random events, such as seed rain timing, non-linear ecological interactions and feedbacks (Hobbs and Norton, 1996; Suding et al., 2004).

An undesirable outcome after overstory disturbance can be the proliferation of dense thickets of understory vegetation, which can delay tree establishment and influence forest succession (George and Bazzaz, 1999; Royo and Carson, 2005). Such stable vegetation states may be undesirable and persistent over long periods of time (Mallik, 2003; Royo and Carson, 2005). This so-called arrested succession occurs when after selected disturbances, such as high-grading (i.e., selective harvesting), understory vegetation dominates the forest for multiple decades or longer and thus, stalls, delays or “arrests” succession by preventing typical turnover from early- to late-successional tree species (sensu Niering and Goodwin, 1974; George and Bazzaz, 1999; Mallik, 2003; Royo and Carson, 2006) (see global examples in Supporting Information; SI 1). Such lack of successional progression can be due to human and

natural disturbance (Royo and Carson, 2006) or plant invasion, of a combination of these factors (Tymen et al., 2016). Arrested succession has been defined as a type of forest degradation because ecosystems processes and functions that underlie successional dynamics have been dramatically reduced (Ghazoul et al., 2015).

In response to arrested succession, a common management strategy is to utilize restoration activities inspired by historical disturbance regimes (Walker and del Moral, 2009; Chazdon, 2014). Goals of such activities typically encourage desirable successional development that eventually leads to pre-disturbance vegetation conditions (Dobson et al., 1997; Falk et al., 2006). However, sometimes successional development after these activities does not follow the expected trajectory, producing inconsistent and sometimes unexpected results (Hobbs and Norton, 1996; Suding and Hobbs, 2009). Such unexpected results can be as a consequence of ignoring changes in biotic (e.g., proliferation of understory vegetation) and abiotic (e.g., limited or overabundant resources; such as light, nutrients and water) factors and their interactions, and feedbacks (e.g., high production of litter prevents germination of tree seeds) (Suding et al., 2004). In addition, many successional studies have been focused on the processes of tree regeneration, growth, mortality, and turnover with less attention paid to understory herbaceous and shrubby vegetation and its influence on successional progression (George and Bazzaz, 1999; Royo and Carson, 2006). Understory vegetation can play an important role in determining speed and direction of succession (George and Bazzaz, 1999; Mallik, 2003; Royo and Carson, 2006). Changes in forest conditions after disturbances, with subsequent extended dominance

of understory vegetation, i.e., arrested succession, can be viewed as an alternative stable state in the context of multiple equilibrium dynamics (Beisner et al., 2003; Suding et al., 2004).

Viewing arrested succession as an alternative stable state in the perspective of successional dynamics has not been studied and provides an opportunity to link practical restoration issues with ecological theory. It will allow to gain a better understanding of impacts of management practices on ecological processes and functions and will help refine and reconcile ecological theories as linked to applications (e.g., Falk et al., 2006). Particularly, in this study we describe arrested succession (Royo and Carson, 2006) in the context of multiple equilibrium dynamics (Scheffer et al., 2001), panarchy cycle, and trap theories (Gunderson and Holling, 2002). An integrated view of theories may improve the understanding of forest dynamics and provide guidelines for management to overcome arrested succession and redirect succession trajectories towards more desirable conditions, i.e., with higher provision of ecosystem goods and services.

Arrested succession examples worldwide

Examples of alternative successional trajectories have been documented in different forest ecosystems after partial disturbances, such as natural treefalls (Royo and Carson, 2006), or in management settings such as selective or shelterwood harvestings (Soto et al., 2015). Arrested succession after disturbance has been

documented due to dominance of bamboo species in mesic temperate rainforests in Chile (Veblen, 1982; González et al., 2002; Soto and Puettmann, 2017) and New Zealand (Rogers and Leathwick, 1997), in neotropical forests of Iguazu (Budke et al., 2010), tropical rainforests in Peru and Bolivia (Griscom and Ashton, 2003) and Amazonian forests in Brazil (Tymen et al., 2016), Atlantic forest in Brazil (Campanello et al., 2007), and in subalpine *Abies-Betula* forest in China (Taylor and Zisheng, 1992). Dwarf bamboo in cold temperate forests in Japan also has been reported to arrest succession (Yoshida et al., 2005). In addition, ferns also have been documented to be responsible for arrested succession in the northwestern Pennsylvania hardwoods (Royo and Carson, 2006), in Puerto Rico (Denslow et al., 1991), in southern Chile (Donoso and Nyland, 2005), in Hawaii (Russell et al., 1998) and in temperate forests in New Zealand (Coomes et al., 2003). Similarly, members of the Ericaceae family have been reported to interfere with successional dynamics in different forest types, such as Salal (*Gaultheria shallon*) in the temperate rain forest of the Pacific Northwest of the USA (Tappenier et al., 1991; Messier, 1993; Pabst and Spies, 1999), *Kalmia* spp. in the Eastern USA (Mallik, 2003), *Empetrum hermaphroditum* (Mallik, 2003) in the European boreal forests, and *Calluna vulgans* in western Europe (Mallik, 1995). Another example arrested succession is the long dominance of *Rubus* spp. in temperate forests the Pacific Northwest (Tappenier et al., 1991) and Europe (Schreiner et al., 2000). More detailed review of the issue can be found in Royo and Carson (2006).

Successional development in the context of arrested succession and restoration

Succession is viewed as forest development in time along trajectories of compositional change (Hobbs and Norton, 1996; Falk et al., 2006). We used four possible trajectory patterns (out of many possible ones; Suding and Gross, 2006) as examples to visually highlight the difference between typical successional patterns and less common arrested succession (Fig. 1). Convergent patterns include trajectories that differ initially but converge rather quickly (Fig. 1.1.) to typical late successional conditions (i.e. forests with multi-aged structure and multi-layered vertical stratification dominated mostly shade-tolerant tree species) (Fig. 1, y-axis label D). However, initial convergent trajectories could switch temporarily to divergent trajectories due to, for example, negative feedbacks. After the temporary divergence, the system could develop similar to the “typical” advanced successional stages if the system attributes are not modified enough in structure and composition (Fig. 1.2) (Suding and Gross, 2006). On the other hand, arrested succession shows divergent trajectories that never converge with the “typical” successional trajectories and are quite stable over time (Fig. 1.3). This condition never reaches an advanced successional stage or stable state or basin of attraction (i.e., a stable state of a system that tend to change towards to a particular attractor; Walker and Salt, 2012) characterized by late successional conditions (Fig. 1.3). However, the successional pathway can be changed through management activities that overcome arrested succession and shift the system towards a desirable succession trajectory (Fig. 1.4).

Regeneration as a prime process to overcome arrested succession

Given that overcoming arrested succession is difficult, we suggest that is convenient to invest more efforts in facilitating tree regeneration (Lamb et al., 2005; Chazdon, 2008; Ghazoul et al., 2015). In this sense, scientists and practitioners might put efforts in encouraging early- and late-seral tree regeneration (Lamb et al., 2005; Chazdon, 2008; Ghazoul et al., 2015), to encourage ecosystem development towards a more desirable successional trajectory (Ghazoul et al., 2015; Soto and Puettmann, 2017). For example, promoting early-seral tree regeneration might be one important restoration goal when succession is arrested (Ghazoul et al., 2015). Examples of practices aiming to achieve that goal include provision of physical space for germination (i.e., microsite conditions) or increasing resource availability (i.e., light, nutrients and water) for regeneration of desired tree species (Luken, 1990; Gray and Spies, 1997), and at the same time constraining space and resources for undesirable understory vegetation (Luken, 1990; Soto and Puettmann, 2017).

Regeneration is a complicated process as tree species establishment and subsequent growth are driven by a complex set of interacting factors and processes (Chase and Leibold, 2003; Grime, 2006). Consequently, plant traits play an important role in determining which successional trajectory an ecosystem takes. In this context, plants are often grouped based on similar plant traits for efficient research and management efforts (Pywell et al., 2003; Herault et al., 2005). For example, early- and late-seral species are characterized by traits (e.g. shade tolerances, leaf habits, crown shape, seed size, among others) that lead to different resources use, which can

determine successional dynamics especially when competition for resources is a major driver (Pywell et al., 2003; Herault et al., 2005).

In addition, a broader, dynamic view of traits through ontogeny appears more useful, because different factors act at “establishment” and various “growth” stages (see Schupp, 1995; Young et al., 2005; Boyden et al., 2009). Such ontogeny differences imply that the relative advantage of one species versus another may change over time, potentially making it very difficult to predict successional trends in any one place (e.g. Fig. 1).

Developing a restoration framework for overcoming arrested succession

Models of ecosystem dynamics to explain the alternative stable state in the context of arrested succession

We focused on multiple equilibrium models (Scheffer et al., 2001; Beisner et al., 2003; Suding et al., 2004) because they have a strong conceptual basis and allow for multiple successional trajectories, where the transitions from one stable state to another can be discontinuous (Scheffer et al., 2001; Beisner et al., 2003; Suding et al., 2004; Suding and Hobbs, 2009). Furthermore, these models can be integrated with successional theory, e.g., the trajectory of arrested succession can be expressed as a basin of attraction over time. The multiple-equilibrium model has been successfully

used to characterize ecosystem dynamics including regime shifts e.g., collapse of corals, fishery stocks, and transitions of forest ecosystems to degraded one or savannah (Scheffer et al., 2001; Suding and Hobbs, 2009, and citation therein).

The multiple equilibrium model describes multiple distinct states or basins of attraction and how ecosystems cross thresholds to move from one basin to another (Scheffer et al., 2001; Beisner et al., 2003). It is well suited to provide insights into ecosystem dynamics, especially in relation to arrested succession. For simplicity, we focus the discussion on two conditions. One “undesirable” condition which represents forests with arrested succession, and a second “desirable” which represents forests following “typical” successional progression towards late successional conditions. We also consider that arrested succession, as an example of an undesirable conditions because often leads people to consider restoration practices to recover the desirable ecosystem services (Lamb et al., 2005; Chazdon, 2008). In contrast, successional development towards desirable condition typically requires little or no management intervention (Lamb et al., 2005; Suding and Hobbs, 2009).

One important feature of this model is hysteresis, i.e. unstable state condition where two or more alternative states can persist in similar environments, e.g., similar climate and disturbance frequencies (Beisner et al., 2003; Suding and Hobbs, 2009) and thresholds have to be crossed to switch between these states (for further clarifications see examples in Scheffer et al., 2001; Beisner et al., 2003; Suding and Hobbs, 2009). In hysteresis, the switch between the stable states is often driven by interactions of variables acting at different spatial and time scales (Scheffer et al.,

2001; Suding et al., 2004). In this context, fast variables typically operate at small scales (e.g., herbivory or fertilization or soil drainage) and can change the forest composition very quickly (Suding and Gross, 2006), e.g., by encouraging and constraining the dominance of species or vegetation groups. In contrast, slow variables are ecosystem drivers, such as climate change (e.g. a year with sudden drought induces tree mortality, such as El Niño events; Holmgren et al., 2001), which can be highly influential on ecosystems in the long term or over larger spatial scales (Scheffer and Carpenter, 2003; Suding and Gross, 2006).

Properties of adaptive cycle phases and traps

Further insights into arrested succession can be drawn from the adaptive cycle model by Gunderson and Holling (2002), which separates ecosystem dynamics in four phases: exploitation, conservation, release, and reorganization. Three properties are defining features as ecosystem develop through the cycle (Table 1; Gunderson and Holling, 2002):

- (1) Potential: stored energy or biomass.
- (2) Connectedness: the rigidity of internal control of the ecosystem to external influences.
- (3) Resilience: the ability of ecosystems to react to disturbances while staying in the same basin of attraction.

The exploitation and conservation phases, are basically representing typical ecological successional dynamics. During these phases, forests gradually increase in

potential and connectedness, but decrease in resilience (Drever et al., 2006). This means that in early stages of succession ecosystems absorb disturbance without shifting to alternative stable state due to its high resilience. On the other hand, during the conservation phase, late successional forests are highly resistant due to high connectedness in absence of large-scale disturbances (Gunderson and Holling, 2002; Drever et al., 2006). For example, after small disturbances the forests typically fill in with late-seral tree species already present in the midstory and overstory, leading to minor changes in structure and composition (Carpenter and Brock, 2008; Puettmann, 2016). A more intense disturbance could initiate a major shift in structure and composition due to low resilience (Holling et al. 2002; Gunderson and Holling, 2002; Carpenter and Brock, 2008).

To understand arrested succession (undesirable condition), it is useful to additionally consider traps in the context of the adaptive cycle (Gunderson and Holling, 2002). Traps are defined as phases when ecosystem development is hindered for several possible reasons (see Holling et al., 2002). The relative importance of potential, connectedness, and resilience in three types of traps “poverty”, “rigidity”, and “lock-in trap” (Allison and Hobbs 2004) are presented in Table 1. Examples of ecosystems in a poverty trap characterized by low potential are landscapes with frequent disturbances that set back succession, free-up new resources repeatedly and thus prevent ecosystem development, e.g. open chaparral or grassland ecosystems that are stabilized through frequent fires. Some late successional forests can be viewed as a rigidity traps due to their high potential and connectedness (Carpenter and Brock,

2008; Puettmann, 2016). Forests with arrested succession with low potential (i.e., as consequence of natural or anthropogenic disturbances) and high connectedness and resilience can be considered a “lock-in trap” (sensu Allison and Hobbs, 2004). In this case, restoration activities should have the goal of overcoming the high connectedness and resilience.

Basin of attraction

Multiple equilibrium models can be easily represented using the metaphor of basin of attraction (Scheffer et al., 2001; Beisner et al., 2003). This metaphor leads to understand how a state is “attracted” to be stable in a bottom of a ball-and-cup landscape (Beisner et al., 2003; Walker and Salt, 2012). The ball remains fairly stable in the bottom of a cup if disturbances are absent or not sufficient to change ecosystem structure, functions and processes (Ghazoul et al., 2015). Disturbances move the ball throughout the cup’s landscape (Scheffer et al., 2001). For example, if a disturbance in a forest disrupt the ecosystem’s structure and composition and/or biotic and abiotic factors sufficiently, the ball may move to another cup in the landscape (Beisner et al., 2003). If a disturbance is not sufficiently intense to overcome the basin threshold or tipping point the ball will return to its pre-disturbance position through the natural processes of succession (Scheffer et al., 2001; Beisner et al., 2003). The stability of a basin of attraction is defined by two attributes: resilience and resistance. Resilience is represented by the horizontal distance between two summit of a basin of attraction (i.e., thresholds) which represent how much a system’ can change without losing its functioning and the capacity to re-organize after disturbance (Walker and Salt, 2012).

Resistance is reflected by the depth of the basin which represents the effort to switching to another state, or for example how much disturbance can cope a system without losing its capacity to re-organize (Walker and Salt, 2012; Ghazoul et al., 2015). As connectedness represent the rigidity of internal control of the ecosystem to external influences, so the depth of a basin can be seen as how much connections the system has to resist disturbance. Late successional forests are the typical example, which have low resilience and but are highly resistant to change due to their high connectedness.

Linking the multiple-equilibrium to the adaptive cycle, specifically in the context of trap characteristics provide a better understanding of ecosystem dynamics in relation to arrested succession as an example of a lock-in trap. In unmanaged systems, lock-in-traps are typically overcome by natural disturbances, such as large-scale disturbances that break the connectedness and thus allow the potential (biomass) to increase through successional development. Thus, it may be useful to view restoration activities with the same principles in mind. Similarly, linking the basin-of-attraction model to successional dynamics highlights that the static nature of the typical ball-and-cup display (e.g., only using time A in Figure 2) provides only limited insights. Instead, it appears more useful to view any ball-and-cup model as part of a landscape, where location, depth, and shape of a cup vary over time in relation to successional development (see Fig. 2.1). For simplicity, we depict only two basins of attraction along successional development in Figure 2. For example, in Figure 2, time A the black ball depicts a late successional forest stage. The deep and narrow basin of

attractions indicates high connectedness (i.e., deeper) and low resilience (i.e., narrow basin), respectively. That means, for example, that small scale or low severity disturbances do not lead to major changes in structure and composition. However, major disturbances, such as high-grading, can overcome the trap and move the system into a new basin of attraction (Fig. 2, time B, red ball). Displays C, D, and E differ between Figures 2.1, 2.2, and 2.3 reflecting three possible successional trajectories over time.

Figure 2.1 represents ecosystem that follows a typical successional development (see Fig. 1.1 or 1.2) leading to buildup of biomass (i.e, potential in this work) and thus moving in a basin of attraction that eventually leads to late-successional conditions (green balls). Figure 2.2 represents an example of an ecosystem that has moved from late successional state (time A) to another alternative stable state (time B), where high connectedness after the initial disturbances prevents development of potential along succession (Fig. 2.2 C-E, blue balls), i.e., an ecosystem that is undergoing arrested succession.

Figure 2.3. is an example how restoration activities can push an ecosystem out of a lock-in trap, i.e., how arrested succession that prevents ecosystem development (blue ball) can be overcome through restoration activities. These activities alter the basin shapes (see details in the next section) and thus move the system into a basin of attraction that leads to more desirable conditions, i.e., late-successional conditions that provide more desirable ecosystem services (white balls).

Modifying the basin shapes to overcome arrested succession state and encouraging succession progression

To move ecosystems out of an arrested succession stable state requires specific disturbances or restoration activities (Suding and Hobbs, 2009). For efficient restoration, such activities should be designed to effectively reduce the system stability by e.g., breaking down the connectedness (Allison and Hobbs, 2004) and erode resilience (Beisner et al., 2003; Ghazoul et al., 2015). Undesirable states can be overcome by 1) moving the ball through the basin of attraction landscape, and 2) by modifying the basin of attraction shape (see details in Beisner et al., 2003). Typically, disturbance moves the ball through the basin of attraction' landscape, because whole community components and variables have been modified (e.g. structure, composition, processes, and functions). For example, if the disturbance is intense enough it can switch from one state to another by moving the ball through the landscape of one basin of attraction to another, which could be the case of arrested succession after high-grading. Second, to modify the shape of a basin of attraction can be done through altering the species composition of a state (Ghazoul et al., 2015).

As was defined early, a basin of attraction' shape is defined by connectedness (depth) and resilience (width). First, one can erode or enhance the connectedness of a basin of attraction by altering the resources (e.g., light, low nutrients and low water) or safe sites conditions (mineral soil, litter or downed wood, and lack of competition) for key dominant species that lead the ball remain stable in a basin of attraction. For example, eroding connectedness can be accomplished by e.g., prevent existing

vegetation from taking up key resources. The free-up resources are then available for other species, which can become established and thus break the system out of the trap (dashed lines in Fig. 2.3C). On the other hand, management may erode or foster resilience. For example, the extirpation of a key species can erode the resilience of a basin of attraction in an irreversible manner. Alternatively, management may foster resilience through altering species composition by e.g., underplanting of species that initiate the successional process (Ghazoul et al., 2015). Thus, restoration activities that modify resources and safe sites conditions can be viewed as deepening (increased connectedness) and widening (increased of resilience) of desirable basins of attraction and vice versa for undesirable ones.

Encouraging ecosystems to stay in desirable basin of attractions

Once a desirable state is reached (e.g., white circle on basin of attraction model on Line E, Figure 3.3) management activities may be used to encourage connectedness, and thus encourage the system to remain stable in the basin of attraction in advanced successional stages (not displayed in Fig. 2). This could include activities to avoid proliferations of vegetation that would promote arrested succession. Other management activities could aim at encouraging resilience and connectedness, such as low intensity canopy removals that encourage regeneration of mid to late seral tree species.

Regardless of whether ecosystems develop without (e.g., Fig. 2.1) or with restoration activities (e.g., Fig. 2.3), management activities may be necessary to increase the provision ecosystem services such as wood (growing stock, carbon

storage), water (quality and quantity), nutrients (stimulating cycles), wildlife habitat and tourism are important outcomes for getting the forest in a desirable basin of attraction (white balls Fig. 2.3E). In such instances, practices are aimed at maintaining biomass and at the same time maintain or encourage connectedness and resilience (Allison and Hobbs, 2004; Carpenter and Brock, 2008; Puettmann, 2016).

Model applications: the case of degraded *Nothofagus* forests in Chile

Background

In temperate rainforests of south-central Chile, a large extent of forests is mostly degraded as a result of high-grading (i.e., removal of trees with high timber quality and growth, leaving trees of poor condition; Donoso and Lara, 1996; Bahamondez et al., 2009; Salas et al., 2016). In these forests, regeneration of *Nothofagus* spp. (southern beeches) is often lacking after anthropogenic disturbances, such as high-grading (Donoso and Lara, 1996; Lara et al., 2003). These conditions are locally viewed as an indication of lack of resilience (i.e., the capacity of the forest to return to pre-disturbance conditions; Bahamondez et al., 2009), and it appears to be at least partially due to the expansion of native *Chusquea* spp. (bamboo species) in understories after harvestings (Soto et al., 2015). In these conditions, *Chusquea* spp. grow in dense thickets and prevent *Nothofagus* spp. natural regeneration over longer periods of time (Veblen, 1982; González et al., 2002). Forests with low-quality trees in overstory and a dominant *Chusquea* understory are considered ecologically

undesirable in terms of structural and compositional conditions (González et al., 2002; Reyes et al., 2013; Soto et al., 2015; Soto and Puettmann 2017). These conditions also have negative long-term consequences, economically (e.g., wood, carbon storage, and tourism) and in terms of other services (e.g., wildlife, nutrient cycling, water, aesthetics), compared to forests managed per sustainability paradigm, i.e., based on strong silvicultural principles to ensure high diversity and productivity (Lara et al., 2003). These high-graded forests are an example of arrested succession as we defined it above.

In the Andean forests of south-central Chile, at low elevation on mesic sites, partial overstory disturbance such as treefall gaps is a typical natural disturbance (sensu Pollmann and Veblen, 2004). This small-scale disturbance promotes intense competition between relatively shade intolerant *Nothofagus* spp. and mid to late successional trees species (e.g., Asteraceae, Atherospermateaceae, Podocarpaceae families). *Nothofagus* species establish more successfully in environments that follow less frequent large scale and intense stand replacing disturbances such as landslides and fire (Pollmann and Veblen, 2004). In some situations, partial overstory disturbances release dense tickets of bamboo species (*Chusquea* spp.) in understories, which prevent establishment of shade intolerant and shade tolerant tree species for extended periods (Veblen, 1982; González et al., 2002; bamboo can dominate the site for 70-120 years until it flowers and dies, but this creates a short time periods for tree regeneration (Veblen, 1982; González et al., 2002). Forest management operations have typically used partial overstory disturbance such as high grading and paid little

attention to the effects of this type of management on tree regeneration (Reyes et al., 2013, Soto et al., 2015). Several studies have documented that a large extent of “degraded forest” that has resulted from this type of forest management and associated understory response (Donoso and Lara, 1996; Lara et al., 2003; Bahamondez et al., 2009; Reyes et al., 2013; Soto et al., 2015).

Model application to degraded Nothofagus-dominated second- and old-growth forests

After high-grading in *Nothofagus*-dominated second- and old-growth forests often are dominated by recalcitrant bamboo species in the understory for over long periods of time (70-120 years) with poor residual forest structure and composition (Reyes et al., 2013; Soto et al., 2015). This can be viewed as shifting forest ecosystems with successional progression (i.e., Fig. 3A in second-growth forests and late successional forests) to another stable state (arrested succession, Fig. 3B). In these forests, high grading is a disturbance intense enough to push an ecosystem over a threshold, and thus out of a desirable basin of attraction (Fig. 2.2, 3B, 3C blue ball), mostly by removing overstory trees (i.e., potential) and thus breaking down the connectedness of this basin of attraction.

High-grading breaks down the connectedness (i.e. rigidity of internal control) of old-growth forests (as an example of a desirable basin of attraction) by not providing the safe sites (i.e., ground conditions) and resource conditions (interaction of light, water and nutrients) needed by early- and late-successional tree species to become established and grow. Proper microsite conditions (e.g., mineral soil or dead wood, without competition with understory vegetation and shallow litter layer) may

encourage regeneration of early (high light, nutrients and water)- and late-successional (low light, water, nutrients) species, but these conditions are not available or common after high-grading (Soto and Puettmann, 2017; Soto et al., 2017).

Typically, after high-grading the connectedness is increasing rapidly through the proliferation of bamboo in understories, mainly due to high light, low water and nutrients availability, and a dense carpet of litter (Veblen, 1982; Gonzalez et al., 2002; Soto and Puettmann, 2017). This condition creates a successional trajectory divergent from the “standard” one (Fig. 1.3), that typically leads to species turnover and build up biomass through time (Fig. 1.1). The high connectedness of this conditions, as evident by dense bamboo thickets that generate low light, nutrient, and water resources available for tree regeneration, lead bamboo to dominate understories over long time periods (Veblen, 1982; Gonzalez et al., 2002).

Specifically, old-growth *Nothofagus* forests are characterized by long-living trees with high biomass. Small-scale natural disturbances will typically not lead to major shifts in species composition and biomass due the high connectedness (Fig. 3A). Instead, the changes in environmental and resource conditions after high grading (environmental conditions are similar to shelterwood harvesting see Figure 3B), in conjunction with the regeneration and competitive traits of bamboo (Veblen, 1982; Gonzalez et al., 2002) and high connectedness and resilience, are apparently responsible for locking-in a trap following this kind of disturbances.

On the other hand, second-growth *Nothofagus* forests are characterized by the dominance of early-seral *Nothofagus* spp. in terms of vertical canopy positions and

biomass (Lusk and Ortega, 2003). After the self-thinning stage, often these forests are filled with late-seral tree species at intermediate and lower canopy layers. In these settings, overstory mortality results in microsite and resources conditions that enhance connectedness (light, nutrient and water) and thus ensure the system develops in a desirable basin of attraction, i.e., towards old-growth (Fig. 3A second-growth forests photo, Fig. 1.1, 1.2 and 2.1) (Lusk and Ortega, 2003). However, after high-grading commonly the understories in these forests are filled with bamboo (Fig. 3B), rather than late seral trees (Gonzalez et al., 2002). In these conditions, early seral tree species are not competitive with bamboo, which prevent establishment of seral tree regeneration (Veblen, 1982; Gonzalez et al., 2002). Thus, the harvesting operation can be considered sufficiently intense to break down the connectedness of the desirable basin of attraction, and move the ball into a different stable state, i.e., a forest dominated by trees of poor form vitality, and dense tickets of bamboo in understories (Fig. 3B-C blue balls).

Restoration activities have been implemented to overcome this undesirable state in some locations of the Andes of South-Central Chile. In high-graded *Nothofagus* old-growth forests restorationists and forest managers have started to mimic natural disturbance patterns that alter the forest floor with the goal to reduce the connectedness and resilience of undesirable arrested succession basin of attraction and promote these conditions for the desirable basin of attraction. Specifically, deep ground disturbance (i.e., topsoil removal through scarification with heavy machinery, Fig. 3C) appears to be successful because: 1) it reduces the resilience of bamboo (main

responsible of arrested succession) through the effective extirpation of rhizomes and culms of these species and thereby by controlling the regeneration process (Reyes et al., 2013; Soto and Puettmann, 2017), 2) the vegetation and topsoil removal releases resources such as light (Soto et al., 2017), nutrients (mostly N, Soto et al., 2017), soil water (Reyes et al., 2013), and improves the microsite (exposed mineral soil) conditions for regeneration of early-seral trees (Soto and Puettmann, 2017), and 3) generates open areas after ground disturbance can be planted with species that promote successional development. Therefore, modifying species composition through such designed disturbances can alter the original properties that define the shape of basins of attraction (i.e. depth, as consequence of connectedness; width, as result of resilience), which expand and constraint the desirable and undesirable basin of attraction, respectively. Thus, this management deepen (increased connectedness) and widen (increased of resilience) the desirable basin of attraction and has the opposite effect for the undesirable basin (Fig. 2.3 and 3).

In secondary forests, the control of undesirable understory vegetation has been done mostly by manual control (Fig. 3.C left display in blue), with some additional entries due to the pervasive nature of bamboo regeneration (e.g. through suckering and re-sprouts; Veblen, 1982). After these management operations, the connectedness and resilience of undesirable basin of attraction can be reduced, thereby shrinking its basin of attraction (Fig. 4C blue to white displays). Subsequently, after vegetation management *Nothofagus* tree species have been underplanted to avoid problems due to seed timing, seed predation or other constraints of natural regeneration (Donoso and

Soto, 2010; Donoso et al., 2013, 2015)). This operation can be seen as increasing the resilience and connectedness of desirable basin of attraction, i.e., widen it (Fig. 3C white display).

To accelerate successional development to desirable conditions, additional management activities can provide more optimal growing conditions for selected species (e.g. *Nothofagus* spp. and late seral trees) (Fig. 3D-E). For example, dense patches of desirable natural or artificial regeneration may result in reduced tree growth due to high intra- and inter-specific competition. In these cases, restoration thinning (Dwyer et al., 2010) or variable density thinning (Puettmann et al., 2016) can be used to accelerate successional progression by decreasing connectedness (i.e. resources releases) which may result in increased tree growth, but not decrease connectedness to the level that prevents regeneration of late-seral trees (Fig. 3D). Below the *Nothofagus* canopy, late seral-tree species can become established and fill the lower canopy tiers of the forests, when the seed sources of these species are already present (Fig. 4E second-growth forest).

Finally, when late successional conditions are reached, managing the forest conditions that maintain a level of connectedness sufficient to maintain the forest in the same basin of attraction might be conducted (Fig. 4E old-growth forests). For example, late successional forest may be managed at low-intensity, i.e., limit the reduction in connectedness while maintain a relatively high potential (biomass) and encourage regeneration of late-seral trees (Puettmann et al., 2009; Schütz et al., 2012; Messier et al., 2013). In that sense, we suggest that treatments with small-scale, low

level removals, such as uneven-aged (Nyland, 2016) or selected close-to-nature (Schütz et al., 2012) management approaches may be better suited that lead to lower understory competition due to the patchiness and relatively high overstory cover. With these management approaches, complex ecological processes and functions would be maintained, i.e., connectedness and resilience (Bauhus et al., 2009; Messier et al., 2013). On the other hand, more intensive or larger scale overstory disturbances—associated with management approaches such as shelterwood and seed-tree silvicultural systems (sensu Nyland, 2016)—result in a higher likelihood of a recalcitrant understory layer and are thus more likely to push the desirable forest state close to its tipping point (sensu Sheffer et al., 2001; Beisner et al., 2003).

Conclusions

Linking the adaptive cycle, especially in the context of traps, with multiple equilibrium dynamics provides a conceptual understanding of succession, including arrested succession. Viewing ecosystems in terms of properties related to phases of adaptive cycle and traps, especially potential (biomass or energy of the system), connectedness (rigidity of internal control to resist external influences), and resilience (the ability of ecosystems to stay in the same basin of attraction after disturbances) can provide important insights into designing restoration activities to overcome arrested succession and move the ecosystem over a threshold into desirable basin of attraction with successional development. Similarly, viewing basin of attractions in a dynamic

context, e.g., where location and shape of a cup changes over time provides a conceptual linkage between the multiple equilibrium theory and successional development. Viewing basin-of-attractions in such a dynamic concept provides insights into designing restoration activities that re-shape the basin of attraction through modifying the species composition and, thereby the attributes that define the basin.

To modify basin of attraction shape restorationists should view their activities in the context of altering connectedness (depth), and resilience (width). Designed disturbances erode or enhance connectedness of a basin of attraction through the release or constraint resources (light, nutrients and water), and by providing suitable microsite conditions needed (exposed mineral soil, dead wood and litter cover) to increase the competitive ability for a desirable plant group. On the other hand, designed disturbances that efficiently remove an undesirable understory competitor species may erode the resilience of this basin. Alternatively, resilience can be encouraged by an external input, such as underplanting species that foster successional dynamics towards a desirable condition. Thus, modifying connectedness and resilience through manipulation of species composition, restorationists may deepen and widen a desirable basin of attraction or vice versa for undesirable one.

The example of degraded *Nothofagus*-dominated second- and old-growth forests in Chile highlights how such a conceptual linkage can be applied to a real-world example. While the integrated model per se should be general and apply to a

broader set of conditions, application to other settings requires more detailed analysis and adjustments.

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TABLE 1. Features of three variables that characterized the phases of the adaptive cycle (Gunderson and Holling, 2002) and for ecological traps (Holling et al., 2002; Allison and Hobbs, 2004).

Phase	Potential	Connectedness	Resilience
Release	Low	High	Low
Reorganization	High	Low	High
Exploitation	Low	Low	High
Conservation	High	High	Low
Ecological traps	Potential	Connectedness	Resilience
Poverty	Low	Low	Low
Rigidity	High	High	High
Lock-in	Low	High	High

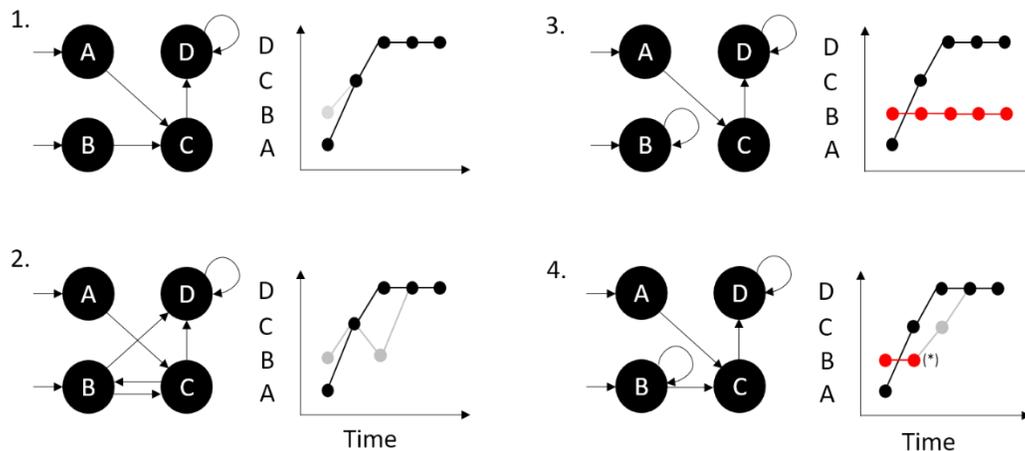


Fig. 1. Four possible patterns of successional dynamics after disturbance. A is the initial successional state (e.g., bare ground) and D is the final basin of attraction, typically stands with late successional composition and structures. The solid black line and black dots reference “typical, standard” successional trajectories leading efficiently to late successional conditions. In contrast, the grey line and dots show alternative trajectories in comparison. 1) Convergent pattern; trajectories differ initially but converge quickly to the same basin of attraction (gray dots and lines), 2) Initially convergent, then divergent trajectory pattern; different trajectories converge over time to the same climax state. 3) Divergent trajectories as consequence of arrested succession; patterns never converge and the arrested succession trajectory never moves into a late successional basin of attraction, i.e., leads to long-term degraded forest (red dots and lines), and 4) Initial divergent trajectory as a consequence of arrested succession (red line and dots) where management creates (*) a shift in the stagnated trajectory towards a late successional basin of attraction (grey line and dots).

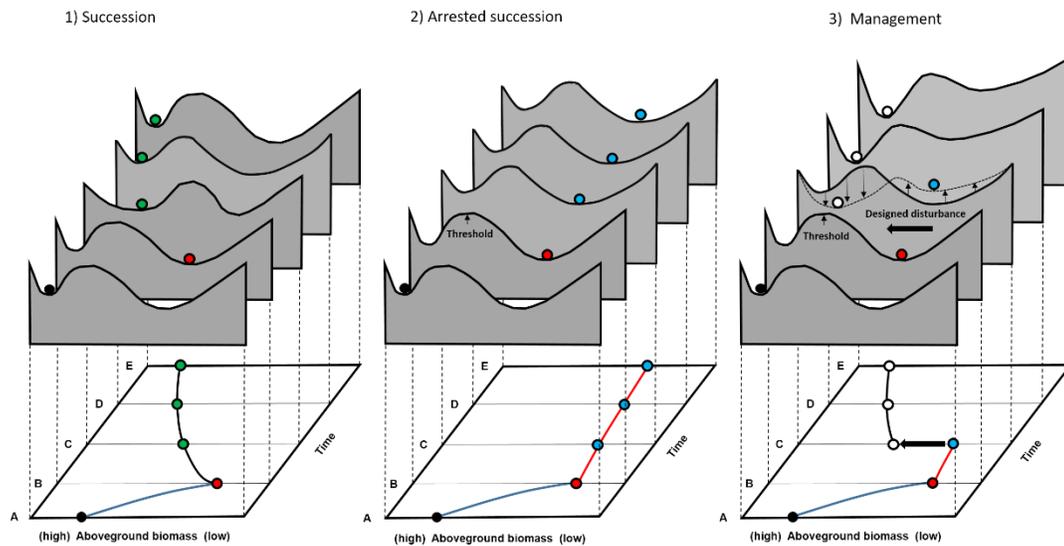


Fig. 2. Multiple equilibrium model and its associated basin of attractions in different successional trajectories following a partial disturbance (A-E in all models). Panel 1 shows when disturbance (red ball) is not intense enough to produce a change in the system state and their attributes (e.g. structure and composition), and the potential to buildup biomass is not affected after disturbance. That means that green balls are kept in the desirable basin of attractions while succession progress. Alternatively, if disturbance is intense enough it may produce a shift in species composition and structure due to changes in biophysical conditions in the forest (panel 2, red ball). In this state the succession is arrested, and potential to build biomass is locked into alternative stable state in the long-term by the high connectedness of this state (blue balls). Restoration activities may overcome this lock-in trap (panel 3, white balls). Designed disturbance alters the basins shape and lead the system move the ball from one basin (blue ball in panel C) to another (white ball in panel C) with successional progression.

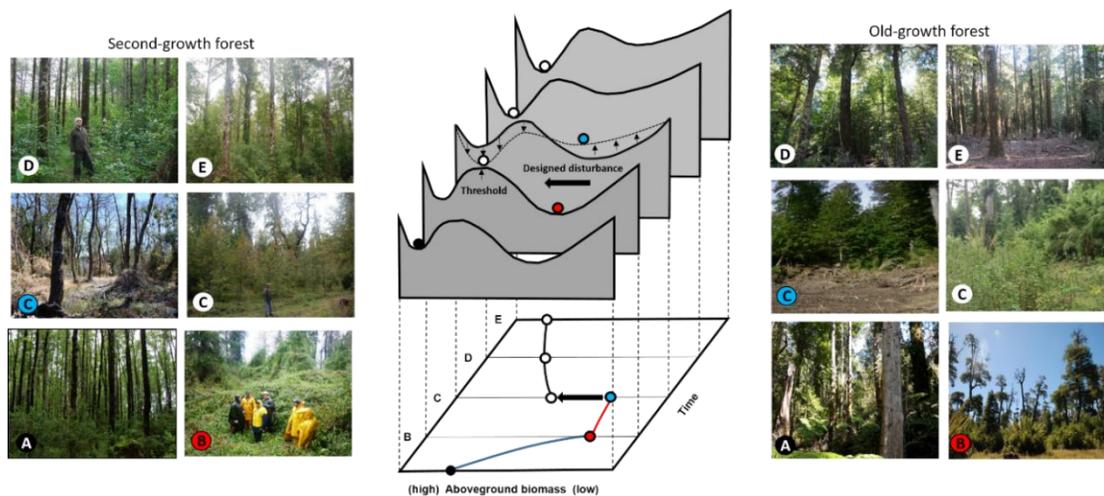


Fig. 3. Multiple equilibrium model represented by basins of attraction and their associated photos depicting how two forest stages reacted to forest degradation (through high-grading) and subsequently dominated by bamboo that arrested forest succession (displays B and C, red and blue balls) in the Chilean Andes. Designed disturbance aided to overcome the arrested succession state and push the forest into successional progression (displays C-E, white balls) in both forest used as examples (second- and growth-growth forests). The restoration treatments reshaped the basin of attraction (display C, black arrow) and allows ecosystems to follow desirable successional patterns through establishment of early-seral tree species (Photo C white balls) through underplanting (second-growth example) and natural regeneration (second- and old-growth examples). Photos D and E show how the successional progression is taking place in both examples after some small-scale disturbances or management actions to promote potential, connectedness and resilience (see text for further details and explanation).

Chapter 3

TOPSOIL REMOVAL THROUGH SCARIFICATION IMPROVES NATURAL REGENERATION IN HIGH-GRADED IN HIGH- GRADED *NOTHOFAGUS* OLD-GROWTH FORESTS

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Abstract

1. High grading by removing mostly trees with superior timber quality has led to losses of productivity and biodiversity in forests. Typically, after high grading little attention is paid to tree regeneration. Thus, undesirable understory vegetation often dominates for a long time, leading to stagnation in forest recovery and so-called arrested succession. In such settings, managing understory vegetation through topsoil removal through scarification has been proposed as a restoration tool to encourage tree regeneration.
2. We investigated the effectiveness of topsoil removal as a restoration technique in high-graded *Nothofagus* old-growth forests in the Chilean Andes. In these forests, high grading often leads to understories be dominated by dense thickets of native bamboo, *Chusquea culeou*. These understory conditions typically delay succession by preventing tree regeneration.
3. T-tests were used to compare vegetation development in areas with and without topsoil removal. Non-parametric multiplicative regression (NPMR) was used to investigate which environmental variables were mainly related to regeneration of different plant groups (short- and long-lived early- and late-seral tree species) and *C. culeou* abundance in areas with and without topsoil removal.
4. Topsoil removal improved the regeneration of early-seral tree species and constrained *C. culeou*. In areas without topsoil scarification, higher abundances of *C. culeou* were reflected in a higher transmitted radiation and litter cover. In

these areas, the presence of early-seral tree species was related to higher soil water content and transmitted radiation. However, topsoil removal altered these response patterns for early-seral trees. For instance, the interaction between higher soil water content and more exposed mineral soil was reflected in a higher likelihood of finding early-seral tree seedlings.

5. *Synthesis and applications.* Topsoil removal was a successful restoration tool for overcoming arrested succession on the study sites by encouraging the regeneration of early-seral trees in high-graded forests. Contrasting environmental conditions of pre- and post-topsoil removal allowed insights into the processes and mechanisms responsible for forests with arrested succession and for succession progression. This understanding provides guidance regarding the range of conditions under which topsoil removal can be used as a successful restoration practice.

Introduction

In many parts of the world, much of the native forest has either been converted to plantations or other land uses and/or has been degraded (FAO 2010). In the Andean forests in Chile, the large extent of degraded forest is mostly a result of high-grade harvesting (i.e., removal of trees with high timber quality and growth, leaving only trees of poor condition, sensu Lara *et al.* 2016), with little attention paid to tree regeneration (Soto *et al.* 2015). Consequently, regeneration in this temperate region (mostly dominated by *Nothofagus* spp., southern beech) was found to be successful in only about 5% of such high-graded forests (Lara *et al.* 2016). This can be viewed as a lack of resilience (i.e. “ability of a system or state to absorb disturbance and maintain its functions” sensu Gunderson & Holling 2002) and appears to be at least partially due to the expansion of native bamboo, *Chusquea culeou* Desvaux. In these conditions (i.e., in 300-800m² canopy gaps after high-grading), *C. culeou* often develops into dense thickets that prevent the natural regeneration of *Nothofagus* spp. and other tree species over longer periods of time (Veblen 1982; González *et al.* 2002). High-graded forests with only damaged and low-vigor trees in the overstory and with understories dominated by *C. culeou* are viewed as ecologically undesirable in terms of structural and compositional conditions (González *et al.* 2002; Soto *et al.* 2015). Specifically, the expansion of *C. culeou* in the understory is of concern because it negatively affects soil fertility through its deleterious effects of litter on soil nutrients (Veblen 1982), soil water availability, and damage to regenerating trees by mechanical crushing (Griscom & Ashton 2002). Compared to forests managed according to sustainability principles

that encourage high diversity and productivity, conditions after high-grading have negative long-term consequences, both economically and in terms of the provision of other ecosystem services, such as a wide variety of habitat conditions and carbon sequestration (Lu & Buongiorno 1993).

Concerns about the ecological and economic implications of high grading and the subsequent understories dominated by *C. culeou* have been growing over the last decades, as reflected in increased political discussions and research and restoration efforts (Donoso, Soto & Fuentes 2015; Lara *et al.* 2016). After such overstory removal, these ecosystems do not follow typical secondary successional patterns, e.g. starting with establishment of early-seral tree species and subsequent build-up of biomass and, in absence of disturbances, over time a shift in species dominance to late-seral tree species. Instead, the dominance of *C. culeou* results in stagnated vegetation dynamics that can last for 70 to 120 years. (González *et al.* 2002; Caccia, Kitzberger & Chaneton 2015). The environmental and resource conditions after overstory removal, in conjunction with the expansion and *C. culeou*, a very competitive species, are considered mainly responsible for locking these forests into an arrested succession conditions (Royo and Carson 2006).

The germination and establishment of early-seral tree species have been shown to be especially sensitive to microsite conditions, e.g., availability of exposed mineral soil or soil water content (Gray & Spies 1997; Yoshida *et al.* 2005; Fahey & Puettmann 2007). In contrast, late-seral species are better able to tolerate the low soil water conditions typically found in *Nothofagus* old-growth forests, but only in areas

without competition from understory vegetation (Veblen, Schlegel & Escobar 1980; González & Donoso 1999). In addition, physical barriers, such as thick litter cover, can negatively influence tree establishment in understories, especially of species with small seeds (Sydes & Grime 1981; González & Donoso 1999; Christie & Armesto 2003), such as *Nothofagus* spp. (Donoso 2006). Thus, ground disturbance (e.g., slash, humus, or topsoil removal by scarification) has been used to manage competitive vegetation and encourage more reliable regeneration of desirable tree species (i.e., mostly early-seral trees) in a number of forest biomes (Örlander, Egnell & Albrektson 1996; Yoshida *et al.* 2005; Löff *et al.* 2012; Reyes, Thiers & Gerding 2014).

In this work, we utilized a field study to investigate whether topsoil removal by scarification (hereafter as topsoil removal) is sufficient to push forests out of arrested succession (after partial overstory removal) by encouraging regeneration of various plant groups, especially early-seral tree species. Furthermore, we documented microsite conditions (small-scale environmental variables, including resource levels) after partial overstory removal and in areas with and without topsoil removal. The relationships between these conditions and vegetation patterns provides insights which processes may be responsible for potential success of restoration treatments and thus help guide future restoration efforts. We asked the following questions:

1. What environmental conditions are mainly related to the abundance of *C. culeou* (as a species responsible for arrested succession) and to early- and late-seral tree species (as indicators of successional processes) after high grading?
2. Can restoration through topsoil removal overcome arrested succession by

reducing undesirable understory vegetation (*C. culeou*) and encouraging tree regeneration, especially of early-seral species?

3. Does the impact of topsoil removal on environmental conditions and tree abundance provide indications about mechanisms responsible for restoration success?

Material and methods

Study sites

Our study sites (see also Soto *et al.* 2017) were located between 39° and 40°S latitude and at elevations of 800 to 1,000 m.a.s.l. in the Andes of south-central Chile, in the Huilo-Huilo biological reserve. Four different sites within the Coihue-Rauli-Tepa forest type in Huilo-Huilo were randomly selected from a pool of sites where the overstory had been partially removed through high grading and where topsoil removal had been subsequently implemented in portions (a quarter to half) of the high-graded areas (see Table 1). We selected sites that had 8 years of understory response to topsoil removal at the time of sampling. The sites were selected to represent the range of productivity in the region (as reflected in tree height growth; Table 1), were at least 10 ha in size and were on flat or gently sloping ground (< 20°). The general characteristics of site and forest conditions are presented in Table 1.

The study conditions were representative of the vegetation zone where *Nothofagus* spp. are most productive. In these types of forests, *Nothofagus dombeyi*

and *Nothofagus alpina* were typically the dominant tree species in terms of basal area in absence of harvesting, with *Saxegothaea conspicua*, *Laureliopsis philippiana* and *Dasyphyllum diacantoides* as minor components found mostly in intermediate and lower canopy layers (Donoso 2006). Under natural conditions two major disturbance types influence these forests. First, small-scale disturbances (e.g. individual tree mortality or small canopy gaps of smaller sizes than openings typically found after high-grading) promotes intense competition between mid to late successional trees species, e.g., *S. conspicua*, *L. philippiana* and *D. diacantoides* and bamboo, *Chusquea* spp. (Veblen, Schlegel & Escobar 1980). Second, less frequent large scale and intense stand replacing disturbances such as landslides and fire (Pollmann & Veblen, 2004) (openings larger than typically found after high-grading with more soil disturbance) lead to very open conditions. After these disturbances *N. dombeyi* and *N. alpina* are more competitive because understory vegetation is mostly removed, and succession follows the model of Bormann & Likens (1979) in terms of biomass buildup and species composition. However, after small- or partial-scale disturbances (e.g. single and multiple treefalls, or high-grading; Soto *et al.* 2015) dense thickets of bamboo species (*Chusquea* spp.) often develops in the understory, which prevent establishment of shade intolerant and shade tolerant tree species for extended periods (Veblen, 1982; González *et al.* 2002). Bamboo species can dominate a site for 70-120 years until it flowers and dies. Such mortality events create a very narrow window for tree regeneration due to the rapid establishment and growth of *Chusquea* spp. (Veblen 1982; González *et al.* 2002; Lusk 2001).

The climate in Huilo-Huilo is considered Andean polar, with short, dry summers (December-March) and humid winters (June-September). Annual precipitation reaches 3,500 mm (Reyes, Thiers & Gerding 2014), mainly as snow during winter. The mean annual temperature is 9°C, with means of 4°C and 16°C for the coldest (August) and warmest (February) months, respectively. Extreme temperatures can range from below -10°C to above 30°C. Thirty to 50 annual frost events are common at 550 m.a.s.l., typically in July and September (Soto *et al.* 2015). Soils on the study sites are a transition between Andisol (Acrudoxic Hapludand) and Inceptisol (Andic Dystrudepts). Both are coarse mixed and mesic soils and have a stratified structure and medium texture through the entire profile (Reyes, Thiers & Gerding 2014).

Overstory removal and subsequent understory response

The overstory trees on the study sites were partially removed during the summer of 2001/2002 (December-March) by high grading. Even high grading operations have to follow the Forest Laws established by the Chilean Forest Service-CONAF, i.e., this management practice legally can only remove up to 35% of pre-harvest basal area. On our study sites, this resulted in average residual basal areas of 50–63 m² ha⁻¹ and 137–273 trees per hectare (measured at the study installation, Table 1) with high patchiness due to the natural variability of tree species, sizes and forms, as well as harvesting and marketing constraints and preferences (Soto *et al.* 2015). High-graded stands contain few large trees of desirable (*Nothofagus*) spp., few trees with vigorous crowns, and a patchy distribution of residual trees (Soto *et al.* 2015).

After overstory removal existing patches of *Chusquea culeou* expanded into dense thickets that covered most of the study sites. In this region, this species reaches 5–6 m in height, an average density of 30–60 culms m⁻², an aboveground biomass of 3,500 g m⁻² (Veblen 1982). The relatively high average Leaf Area Index of 6 (Lusk 2001) is also reflected in a dense litter layer on the ground (González & Donoso 1999). This dense vegetation layer limits diffuse light levels underneath thickets of *C. culeou* to around 1.5%. Examples depicting the residual structure after overstory removal are shown in Fig. S1 in Supplemental Information.

Topsoil removal through scarification

Topsoil removal through mechanical scarification was conducted with heavy machinery (Komatsu D4 bulldozer of 5,400 kg, with a horizontal blade) in the summer of 2005–2006. This treatment has the goals of 1) controlling dense tickets of *C. culeou* and remove the dense litter layer, 2) exposing mineral soil as safe sites for germination and establishment of *Nothofagus* spp., and 3) creating open areas for underplanting when seed sources are lacking (Soto *et al.* 2015). These operations removed the upper soil layers (20–40 cm), including rhizomes and culms of *C. culeou* (Reyes, Thiers & Gerding 2014). Topsoil removal created a complex spatial pattern of soil conditions. This disturbance affected portions of all study sites (24–45% of the study areas, Table 1), i.e., left many small and large openings untreated. The disturbed proportion and spatial distribution varied among sites reflecting the spatial distributions of residuals trees, snags and downed wood (Table 1, Fig. 1). In addition, such operations typically avoid removing already existing *Nothofagus* spp. regeneration. This spatial variability,

in conjunction with the inherent variability in soils, e.g., due to microtopography, results in a wide range of conditions for tree regeneration. The topsoil removal did not extirpate *C. culeou* from the sites completely, however; in our study sites (Table 1). More information about the effects of topsoil removal through scarification on soil chemical and physical properties on our study sites right after treatments can be found in Reyes, Thiers & Gerding (2014).

Measurements

Trees and seedlings. Eight years after topsoil removal (i.e., December 2014 to March 2015), one permanent square plot of 1 ha (plus a buffer of 10 m on each side) was located randomly in each of the four sites. A 10- by 10-m grid was laid over the 1-ha plots, and centers of regeneration plots of 2 m² (radius of 0.8 m) were positioned on all grid intersections (100 regeneration plots in all permanent plots). Regeneration plots were classified based on their location in areas with or without topsoil removal, which after 8 years were still clearly identifiable in field (Fig. 1). In the regeneration plots, the percentage of *C. culeou* cover was assessed using ocular estimation (% of cover, accuracy ~5%). The regeneration (seedlings: 5–130 cm in height) was documented using presence (0 = not present, 1 = present) for each of the study species.

Environmental conditions. We measured the following variables in the regeneration plots: exposed mineral soil (%); litter cover (%); coarse woody debris (woody debris above 10 cm in diameter, %); microtopography (flat, convex, concave and mixed); soil resistance to penetration (kPa); soil volumetric water content and total transmitted radiation (% total light). Soil resistance to penetration was considered an integrated

measure of soil disturbance (Soto *et al.* 2015). We used a cone Fieldscout SC 900 soil compaction meter (Spectrum instruments, Inc.) with a resolution of 35 kPa and an accuracy of ± 103 kPa. Resistance to penetration was measured in five random spots in each regeneration plot. Soil volumetric water content was measured in five random spots in all regeneration plots with a time-domain reflectometer (TDR 100 soil moisture meter; Field Scout TM, Spectrum Technologies, Inc.), using peer rods of 20 cm. At the center of regeneration plots, we took hemispherical photographs at 1.5 m above ground. Light availability was estimated from these photos as total transmitted radiation (a combination of diffuse and direct radiation). For more details about soil resistance to penetration sampling, soil water content sampling and light measurements and calculations, see Appendix S1 in Supplemental Information.

Data management

Chusquea culeou abundance (cover, %) were log transformed to improve data normality (zero percent cover values were replaced by the smallest non-zero value: one percent). Plant species (presence and absence) were divided into three categories based on lifespan, shade tolerance, maximum height, crown characteristics, rooting patterns and seed size and dispersal (Donoso 2006):

(1) SLES—short-lived early-seral plants (*Ribes* spp. and *Fuchsia* spp.), lifespan ~30–50 years, small maximum height (<3 m), small, flat root system and fleshy fruits dispersed by birds and small mammals.

(2) LLES—long-lived early-seral tree species (*Nothofagus dombeyi*, *N. alpina*, *N. pumilio*), lifespan >500 years, shade-intolerant, tall maximum height, small crown depths, flat and shallow root system and small, wind-dispersed seeds.

(3) LLLS—long-lived late-seral tree species (*Laureliopsis philippiana* and *Dasyphyllum diacantaoides*), lifespan >500 years, shade-tolerant, intermediate maximum height, large tree crowns, deep root system and wind-dispersed seed.

Statistical analysis

General overview. First, we tested data normality for species responses individually, using the Shapiro-Wilk test, and we assessed homoscedasticity with Levene's tests (Dytham 2003). To assess the effectiveness of topsoil removal, we performed paired *t*-tests for abundance of *C. culeou* and plot counts of SLES, LLES and LLLS regeneration separately. All tests used an $\alpha \leq 0.05$.

Species group - habitat relationships. We used nonparametric multiplicative regression (NPMR) in HyperNiche (McCune & Meford 2009) to quantify the relationships between plant groups (abundance of *C. culeou* and presence of SLES, LLES and LLLS) and environmental predictors (McCune 2006). NPMR avoids distributional assumptions, can accommodate a wide range of response surface shapes, unbalanced data and uses a free search of the best predictor combination (McCune 2006). We used the Gaussian weighting kernel and local mean estimator (LM-NPMR; for further details see McCune 2006). The predictor variables used to address questions 1 and 2 included exposed mineral soil, litter cover, coarse woody debris,

microtopography, soil resistance to penetration, soil water content and transmitted radiation.

Evaluation procedures in NPMR differ for continuous (abundance) and binary (presence/absence) data. Thus, the model was optimized for the abundance of *C. culeou* cover (continuous data) by minimizing minimum average neighborhood sizes (i.e., N^* , see McCune 2006). Standard deviations (tolerance) of the kernel functions were optimized by improving the cross-validated coefficient of determination R^2 (xR^2). xR^2 has the same interpretation as the classical R^2 , but its calculation differs from R^2 because it is penalized by leave-one-out cross-validation and thus controls for overfitting (see McCune 2006).

For assessing occurrences (presence/absence, i.e., binary response variables), NPMR uses the Bayes Factor to evaluate model quality, comparing a candidate model (M_1) against a “naïve model” (M_2) to determine which provides a higher probability of correctly predicting occurrences of groups (McCune 2006). For model comparisons, this approach uses the log-likelihood ratio to compare the presence or absence of seral groups in a given plot, using the same probability of the two tested models: i.e., $P(M_1) = P(M_2) = 0.5$. Thus, the ratio likelihood B_{12} from observed occurrences ($\mathbf{y} = y_1, y_2, \dots, y_i$) against the likelihood of the M_2 model is calculated as follows:

$$B_{12} = \frac{P(\mathbf{y}|M_1)}{P(\mathbf{y}|M_2)} \quad \text{eqn 1}$$

where,

$$P(\mathbf{y}|M_j) = \prod_{i=1}^n \hat{y}_i^{y_i} (1 - \hat{y}_i)^{1-y_i} \quad \text{eqn 2}$$

\hat{y}_i is the fitted and y_i is the observed values for the likelihood from the i th occurrence data for each model, $M_j, j=M_1, M_2$. Equation 2 is the joint probability function of n observations of y_i , where each observation is an ordinary Bernoulli random variable (McCune 2006). For a better interpretation of Bayes Factor values, we used $\log(B_{12})$, where $\log B_{12}$ values of 0–0.5 indicate minor, 0.5–1 substantial, 1–2 strong and >2 decisive support (McCune & Mefford 2009). Because of the nonparametric nature of this approach, we conducted sensitivity analyses in Hyper Niche to evaluate the relative contribution of predictors for candidate models (McCune & Mefford 2006).

Results

General trends

Topsoil removal was successful in reducing the abundance of *C. culeou* from an average of 36% of cover in areas without topsoil removal to 5% cover in areas with topsoil removal and at the same time encouraged regeneration of early successional species (Fig. 1, Table 2). Topsoil removal also lead to areas without any *C. culeou*; the number of plots with *C. culeou* cover was significantly lower in areas with topsoil removal compared to areas without topsoil removal ($P < 0.001$, Table 2). In contrast, SLES and LLES were found in significantly more plots in areas with disturbed soils than in areas with undisturbed soils ($P < 0.05$). The occurrence of LLLS species did not appear to be influenced by this ground disturbance ($P > 0.05$).

Chusquea culeou responses to environmental conditions in undisturbed and disturbed soils

The abundance of *Chusquea culeou* showed similar (but not equivalent) patterns in soils with and without topsoil removal. It was significantly positively correlated to transmitted radiation and litter cover in areas without topsoil removal (Fig. 2). The cross-validated R^2 for the prediction of abundance of *C. culeou* cover ($xR^2 = 23.5\%$, $P < 0.001$) in undisturbed soils and was higher when information from both predictors transmitted radiation and litter cover were incorporated into the model (Table 3), suggesting that the interaction between these two variables is a major influence on *C. culeou* dominance in undisturbed soils (Fig. 2). However, the sensitivity analyses showed that in undisturbed ground conditions, the amount of transmitted radiation was more influential on *C. culeou* cover than was litter cover (Table 3). In contrast, for topsoil removal conditions the NPMR model for the abundance of *C. culeou* was not significant ($xR^2 = 6.4\%$, $P > 0.05$). Even with the low variance explained by these models, transmitted radiation had a higher influence on *C. culeou* than litter cover (Table 3) in areas with topsoil removal.

Plant groups' responses to environmental conditions in undisturbed and disturbed soils

In areas with topsoil removal, soil water content was the main driver for the presence of all plant groups (except *C. culeou*), followed by transmitted radiation (Fig. 3a, c, e). All models with both predictor variables showed a better fit in predicting occurrences of SLES, LLES and LLLS species groups (Table 3). The model

predicting the probability of finding LLES species had decisive support ($\text{Log}B_{12} = 2.9$; for interpretation of values, see statistical analysis section) and the model for SLES species had strong statistical support ($\text{Log}B_{12} = 1.7$) (Table 3). Sensitivity analyses and low tolerance (standard deviation) suggested that soil water content was a more influential (positive) predictor variable for these two early-seral species groups than was transmitted radiation (positive) (Table 3). Similarly, the model predicting the likelihood of finding a seedling of the late-seral species group had decisive statistical support ($\text{Log}B_{12} = 4.6$), and predictions improved when soil water content and transmitted radiation variables were used (Table 3). In contrast to the SLES and LLES species groups, however, low soil water content and higher transmitted radiation were related to a higher probability of finding a seedling of the LLLS species plant group (Fig. 3e). Just as for the early species groups, the sensitivity analysis showed that soil water content was more influential than transmitted radiation for late-seral species (Table 3).

The predictive ability of NPMR-estimated models for all seral species groups was higher in areas with topsoil removal (Fig. 3b, d, f). However, different environmental conditions were responsible for the occurrence of early-seral species (Table 3). For example, influential predictor variables for SLES occurrence ($\text{Log}B_{12} = 2.7$) included transmitted radiation (positive) and to a lesser extent exposed mineral soil (positive). In contrast, LLES occurrence ($\text{Log}B_{12} = 4.3$) was mostly influenced by soil water content (positive) and to a lesser extent by exposed mineral soil (positive) (Fig. 3). Finally, the model for predicting LLLS occurrence had decisive statistical

support ($\text{Log}B_{12} = 5.6$). Similar to the relationships in undisturbed soil conditions, low soil water content and higher transmitted radiation increased the probability of finding seedlings of this group (Fig. 3f).

Discussion

Our study showed that topsoil removal was a successful treatment in high-graded *Nothofagus* forests in the Andes of south-central Chile, as it reduced the abundance of *C. culeou* and at the same time encourages the regeneration of desirable LLES tree species. This supports findings in a number of forest biomes that this ground disturbance can be an effective practice for altering understory vegetation to encourage tree regeneration (Örlander, Egnell & Albrektson 1996; Yoshida *et al.* 2005; Löf *et al.* 2012; Reyes, Thiers & Gerding 2014). Research has shown that a variety of environmental conditions can be responsible for this effect, including the amount of soil exposure needed to provide safe sites (Cornett *et al.* 2000), degree of soil compaction (Ampoorter *et al.* 2010; Soto, Donoso & Puettmann 2014) and soil fertility (Ampoorter *et al.* 2010; Reyes, Thiers & Gerding 2014). We showed that the relevant factors may not only vary due to environmental conditions, as suggested by the studies above, but also varied for different species groups, likely due to the different traits for each group, such as shade tolerance and seed dispersal patterns (Pywell *et al.* 2003).

Environmental and ecological conditions influencing of plant groups

Given that all study species are frequently found in nearby forests, we assumed that propagules were readily available and that their regeneration dynamics were responding to changes in environmental conditions, as influenced by disturbance (overstory and topsoil removal) and other plant interactions, such as competition. In this light, our study confirmed that *C. culeou* was dominant – to the detriment of other species, even late-seral species – after partial overstory removal (high-grading) and before (or without) topsoil removal (Veblen 1982; González *et al.* 2002). The expansion of *C. culeou* cover during the first few years after partial overstory removal (without topsoil removal) has previously been attributed mainly to increases in light availability (Veblen 1982; González *et al.* 2002), with less attention paid to other environmental variables (Royo & Carson 2006). Our results also suggest that the dense cover of leaf litter, low soil water content, and increases in light availability interact to promote the dominance of *C. culeou* in forests without topsoil removal. Thus, this dominance in undisturbed soils was likely facilitated by the fact that early-seral species are not competitive in late successional understory settings (González *et al.* 2002; Caccia, Kitzberger & Chaneton 2015). At the same time, the dense *C. culeou* thickets led to high accumulation of litter on the ground, suggesting a positive feedback loop that further reduces the likelihood of tree regeneration (González & Donoso 1999). Both competition for belowground resources (soil water and nutrients) and negative impacts on seed germination through litterfall appeared important (Sydes & Grime 1981; Christie & Armesto 2003). However, the study setup did not allow us

to separate these two processes. Despite this limitation, our results confirmed that a second disturbance that impacts both factors is needed after partial overstory removal to encourage the early-seral tree regeneration.

In contrast to earlier findings (Pollmann & Veblen 2004; Soto *et al.* 2015), our study pointed out that the interaction of exposed mineral and soil water content with light availability are related to the regeneration of early-seral species (LLES and SLES). Light availability in isolation has been commonly assumed to be the major driver for establishment and growth of these species (Veblen, Schlegel & Escobar 1980; Pollmann & Veblen 2004). In this study, we found that transmitted radiation did not play such a dominant role in the establishment process. Instead, our results pointed out that the presence of regeneration was related to an interaction of soil water content with transmitted radiation for all species groups in undisturbed soil conditions. In contrast, the interaction of exposed mineral soil (LLES and SLES), soil water content (LLLS) and transmitted radiation was influential in disturbed soils, highlighting the complexity of factors influencing plant regeneration (Schupp 1996).

Studies have shown the growth plasticity of *Nothofagus dombeyi* and *N. alpina*, in terms of light requirements during early stages of regeneration, allowed seedlings to establish and persist under deep shade in areas with relatively little competition from other understory species (Pollmann & Veblen 2004; Donoso, Soto & Fuentes 2015). Thus, topsoil removal that constrained the abundance of *C. culeou* led to an increase in the regeneration of early-seral *Nothofagus dombeyi* and *N. alpina*,

likely due to a combination of providing more soil water and exposed mineral soil, and increased light.

Partial overstory removal and ground disturbance in a larger ecological perspective

To properly place our findings on the influence of disturbances (overstory removal and topsoil removal) and their associated impact on environmental variables into the context of vegetation dynamics, the dynamics themselves must be placed within a larger theoretical perspective, reflecting the importance of cross-scale hierarchies in complex adaptive systems (Messier, Puettmann & Coates 2013). As our study pointed out, one of the main drivers of vegetation development was the presence of *C. culeou*, which is a common component (typically found in patchy distributions) in almost all undisturbed, late-successional, temperate old-growth forests in South America (Veblen 1982; González *et al.* 2002; Caccia, Kitzberger & Chaneton 2015). Partial overstory removal through high grading appeared to create conditions that were suitable for the expansion of *C. culeou* and consequently unsuitable for the regeneration of early- or late-seral tree species that otherwise would replace the harvested trees to achieve full stocking. Rather than moving relatively quickly through the reorganization phase (*sensu* Gunderson & Holling 2002) and following more standard successional development patterns, the environmental conditions in high-graded *Nothofagus* forests are instead suitable for the expansion and dominance of *C. culeou*. Due to the longevity of *C. culeou*, these conditions typically lead to an extended dominance of dense thickets of *C. culeou* within many high-graded old-growth *Nothofagus* forests. Such stagnation in ecosystem development exemplifies a

rigidity trap. In such traps “strong self-reinforcing controls prevent the flexibility needed for the system to adapt” to external changes (Carpenter & Brock 2008). The high connectedness (i.e. rigidity of internal control; sensu Gunderson and Holling 2002) of ecosystems in rigidity traps is evident, when e.g., typical small-scale disturbances in these forests, such as a single treefall gap, snow and ice breakage, animal damage, etc., do not initiate a substantial shift in forest structure and composition. Instead, as long as this internal control is still “rigid”, any impacted areas are relatively quickly filled with more *C. culeou*. In these forests, the internal control apparently is overcome by larger or more intensive disturbances, e.g., the topsoil removal and thus removal of a large proportion of *C. culeou*. Only then can standard successional patterns resume (Carpenter & Brock 2008).

Implication for forest restoration

Our study showed that topsoil removal by mechanical scarification can be an effective restoration tool for overcoming arrested succession after high grading in the studied forests. In addition, our findings provide insights into how environmental conditions are influenced by overstory removal and topsoil removal and, in turn, how these changes in conditions are reflected in vegetation dynamics. Specifically, our study showed that other resources besides light, e.g., soil moisture, may also be influential in driving tree regeneration in the studied forests and restoration treatments should reflect this. Thus, a close examination of soil conditions, specifically nutrient and soil water conditions will provide insights into the likelihood of success when applying topsoil removal as a restoration treatments. Earlier work (Reyes, Thiers &

Gerding 2014) also pointed out that soil structure, specifically the potential for soil compaction, needs to be considered when such restoration treatments are applied across a broader landscape.

A basic understanding of these conditions and their interactions and influences is especially helpful when restoration treatments are applied to novel conditions (Hobbs, Higgs & Harris 2009), where past experiences are not necessarily helpful or sufficient for a current treatment selection. For example, if climate change leads to more drought events the prominent influence of soil moisture conditions suggests a higher need for restoration treatments, such as ground disturbance, in order to overcome *C. culeou* dominance in high-graded stands. Additionally, viewing plants in terms of traits related to regeneration processes, rather than focusing on life forms, appears to be useful when selecting restoration treatments (Pywell *et al.* 2003). Plant traits that are directly linked to resource use or environmental conditions can provide a more mechanistic understanding of vegetation dynamics. Such understanding also facilitates the extrapolation of study findings to other ecosystems (Pywell *et al.* 2003).

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TABLE 1. Study site descriptions.

Characteristic	Rincón del diablo	Lago chan-chan	Piedras negras	Valle Hermoso
Latitude (°)	39°49'20	39°49'53	39°54'33	40°01'07
Longitude (°)	71°52'27	71°50'34	71°56'50	71°52'32
Altitude (masl)	1050	1200	1030	970
Top-height* (m)	41	34.6	39	44
Density (trees per ha)	145	137	273	285
DBH (cm)	44.0	40.5	34.1	35.4
Basal area (m ² ha ⁻¹)	50.6	55.8	54.9	63.3
Density of dead trees (trees per ha)	13	25	13	20
Dead tree basal area (m ² ha ⁻¹)	13.9	19.7	7.5	20.9
Scarified area (%)†	45.8	32.5	33.8	24.1
Number of plots with/without ground disturbance	48/52	33/67	39/61	26/74
Slope (%)	0–15	0–20	0–15	0–20
Aspect	SE	SW	E	SE
Soil texture	Sandy loam	Sandy loam	Coarse sands	Loam

* Top-height based on ten largest trees per site. † Scarified soil was mapped with a resolution of 1 m².

TABLE 2. Means (standard deviation) for species occurrence (SLES, LLES and LLLS) and abundance (% cover of *C. culeou*). *P*-values indicate the results of paired *t*-tests comparing occurrence in plots with and without ground disturbance for each species group.

Species group	Ground disturbance		
	Without	With	<i>P</i> -value
SLES	13.5 (7.9)	28.5 (9.9)	*
LLES	10.5 (6.3)	31.7 (11.0)	*
LLLS	8.2 (10.5)	15.5 (18.6)	ns
<i>C. culeou</i>	49.5 (15.9)	8.0 (5.2)	**

ns: not significant, * $P < 0.05$, ** $P < 0.01$

TABLE 3. Best fitted NPMR for abundance of *Chusquea culeou* (Log %). xR^2 is the cross-validated coefficient of determination, $\text{Log}B_{12}$ is the Bayes Factor coefficient and N^* is the neighborhood size in the fitting. Tolerance values are for the best predictors (in parentheses) in the free searching procedure using Hypeniche (McCune & Mefford 2009).

Ground conditions	Model	xR^2	N^*	Tolerance 1	Tolerance 2
Without ground disturbance	<i>C. culeou</i>	0.235***	25.7	14.3 (light)	20.0 (litter cover)
With ground disturbance	<i>C. culeou</i>	0.064ns	22.1	14.1 (light)	20.0 (litter cover)
Ground conditions	Model	$\text{Log} B_{12}$	N^*	Tolerance 1	Tolerance 2
Without ground disturbance	LLES	2.9**	45.5	8.3 (SWC)	14.2 (light)
	SLES	1.7*	31.9	8.3 (SWC)	14.3 (light)
	LLLS	4.6***	43.6	8.3 (SWC)	28.5 (light)
With ground disturbance	LLES	4.3***	10.5	8.4 (SWC)	38.0 (SM)
	SLES	2.7**	65.9	14.1 (light)	38.0 (SM)
	LLLS	5.6***	13.5	8.3 (SWC)	16.0 (light)

ns: no significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

light = transmitted radiation

SWC = soil water content

SM = exposed mineral soil

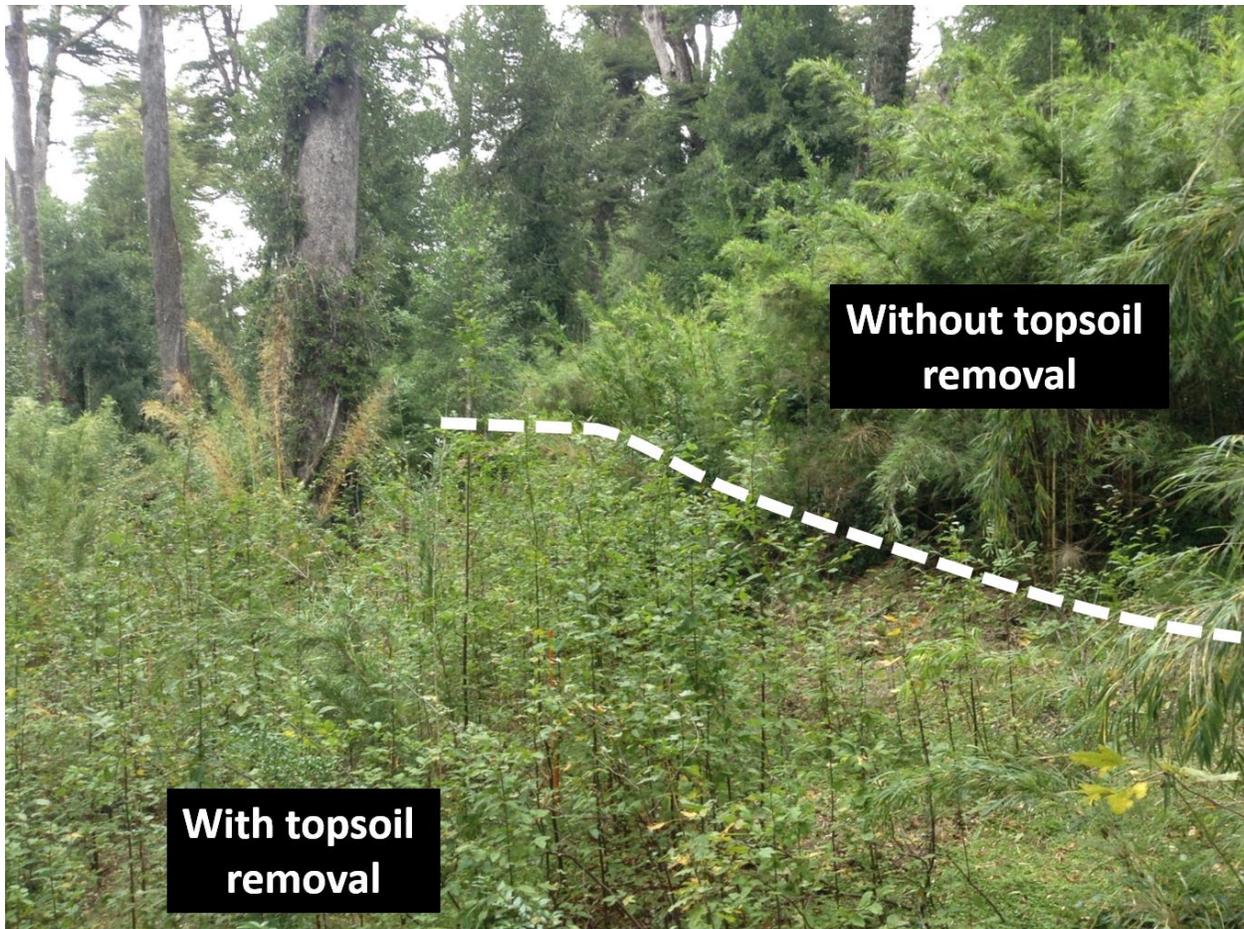


Fig. 1. Photo depicting the effects of topsoil removal after eight years in the Valle Hermoso site. Note the clear edge (dashed line) between areas with topsoil removal (to left of line; showing regeneration of SLES and LLES) and areas without topsoil removal (to right of line; showing dense thicket of *Chusquea culeou*).

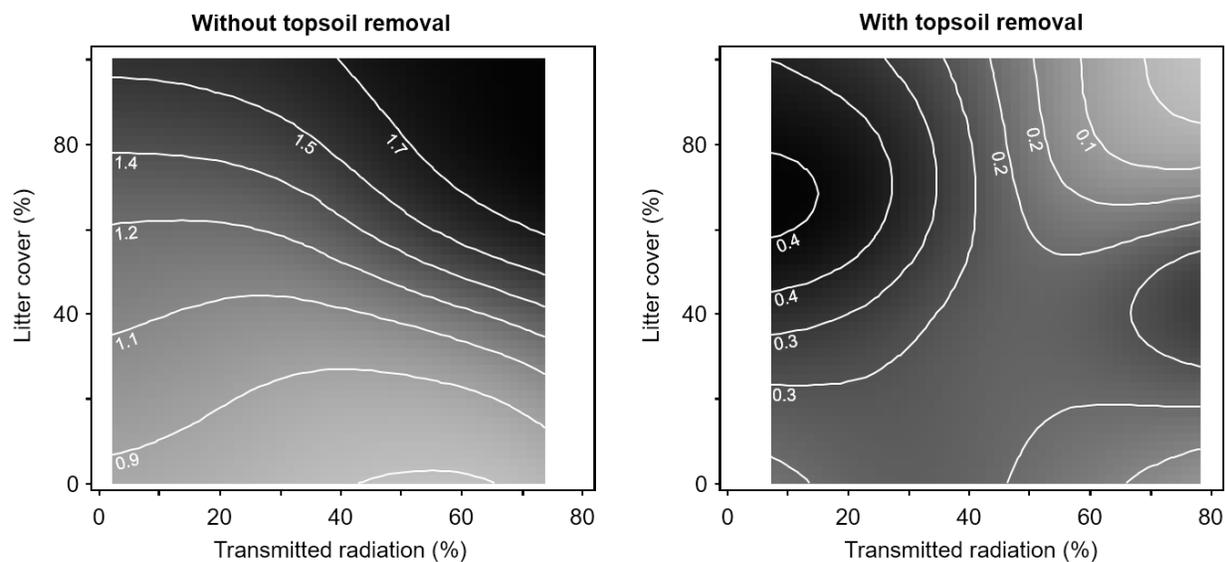


Fig. 2. NPMR-LM contour plots showing abundance of *Chusquea culeou* (log % of cover) as a function of the best supported predictors for areas with and without topsoil removal through scarification. Darker areas indicate higher abundance.

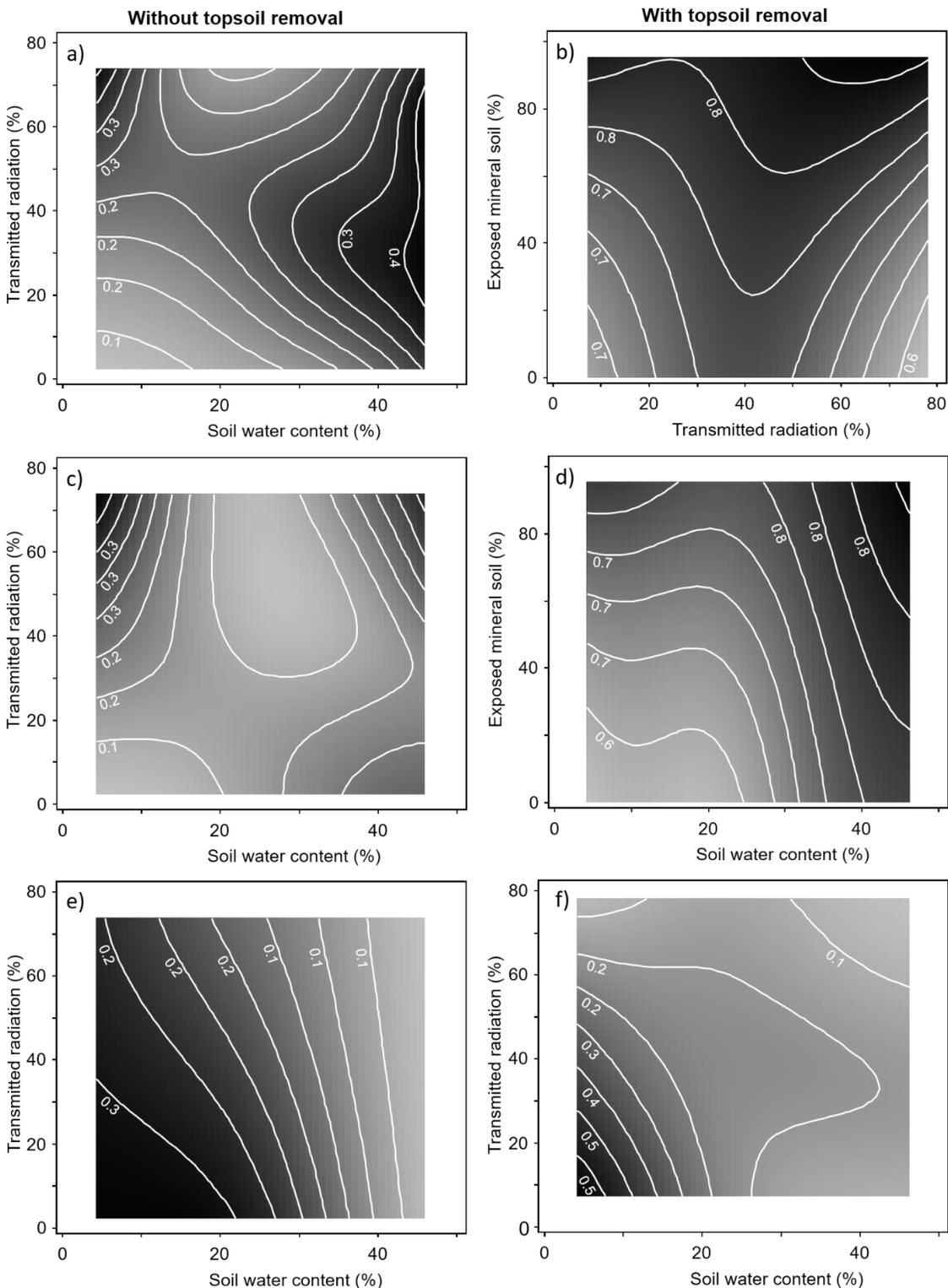


Fig. 3. NPMR-LM contour plots showing the probability of seedling presence as a function of the best supported predictors for areas with and without ground disturbances. Panels a and b show results for SLES, c and d for LLES, and e and f for LLLS. The gradual darkness show higher probability to find a seedling.

Supporting Information



Fig. S1. Study site conditions after high-grading on the four selected sites in the Chilean Andes.

a) Rincon del diablo, b) Lago Chan-Chan, c) Piedras Negras forests, and d) Valle Hermoso.

Note, the understories on all sites are dominated by a dense cover of *Chusquea*. Also all sites had similar residual stand structures and overstory composition, e.g., *Nothofagus* spp. which can provide effective seed sources for potentially rapid regeneration of *Nothofagus* species.

Supporting Information

Appendix S1. Field measurements of soil resistance to penetration, soil water content, and light availability

1) Soil resistance to penetration

We used a cone Fieldscout SC 900 soil compaction meter (Spectrum instruments, Inc.) with a resolution of 35 kPa and an accuracy of ± 103 kPa. Resistance to penetration was measured in five random spots in each regeneration plot by pressing down the Fieldscout with a uniform speed of ~ 3 cm sec⁻¹; otherwise, the instrument shows an error. To take readings, we used a cone with a base area of 1.25 cm²; readings were taken once the cone reached soil depth of 20 cm, a depth that contains most of the root systems of regenerating plants (sensu Puettmann et al. 2008; Soto et al. 2015). These measurements were taken in late summer (March) during the driest period of the year on two contiguous days per site (sensu Berger, Puettmann & Host 2004; Puettmann et al. 2008; Soto, Donoso & Puettmann 2014). Ares et al. (2005) and Soto et al. (2015) documented that penetration readings during dry periods are likely to be near the maximum values for the year, thus best reflecting stressful condition for seedlings.

2) Soil water content

The soil volumetric water content (SWC) was measured in five random spots in each regeneration plot with a time-domain reflectometer (TDR 100 soil moisture meter; Field Scout TM, Spectrum Technologies, Inc.) using peer rods of 20 cm. The resolution of this TDR soil moisture meter is reported to be 0.1%, accuracy $\pm 3\%$ SWC, with electrical conductivity < 2 dSm⁻¹, and range of from 0% to 50% of volumetric SWC, where 50% is typically maximum value (Spectrum Technology, Inc.). Three readings were taken during late summer (March), and

the average value for each regeneration plot was used as an integrated measure of SWC during the driest or most stressful period of the growing season.

3) Light availability

A hemispherical photograph was taken at the apex of all selected seedling to estimate the light availability using WinSCANOPY Pro 2013c software (Regent instruments, 2013). The software works with 24MP DSLR compact self-labeling O-Mount system with a calibrated fisheye lens, and automatic north finder (for further details about software and hardware see Regent instruments webpage (http://www.regentinstruments.com/assets/winscanopy_about.html)). Light availability was estimated as the total transmitted radiation (the sum of diffuse and direct beam radiation) computed as the percentage of growing season incident radiation (e.g., light index as % of full sun; Canham 1988). Photographs were taken during the growing season under homogeneous diffuse sky light conditions, i.e., during cloudy days or at dawn or dusk. Input parameters into WinSCANOPY included the solar constant ($1370 \text{ W}\cdot\text{m}^{-2}$), cloudiness index (0.5), spectral fraction (0.45), beam fraction (0.85), clear sky transmission coefficient (0.65), and standard overcast sky-regions brightness.

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Chapter 4

LIGHT AND NITROGEN INTERACT TO INFLUENCE THE REGENERATION IN NOTHOFAGUS OLD-GROWTH FORESTS AFTER PARTIAL DISTURBANCES

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Abstract

Light is one of the most important factors governing development of understory vegetation in forest ecosystems, including tree establishment and growth. Information about interactive effects of light with other resources such as water and nutrients is relatively scarce. How varying resources affect tree growth in forest understories is still unclear and current knowledge is largely confined to the northern hemisphere. A field experiment in which high-grading of an old-growth forest in the Andes of south-central Chile was followed by ground disturbance provided data about tree basal diameter growth responses under a wide range of light conditions, total nitrogen (tN) concentration in leaves, and water potential. We used a model selection approach to determine whether light is co-limiting with tN and water potential (or their interactions) for three species typically found in these forests and are known to vary in resource-use strategies. Species differed in growth response to light and tN, but not to water potential. For instance, radial growth of the tree species (*Nothofagus dombeyi*) with greatest light demand was strongly related to tN at high-light conditions only. The mid-shade tolerant species (*Nothofagus alpina*) had better basal diameter growth with high tN at high- and low-light environments. Contrary to expectations, radial growth of the late-successional shrub species (*Drimys andina*) was positively affected by light and tN in low-light environments only. Our results suggest that the species differences in regards to the impact of tN concentration along a light gradient are important factors that could influence plant community development. Restoration and management treatments can be more efficiently targeted if they are based on information about species sensitivities to interacting resource levels.

Introduction

Resource availability affects plant growth, thereby potentially influencing successional trajectories of forest ecosystems (Canham et al., 1996; Pacala et al., 1996) depending on the set of interacting ecological and environmental variables (Lambers et al., 2008; Harpole et al., 2011). Among these variables, light availability is considered one of the most important limiting factors in determining seedling and sapling growth in understories of forest stands (Canham et al., 1990; Pacala et al., 1996). However, studies have also shown a consistent association between tree species performances and light and soil conditions (Coomes and Grubb, 2000; Finzi and Canham, 2000; Hostle et al., 2011), specifically nutrient and water availability (Carter and Klinka, 1992; Bigelow and Canham, 2007), but these effects vary according to species-specific resource requirements (Drever and Lertzman, 2001; Kobe, 2006; Hostle et al., 2011). Thus, plant growth may be influenced by an interaction of soil moisture, nutrient and light availability (Carter and Klinka 1992; Kobe, 2006). Nitrogen (N) has been recognized as the element that globally is most limiting to plant growth in natural (Waring and Schlesinger, 1985; Catovsky and Bazzaz, 2002; Lambers et al., 2008) and managed temperate forest ecosystems (Binkley, 1985; Harpole et al., 2011; Goodman et al. 2013a; Mainwaring et al., 2014). In many settings, water availability limits N uptake and this co-limitation affects plant growth, and thus the development of forest communities (Waring and Schlesinger, 1985; Drever and Lertzman, 2001; Lambers et al., 2008). Although several studies have provided insights into the mechanisms how light limitations affect plant growth and its subsequent influence on forest ecosystem dynamics (Pacala et al., 1996; Bloor and Grubb, 2003), understanding the processes of how light is in co-limitation with other resources, such as N and water availability, is still unresolved.

The effects of water and nutrient limitations on tree growth in forest understories are complex and responses vary by species, associated with species' life history traits and the combination of the specific resource levels (Chapin et al., 1987; Reich et al., 1997; Lambers et al., 2008). For example, high foliar N content influenced growth at high light conditions in temperate conifers and hardwoods forests, while soil water availability affected growth in low-light conditions (Carter and Klinka, 1992; Drever and Lertzman, 2001; Finzi and Canham, 2000; Kobe, 2006). In contrast, multiple resource limitations in northern hardwoods in North America produced differing results. For example, calcium and N were equally important for growth of some tree species, while at other times, N alone had the greatest effect (Kobe, 2006; Bigelow and Canham, 2007). Such reports of contrasting growth responses within a species highlight the ambiguity of our understanding of tree responses to multiple resources. On the other hand, a consistent positive relationship between high foliar N levels and high light conditions has been observed in studies that focused on photosynthesis (Walters and Reich, 1997; Lambers et al., 2008; Goodman et al., 2013b). In contrast, soil nutrients and water availability do not appear to have a major influence on plant growth under low light conditions (Walters and Reich, 1997). Thus, plant reaction and its synergistic interactions with varying resource availability in ecosystems are complex and not well understood. Furthermore, most current knowledge is based on results from studies in northern hemisphere forest ecosystems.

In this study, we investigated how co-existing species of differing successional status respond to multiple, interacting resource limitations. These data will enable us to better predict differential responses to disturbance within managed forests. This will provide insights about possible mechanisms and implication for plant community development in disturbed forests. To this end, we used a gradient of light, leaf tN concentration and plant water potential conditions in

disturbed, high-graded stands in the south-central Chilean Andes to investigate how multiple conditions and their interactions influence basal diameter growth patterns of *Nothofagus dombeyi*, *N. alpina* and *Drimys andina*, species that are known to differ in terms of their resource use. Specifically, we hypothesized that: (a) the light demanding tree species (*N. dombeyi*) is more sensitive to tN limitations under high-light conditions than the late successional species; (b) the basal diameter growth of species with intermediate shade tolerance (*N. alpina*), but high sensitivity to tN concentration under the full light gradient, i.e., between the light demanding species and the shade tolerant species, respectively; (c) the shade tolerant species (*D. andina*) is less sensitive to tN and water potential levels under any light level.

Methods

Study sites

We selected four disturbed *Nothofagus* old-growth forest stands with a wide range of site productivity within the Coihue-Rauli-Tepa forest type in the Huilo-Huilo biological reserve (between 39-40°S and 500 to 1,400 masl). Each stand consists of a homogeneous patch dominated in most cases by *Nothofagus dombeyi* (coihue) and *Nothofagus alpina* (rauli). The general stand and soil characteristics for each site are presented in Table 1.

The climate in Huilo-Huilo is considered as Andean polar, with short and dry summers (December-March) and humid winters (June-September). The annual precipitation reaches 3,500 mm (Reyes et al., 2014) mainly as snow during winter months. The mean annual temperature ~9°C, with a mean of 4°C and 16°C for the coldest (August) and warmest month (February), respectively. Extreme temperatures can range from below -10 °C to above 30°C, and

30-50 annual frost events concentrated from August through September are common above of 550 m a.s.l. (Soto et al., 2009). On the other hand, soils in these sites correspond to a transition between Andisol (Acruoxic Hapludand) and Inceptisol (Andic Dystrudepts); both are coarse mixed and mesic soils that have a stratified structure and medium texture through the entire profile (Reyes et al., 2014).

In high altitudes, the studied forests are dominated by *N. dombeyi*, *N. alpina* and *Nothofagus pumilio* (lenga), which is a species adapted to harsh environmental conditions in the treeline (Donoso, 1993; Pollmann and Veblen, 2004). At lower altitudes this forest consists in a more complex and stratified vertical structure, showing the typical uneven-aged stand structure (i.e. reverse j-shape diameter size structure), where *N. dombeyi* and *N. alpina* are the dominant trees, and mid canopies are comprised mainly of shade-tolerant tree species, such as *Saxegothaea conspicua* (manio hembra or manio de hojas cortas), *Laureliopsis philippiana* (tepa) and *Dasyphyllum diacantoides* (trevo) (Donoso and Lusk, 2007). The understory vegetation in these forests is commonly comprised of bamboo (*Chusquea* spp.) and the shrub *Drimys andina* (canelo enano). Dense thickets of bamboo (*Chusquea* spp.) that proliferate quickly in understories affects ecosystem dynamics (Veblen et al., 1980; Veblen, 1982; González et al., 2002) by stalling forest recovery and succession (González et al., 2002; Reyes et al., 2013; Soto et al., 2015). To overcome this condition, forest managers started to implement ground disturbance through topsoil scarification with heavy machinery (i.e., bulldozer) after harvesting. Goals of these operations include to creation of “safe sites” for establishment and growth of early-seral *Nothofagus* tree species during the initial stages of post-disturbance succession by effectively controlling bamboo (Reyes et al., 2014; Soto et al., 2015). Further details about structure,

composition and stand dynamics of these forests can be found in Veblen et al. (1980) and Pollmann and Veblen (2004).

Overstory removal and ground disturbance

The four stands were disturbed through operational high-grading harvests during southern summer of 2000-2001, leaving on average residual basal areas between 50-63 m² ha⁻¹ and 137-273 trees ha⁻¹ (Table 1). Due to natural variability of spatial arrangement and size and quality of trees, harvesting only the largest, high quality trees led to spatial heterogeneous conditions, e.g., light conditions ranged from 4.5% to 80.5% of full sunlight (Table 1).

Topsoil removal through mechanical scarification was conducted by heavy machinery (Komatsu D4 bulldozer of 5,400 kg, with a horizontal blade) in the summer of 2005-2006. These operations removed the rhizomes and culms of *Chusquea* spp. and 20–40 cm of the upper soil layers (Reyes et al., 2014; Soto et al., 2015). As indicated above, ground disturbance of this type creates a complex spatial pattern, as the machine movement depends on the distribution of residuals trees and the presence of snags and logs on the forest floor. This typically leads to larger treatment areas connected by narrower pathways, reflecting a node-network (D. Soto, personal observation). In addition, such operations typically avoid removing already existing *Nothofagus* spp. regeneration. Scarification will not extirpate *Chusquea* spp. from the sites, and impacted around 24% to 46% of the total area in our study sites (Table 1). Technically, ground disturbance altered the chemical and physical properties of the remaining soil. Reyes *et al.* (2013, 2014) documented that in the top 20 cm of the soil, nutrient supply decreased (organic matter: 4 ± 2.8 %, total N: 0.07 ± 0.05 %, P (Olsen) 3.2 ± 2.0 mg kg⁻¹, K: 19 mg kg⁻¹), and Al saturation increased (30%); physically, the soil increased in bulk density (0.8 ± 0.1 g cm⁻³) and

penetration to resistance ($1.1 \pm 0.2 \text{ kg cm}^{-2}$). Further details on the effects that this restoration technique has on soil chemistry are given in Reyes et al. (2013, 2014).

Study design, species and measurements

In each of the four selected stands, we installed a 1-ha permanent rectangular plot with 100 circular regeneration plots of 2 m^2 (radii 0.8 m) in a 10 m by 10 m grid. The four stands exhibited a range of productivity, as reflected in top heights of the 10 tallest trees of *Nothofagus dombeyi* per stand, Table 1). We selected the tallest sapling of the three species (see below) in each regeneration plot (Table 4). Furthermore, measurement trees had to be free-to-grow, i.e., without apparent lateral understory competition quantified as having at least 75% of the upper crown free of competition, and any biotic and abiotic damage (e.g., chlorosis and clipping by browsing).

Characteristics of the species under study

We chose three species common in scarified and unscarified soil conditions in the four stands selected; these species are known to differ in resource utilization strategies (Table 2): 1) *Nothofagus dombeyi*, an evergreen, light demanding, early seral, tree species, considered plastic in terms of below-ground resource use. The plasticity in terms of resource use is evident by the variety of resource conditions in which the species can be found (Donoso et al., 2005, 2006a); 2) *Nothofagus alpina*, a deciduous early seral species that is mid-shade tolerant when young (Donoso et al., 2006b, 2013, 2015). This species is known to be very sensitive to below-ground resource, as it can only be found on soils that are well aerated with medium to high nutrient availabilities and high soil water holding capacity (Donoso et al., 2006b; Reyes et al., 2007; Soto et al., 2015). Finally, *Drimys andina* is a shade tolerant, late successional understory shrub

species with low water and nutrient requirements. It is considered a species with a plastic response to environmental stresses such as those characteristics of high mountain conditions near timber line (Veblen et al., 1977; Donoso, 2006). More details about species resource requirements are presented in Table 2.

Plant sampling

We harvested a total of 250 saplings and seedlings: 90 *N. dombeyi*, 100 *N. alpina*, and 60 *Drimys andina*. The harvesting and soil disturbance treatment and the grid sampling design ensured that the harvested plants had grown in a wide range of light, nutrients, and water availability (Table 3). A basal disc was removed from selected seedlings (1 cm above the seedling root collar) and we measured periodic annual radial growth for the last five years. Basal radial growth has been widely used as an integrated measure of whole-plant carbon balance in seedlings, which has been shown to be sensitive to resources (Coates and Burton, 1999; Drever and Lertzman, 1999; Finzi and Canham, 2000; Soto et al., 2015). The sampled discs were air dried for 2 weeks in a well-aerated environment (to avoid infection by fungi), and then gradually sanded in the laboratory. The tree ring widths were measured in two directions (wider and thinner, used the average of both as radial growth) of the sampled discs using a high precision digital caliper (resolution of 0.01 mm; Mitutoyo Absolute Digimatic caliper Series 500).

Light conditions

Before the plant harvest, a hemispherical photograph was taken at the apex of each selected seedling to estimate the light availability using WinSCANOPY Pro 2013c software (Regent instruments, 2013). The software works with 24MP DSLR compact self-labeling *O-Mount* system with a calibrated fisheye lens, and automatic north finder (for further details about

software and hardware see http://regent.qc.ca/assets/winscanopy_about.html). Light availability was estimated as the total transmitted radiation (the sum of diffuse and direct beam radiation) computed as the percentage of growing season transmitted radiation (e.g., light index as % of full sun; Canham, 1988). Photographs were taken during the growing season under homogeneous diffuse sky light conditions, i.e., during cloudy days or at dawn or dusk.

Water potential

Prior to plant harvest, we collected the terminal shoots and measured midday xylem water potential (Ψ_{xylem} , MPa) as an indicator of plant water status. At least three complete leaves were cut from each terminal shoot and immediately measured with a portable pressure chamber (PMS Instrument Co., Corvallis, Oregon) in the field. All measurements were taken between the end of March and early April (the driest period of the year in that location) and between 11 to 15 hours. Thus, sampling conditions should reflect highest water limitations during the yearly and daily water use cycle.

Nitrogen concentration

Total nitrogen (tN) concentration (%) was measured following standard Kjeldahl digestion procedures with colorimetric determination (Binkley, 1985; Sadzawka et al., 2004) for all plants used for measuring water potential and growth. We collected the plant material during the end of the growing season to ensure exposure to stressful conditions and the fluctuations of nutrient concentrations typically present during the growing seasons (*sensu* Sadzawka et al., 2004; Goodman et al., 2013a). We sampled a minimum of 10 g of green leaves without signs of chlorosis or mechanical damage by defoliation or herbivory from the upper crown (1/3 crown position) from each seedling. Leaves were stored in polyethylene bags and placed in an ice

container to avoid sample degradation and desiccation for a period not exceeding 24 hours in the field. Subsequently, plant material was air dried in an open and ventilated environment for 2 weeks. Next, the samples were dried for 24 hours in a drying oven at $72^{\circ} \pm 5^{\circ}\text{C}$ and then pulverized into small particles. The analysis was carried out by the Laboratory of Forest Soils and Plant Nutrition, Universidad Austral de Chile.

Statistical analysis

For each one of the species, we considered different models using the periodic (last 5 years) annual radial increment (hereafter radial growth) at the root-collar diameter as a measure of the plant response to growing conditions. Specifically, we used variations of the non-linear Michaelis-Menten model to describe radial growth as a function of various variables, including light availability (% transmitted radiation), water potential (MPa) and tN concentration (%), as fixed effects variables, and ground disturbance (disturbed and undisturbed soil conditions; categorical variable) and site quality (4 stands; categorical variable) as random effects. The inclusion of random effects terms helps account for possible correlations in the error structure. The choice of Michaelis-Menten model is partially justified because of its flexibility and parsimony to describe non-linear relationships, and the biological interpretability of its parameters. For these reasons, they have been widely used in forestry and ecological studies and allow for statistical assessment of interspecific differences in growth response as a function of light availability (see Pacala et al., 1994; Coates and Burton, 1999; Drever and Lertzman, 2001; Coomes et al., 2009; Soto et al., 2015).

We consider first the model:

$$y_i = d_i^\theta \frac{\alpha L_i}{\left(\frac{\alpha}{\beta}\right) + L_i} + \varepsilon_i, \quad (1)$$

where y_i is radial growth (mm/yr), L_i is light availability (transmitted radiation, %) and d_i is the plant size (root-collar diameter, mm), for the i th seedling. The coefficients α , β and θ are unknown parameters of interest and ε_i is the error term, which we assume to be normally distributed and with mean zero and constant variance (Pacala et al., 1994; Coates and Burton, 1999). The biological interpretation of the parameter α is the growth rate at a high-light level (model asymptote), and β is the growth rate at a low-light level or statistically the slope of the relationship at zero light (Pacala et al., 1994; Coates and Burton, 1999; Drever and Lertzman, 2001). Finally, the parameter θ corresponds to the initial plant size and is introduced to control the disproportionate size effects of plants (Kobe, 2006). Values of $\theta < 0$ reflect conditions where larger saplings induce less growth per unit of initial size than smaller saplings, while values of $\theta > 0$ indicates that larger saplings produce greater growth per unit of initial size than smaller seedlings (Kobe, 2006; Coomes et al., 2009).

To incorporate effects of additional single (i.e., water potential and tN) or multiple conditions (i.e., water potential \times tN) we considered the following variations of the model, as proposed by Kobe (2006):

1. - *High-light growth effects*: non-linear positive effect of light on growth with effects of other variables (R_i : 1.- water potential, 2.- tN and 3.- its interaction) more pronounced at high light.

2. - *Low-light growth effects*: variables (R_i) modify growth at low-light levels only.

3. - *Proportionate effect at high-and low-light*: proportional effect of variables (R_i) on growth along the light gradient, i.e., higher effect at high light levels than at low light levels.

4. - *Simultaneous growth limitation at high- and low-light*: simultaneous limitation of light and other variables (R_i) on plant growth (see Kobe, 2006; Finzi and Canham, 2000). For instance, below-ground resources could affect growth negatively at low light and positively at high light levels, or vice versa.

The mathematical expressions of all the models and the corresponding interpretation of the parameters are shown in Table 4. Model parameters were estimated using maximum likelihood and model comparisons were made using the corrected Akaike's information criterion (AICc), in order to avoid possible issues with the approximations due to the sample sizes. In this context, models with smaller AICc values are better supported by the data, and models within 2 units of AICc are considered equivalent (Burnham and Anderson, 2002). To facilitate comparisons, we also computed the Δ AICc, that is, the difference between AICc values of the best-fitting model and the other models, and the AICc-weights (w_a) that can be interpreted as a measure of strength of evidence favoring a specific model (Burnham and Anderson, 2002). Finally, we used the coefficient of determination R^2 as an additional indicator of model performance. All modeling was conducted in nlme package in R (Pinheiro et al. 2016).

Results

General resource and resource-growth patterns

The levels of light, water potential, and tN showed no evidence of multicollinearity (even when data were separated by species). On the other hand, preliminary examinations also showed evidence of association between radial growth and all predictors (i.e., light, tN, water potential) for *N. dombeyi* and *N. alpina* (Fig. 1). In contrast, radial growth of *D. andina* was only significantly related to light availability ($r = 0.380$, $p = 0.002$). The correlations between radial growth with light availability ($r = 0.578$, $p < 0.001$), tN ($r = 0.497$, $p < 0.001$) and water potential ($r = -0.457$, $p < 0.001$) were stronger for *N. alpina* than *N. dombeyi* (Fig. 1). Also, in isolation tN had a stronger influence on plant growth ($r = 0.615$, $p < 0.001$) in *N. dombeyi*, even more than light ($r = 0.522$, $p < 0.001$) and water potential ($r = -0.219$, $p = 0.038$). The strength of association between these variables becomes more evident when the nonlinear Michaelis-Menten model was used, as shown in Figure 2.

Effect of initial plant size on plant growth

All species showed the trend that smaller plants produced less radial growth per unit radius than larger plants ($\theta > 0$ in all cases, $p < 0.001$). In general, (based on the performance of the base model and the best supported model) *N. alpina* was the most sensitive to initial size differences, followed by *N. dombeyi* and by *D. andina* (see A.1). Thus, size of plant evaluated for the studied species played an important role in determining growth patterns.

Effect of light availability on plant growth

All parameters were significant ($p < 0.001$) in the base models for the three species, when only light was used as predictor variable (A.1). The models for the different species had similar

statistical support, as evident by the overlapping confidence intervals (A.1). However, *N. alpina* had the lowest growth under high light conditions, as reflected by $\hat{\alpha} = 0.181$, followed by *D. andina* ($\hat{\alpha} = 0.276$) and *N. dombeyi* ($\hat{\alpha} = 0.333$). Similarly, *N. alpina* had the lowest low light parameter $\hat{\beta}$ (0.03) followed by the *N. dombeyi* ($\hat{\beta} = 0.036$) and *D. andina* ($\hat{\beta} = 0.069$), even though the three confidence intervals overlapped (see A.1).

Species-specific growth responses to light availability, tN and water potential

The best model for *N. dombeyi* (light demanding species) was the model that reflected a tN concentration effect on radial growth mostly in high light environments (Table 5). There was high evidence that this model was superior $w_i = 0.892$ and had a high predictive ability (i.e., relationship between observed and predicted radial growth; $R^2 = 0.797$, $p < 0.001$). The second best supported model was the simultaneous effect of N at high- and low-light environments ($\Delta_i = 4.400$), supporting the notion that – in addition to light – tN concentration have a strong effect on radial growth (Table 5, Fig. 3).

For *N. alpina* (the intermediate shade-tolerant species with high sensitivity to N and water availability), the best supported model reflected a proportionate effect of N in low- and high-light environments ($w_i = 0.768$) and a high predictive ability ($R^2 = 0.880$, $p < 0.001$). The second best supported model reflecting tN concentration effects only at high light had a Δ_i of only 2.4, but these models differed when compared with likelihood ratio test ($p < 0.05$). This species also showed that high tN concentration increased the radial growth (Table 5, Fig. 3).

The best model for *D. andina* (late successional species) reflected a tN concentration effect only at low light environments ($w_i = 0.758$) and a high predictive ability ($R^2 = 0.569$, $p < 0.001$, Table 5). The base model was the second supported model with a Δ_i of 2.4 (Table 5).

Despite the minor differences in terms of AICc values, these models differed according to the likelihood ratio test ($p < 0.05$). The tN concentration effects in the best model are shown in Figure 3.

Discussion

Species-specific growth responses to resource availability

Our study highlights the sensitivity of light demanding species (*N. dombeyi*, coihue) to N under high conditions. This behavior appears to be generally accepted, as has been documented for different functional groups and individual tree species worldwide (Grubb et al., 1996; Finzi and Canham, 2000; Catovsky and Bazzaz, 2002; Kobe, 2006). Light demanding species have been shown to increase their metabolism as light availability increases (Lambers et al., 2008). This mechanism allows increased nutrient and water uptake and thus enhanced photosynthesis and carbon fixation (Field and Mooney, 1986; Lambers et al., 2008). Thus, light demanding species take advantage of the increased N that is often released after disturbances (Bormann and Likens, 1979; Kimmins, 1997). According to our results, growth of the light demanding species (*N. dombeyi*) benefitted from higher tN concentration when light levels were above 10-15% of light availability. Under lower light levels, increases in tN concentration in leaves did not result in increased growth, likely because these light-demanding species are not able to allocate carbon under low light conditions (Water and Reich, 1997; Lambers et al., 2008).

The proportionate response of the mid shade-tolerant, N-demanding tree species (*Nothofagus alpina*, rauli) reflected the species' known niche, i.e., its reputation for being sensitive to resource availability and as a poor competitor in natural forests and planted settings

when resources are not highly available (Reyes et al., 2007; Donoso et al., 2011, 2015; Soto et al., 2015). Under high light conditions this species acted similar to the light demanding species in terms of the response to tN concentration in leaves (see Fig. 2). However, in contrast to the light-demanding species, this species was extremely sensitive to tN under all light conditions, which is indicative of the resource demanding nature (Donoso et al., 2006b; Soto et al., 2015). Thus, even though not considered a late successional species, this species reacted positively to N inputs in shaded conditions, likely because high levels of N increased leaf chlorophyll concentration and thus photosynthesis, albeit modestly (Field and Money, 1986; Walter and Reich, 1997; Holste et al., 2011). This finding may contradict the postulates of previous studies showing that increased N availability reduces the growth and, in extreme cases increase the mortality at low light conditions for light demanding and mid shade-tolerant tree species (Grubb et al., 1996; Catovsky and Bazzaz, 2002), indicating that these mechanisms still need more ecological and functional clarification.

Contrary to our hypothesis, the late successional shrub species (*Drimys andina*, canelo enano) was most influenced by light availability and showed only minor impact of tN concentration on plant growth under low light conditions. These results are consistent with postulates that late-successional species are unresponsive to light, water and N availability, such as that documented for eastern hemlock (*Tsuga canadensis*) (Walters and Reich, 1997; Catovsky and Bazzaz, 2000; Bigelow and Canham, 2007). However, contrary to our expectations, this late successional species reacted positively to light after disturbance (see Fig. 2), despite being known as a shade tolerant species that typically suffers photo-inhibition in response to canopy openings (*sensu* Strauss-Debenedetti and Bazzaz, 1991; Valladares et al., 2002). The potential explanations include that this species adapts to mid-to-high light conditions presumably through

light acclimation mechanisms at the leaf level by increasing tN concentration and light availability (Chazdon, 1992). This finding for this late successional species contradicts previously published claims that species in this functional group are less plastic than co-occurring light demanding species (Strauss-Debenedetti and Bazzaz, 1991; Valladares et al., 2002), although there have been some exceptions reported from tropical rain forests in Panama (Chazdon, 1992) and northern hardwoods in the USA (Abrams and Mostoller, 1995). This shows that more research into these mechanisms is needed to clarify this functional behavior in late successional species.

Effects of species' differential resource use upon secondary succession

Our study provides insights how autecological species characteristics, specifically light and N requirements in conjunction with an understanding of disturbance effects on light, tN concentration, water potential provide insights about the processes governing plant growth in early stages of succession. The differences in species sensitivities and resource levels found on the study sites were strong enough to have implications for future stand composition and structure (Finzi and Canham, 2000; Kobe, 2006). For example, we found that the fast growth of light demanding species (*N. dombeyi*) during early stages of succession is strongly dependent on N. Similarly, the proportionate growth effects of tN concentration along a light gradient for intermediate shade-tolerant species with a high sensitivity to below-ground resources show that *N. alpina* may have lower competitive ability than light demanding species on dry slopes with heavy and poor nutrients soils that are typical conditions after large-scale disturbances such as landslides, fires, or volcanic eruptions (sensu Veblen et al., 1996; Franklin et al., 2002). Therefore, *N. alpina* and tree species with similar traits are strongly dependent of tree-fall gaps in mesic sites, which have high N and water availability (Kimmins, 1997; Thiel and Perakis,

2009). Obviously, the whole suite of species needs to be considered in such settings. For example, in the study region, severe competition can occur with released understory vegetation, such as the case of bamboo species in Chile (*Chusquea* spp.), creating a narrow window for regeneration and growth in competitive mesic environments (González et al., 2002; Soto et al., 2015).

In this study, we found that late successional species acclimate well to new conditions after disturbances, and are able to establish and grow in larger openings and disturbed soils, i.e., in areas considered suitable for light-demanding species. Our results also suggest that the late successional species may be well adapted to establishment in areas with little or low disturbance. This is likely due to its adaptation to low N and water along the light gradient and its acclimation mechanism at high light levels. Consequently, we found this species not only in most disturbed soils in areas with low to high light availability, but also in undisturbed and very shaded conditions (D. Soto, personal observation). This observation is consistent with the theory that successional patterns vary as a function of soil conditions, i.e., that the occurrence of light demanding species is greater in high-fertility soils (i.e., N in this study), and late successional species in low-fertility soils (Aerts & Chapin 2000; Lusk & Matus 2000; Coomes et al. 2009). The dominance of late successional species in low fertility soils is hypothesized to be a consequence of their nutrient and water conservation strategies (e.g., long-lived sclerophyllous leaves with low carbon assimilation rates) (Valladares et al. 2000; Lusk et al. 2014). This trait makes these species relatively unresponsive in high fertility soils, possibly resulting in low competitive abilities compared to with resource demanding species (Aersts & Chapin 2000; Valladares et al. 2000; Lusk et al. 2014). Therefore, the existing tradeoff between species' light preference and demand of soil resources may aid in understanding the compositional shifts at

different soil fertility gradients (Russo et al. 2005; Coomes et al. 2009). Thus, the stand dynamics of these forests are strongly impacted by the range of resource availability, in addition to light, but also (and may be more importantly) by acclimation mechanisms of the species to resources after disturbances.

Implication for forest management

Forest management operations have the ability to alter ecological processes and functions and thus successional pathways (Coates and Burton, 1999; Haeussler et al., 2013). This study evaluated the effects of ground disturbance upon regeneration growth in a forest ecosystem where succession had been sequestered after a partial and incomplete shelterwood cut (a partial disturbance) in the Andes of southern South America. These practices generated variable levels of tN, light and soil moisture, but the latter did not have an effect on regeneration growth, while the interaction of tN and light differed for the three relevant species. Silvicultural practices, such as overstory and understory treatments, have different impacts on resource levels and availability that are likely to affect seedling development of these three species, as demonstrated in our study herein. Understanding these differences and interactions, specifically the sensitivity to available resources, can help when designing silvicultural practices to encourage the development of desired stand structures and compositions.

The interacting effects of resources (in our study light and N) is of special importance, suggesting that the emphasis on managing light conditions may be warranted in some regions (e.g., Ligot et al., 2014; Klopčič et al., 2015) but may need to be expanded in other regions to include other factors, especially nutrients and water (Drever and Lertzman, 2000; Kobe, 2006; Bigelow and Canham, 2007). Thus, simple models, such as prescriptions based only on shade tolerance of a species (e.g., Table 2 in Silviculture Interpretations Working Group, 1994) may

not warrant the desired regeneration and could lead to alternative successional pathways in some regions if other relevant factors are not considered into these models. Similarly, guidelines that define species tolerance (in general) only by their sensitivity to low light levels (e.g., Hopper and Applegate, 1995) may need to be expanded to also address other resources (and environmental conditions) and their interactions (see also Valladares and Niinemets, 2008). Our study highlights the benefits when assessing silvicultural practices in terms of how they impact several factors that affect growth, both in terms of their individual and interactive effects.

Conclusions

In our study, leaf tN concentration played an important role in the radial growth of distinct species in terms of resource use. Leaf tN concentration was strongly related to the growth of shade-intolerant and plastic tree species to N availability at high-light levels. On the other hand, tN concentration was related with the radial growth of mid tolerant and high N demanding tree species to low- and high-light levels. Contrary to our expectation, shade-tolerant growth was related to light and N at low-light levels. On light of our results, we can infer that community organization after disturbances (i.e., overstory harvesting and ground disturbance) in *Nothofagus* old-growth forests is highly impacted by light and N. Higher N availabilities may have an important influence on the presence and dominance of shade-intolerant and (more importantly) in resource demanding species. However, release of understory plants after disturbance could influence the community organization after these disturbances. Therefore, management practices in these forests should consider this ecological information (i.e., species requirements in

availability of nutrients (tN), water and light) to design silvicultural practices to promote desirable tree regeneration and early growth.

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TABLE 1. Study site and stand characteristics.

Characteristic	Rincón del diablo	Lago Chan-chan	Piedras negras	Valle Hermoso
Latitude (°)	39°49'20	39°49'53	39°54'33	40°01'07
Longitude (°)	71°52'27	71°50'34	71°56'50	71°52'32
Altitude (masl)	1050	1200	1030	970
Top-height* (m)	41	34.6	39	44
Density (trees per ha)	145	137	273	285
DBH (cm)	44.0	40.5	34.1	35.4
Basal area (m ² ha ⁻¹)	50.6	55.8	54.9	63.3
Slope (%)	0-15	0-20	0-15	0-20
Aspect	SE	SW	E	SE
Soil texture**	Sandy loam	Sandy loam	Coarse sands	Loam
pH (water)**	5.3	5.0	5.7	5.7
tN (%)**	0.12	0.28	0.12	0.18
tC (%)**	8.4	10.2	5.2	6.5
SB (cmol+ kg ⁻¹)**	2.9	4.0	1.5	5.6
CEC (cmol+ kg ⁻¹)**	3.7	5.7	1.9	5.7

*: measured to the 10 highest trees in 1 ha, : variables without ground disturbance mapped in 1 ha permanent plot. CEC: cation-exchange capacity, and SB: sum of basis.

TABLE 2. Ecological niche requirements for the study species. The number of + signs indicates the strength of the sensitivity for a given resource (maximum degree for each category is 3 + signs).

Species	Shade-tolerance	Light	Water	Nitrogen	Sources
<i>Nothofagus dombeyi</i>	Intolerant	+++	+	++	Donoso (1993); Donoso et al. (2006a, 2011, 2015); Soto et al. (2014, 2015); Piper et al. (2009)
<i>Nothofagus alpina</i>	Mid	++	++	+++	Donoso (1993); Reyes et al. (2007); Donoso et al. (2006b, 2011, 2015); Soto et al. (2014, 2015)
<i>Drimys andina</i>	Tolerant	+	+	+	Veblen et al. (1977); Donoso (2006)

TABLE 3. Seedling size, light availability, water potential, and tN concentration (mean (standard deviation) and minimum and maximum) of the study plants. *d* is the root-collar diameter; *h* is total height. Light was estimated with hemispherical photographs. Water potential was measured with pressure bomb. tN was determined as total N concentration in leaves through Kjeldahl digestion.

Species	<i>N</i>	<i>d</i> (mm)	<i>h</i> (mm)	Light (% transmitted radiation)	Water potential (MPa)	tN (%)
<i>Nothofagus dombeyi</i>	90	17.2 (15.4)	155.4 (44.8)	36.4 (18.6)	0.8 (0.3)	1.3 (0.2)
		3.2-84.2	20.2-214.0	4.5-80.5	0.3-1.8	0.8-1.9
<i>Nothofagus alpina</i>	100	19.5 (13.3)	169.8 (87.8)	33.4 (18.1)	1.1 (0.4)	1.7 (0.3)
		3.5-63.1	30.0-330.2	5.0-80.2	0.4-2.6	0.7-2.7
<i>Drimys andina</i>	60	10.6 (3.5)	91.2 (34.5)	28.87 (17.5)	0.9 (0.3)	1.3 (0.2)
		3.8-30.1	15-210	4.6-78.0	0.3-2.2	0.8-1.7

TABLE 4. Selected models and ecological interpretation of their parameters and of the model as a whole (modified from Kobe, 2006).

Model	Parameters	Biological interpretation
1.- Base $y_i = d_i^\theta \frac{\alpha L_i}{\left(\frac{\alpha}{\beta}\right)^{+L_i}} + \varepsilon_i,$	α : asymptotic growth. β : growth at low light. d : power constant of tree size. θ : plant size effect.	Non-linear positive effect of light. Saturation of growth at high light levels.
2.- High light growth effect $y_i = d_i^\theta \frac{(\hat{\alpha} R_i) L_i}{\left(\frac{\hat{\alpha} R_i}{\beta}\right)^{+L_i}} + \varepsilon_i,$	$\hat{\alpha}$: Resource term affects high light asymptotic growth. β : see model 1. d : see model 1. θ : see model 1.	tN or water potential or both modifies high-light growth.
3.- Low light growth effect $y_i = d_i^\theta \frac{\alpha L_i}{\left(\frac{\alpha}{\beta R_i}\right)^{+L_i}} + \varepsilon_i,$	α : see model 1. $\hat{\beta}$: Resource term affects low light term. d : see model 1. θ : see model 1.	tN or water potential or both modifies low-light growth.
4.- Proportionate effect at high- and low- light $y_i = d^\theta \frac{(\hat{\alpha} R_i) L_i}{\left(\frac{\hat{\alpha} R_i}{\beta R_i}\right)^{+L_i}} + \varepsilon_i,$	$\hat{\alpha}$: see model 2. $\hat{\beta}$: see model 3. d : see model 1. θ : see model 1.	tN or water potential or both proportionally modifies low- and high-light growth.
5.- Simultaneous limitations at high- and low- light $y_i = d_i^\theta \frac{\alpha L_i R_i}{\left(\frac{\alpha}{\beta}\right)^{+L_i} \left(\frac{\alpha}{\beta_{low}}\right)^{+R_i}} + \varepsilon_i,$	α : asymptotic growth term at high light and high resource terms (N or water or both). β : see model 1. d : see model 1. θ : see model 1. $\hat{\beta}_{low}$: Growth term at zero resource (N or water or both).	Simultaneous limitation of light and a tN or water potential or both).

TABLE 5. AICc results for the various models, separated by the hypotheses that the models represent and by species. Δ_i is AICc difference between best supported model (bold numbers) with competitive ones. w_i is the AICc weights. R^2 is the coefficient of determination between observed and predicted values. In bold is shown the best supported model.

Models	<i>Nothofagus dombeyi</i>				<i>Nothofagus alpine</i>				<i>Drimys andina</i>			
	AICc	Δ_i	w_i	R^2	AICc	Δ_i	w_i	R^2	AICc	Δ_i	w_i	R^2
Base												
1. Light	139.5	32.0	0.000	0.710	104.8	36.8	0.000	0.816	-4.7	2.4	0.228	0.552
High-light resources effect												
2. Light, nitrogen	107.5	0	0.892	0.797	70.4	2.4	0.231	0.877	12.8	19.9	0.000	0.435
3. Light, water	-	-	-	-	-	-	-	-	15.3	22.4	0.000	0.490
4. Light, water, nitrogen	177.0	69.5	0.000	0.591	175.4	107.4	0.000	0.702	19.0	26.1	0.000	0.446
Low-light resources effect												
5. Light, nitrogen	145.9	38.4	0.000	0.689	110.7	42.7	0.000	0.816	-7.1	0	0.758	0.569
6. Light, water	136.4	28.9	0.000	0.719	90.9	22.9	0.000	0.849	2.9	26.1	0.000	0.491
7. Light, nitrogen, water	144.2	36.7	0.000	0.695	100.0	32.0	0.000	0.834	1.3	8.4	0.011	0.504
Proportionate effect of resources at low- and high-light environments												
8. Light, nitrogen	116.8	9.3	0.008	0.777	68.0	0	0.768	0.880	6.0	13.1	0.001	0.485
9. Light, water	-	-	-	-	141.0	73.0	0.000	0.778	10.2	17.3	0.000	0.499
10. Light, nitrogen, water	166.8	59.3	0.000	0.613	131.1	63.1	0.000	0.796	14.5	21.6	0.000	0.460
Simultaneous limitation at low- and high-light environments												
11. Light, nitrogen	111.9	4.4	0.098	0.787	87.5	18.5	0.000	0.857	24.4	31.5	0.000	0.364
12. Light, water	249.1	141.6	0.000	0.281	-	-	-	-	32.5	39.6	0.000	0.449
13. Light, nitrogen, water	-	-	-	-	-	-	-	-	-	-	-	-

‘-’: do not converge

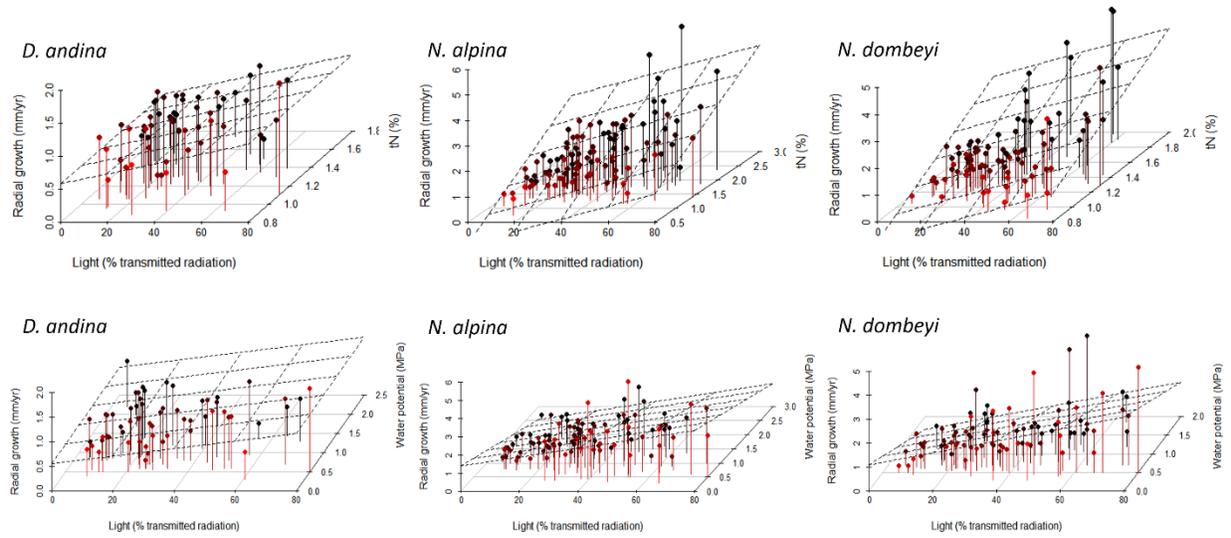


Fig. 1. Tridimensional relationship between radial growth (mm/yr) with light (% transmitted radiation), N concentration (tN%), and water potential (MPa) for the study species. Gradient from red to black dots represent the low to high conditions in tN and water potential, respectively. The surface planes are the linear relationships among variables.

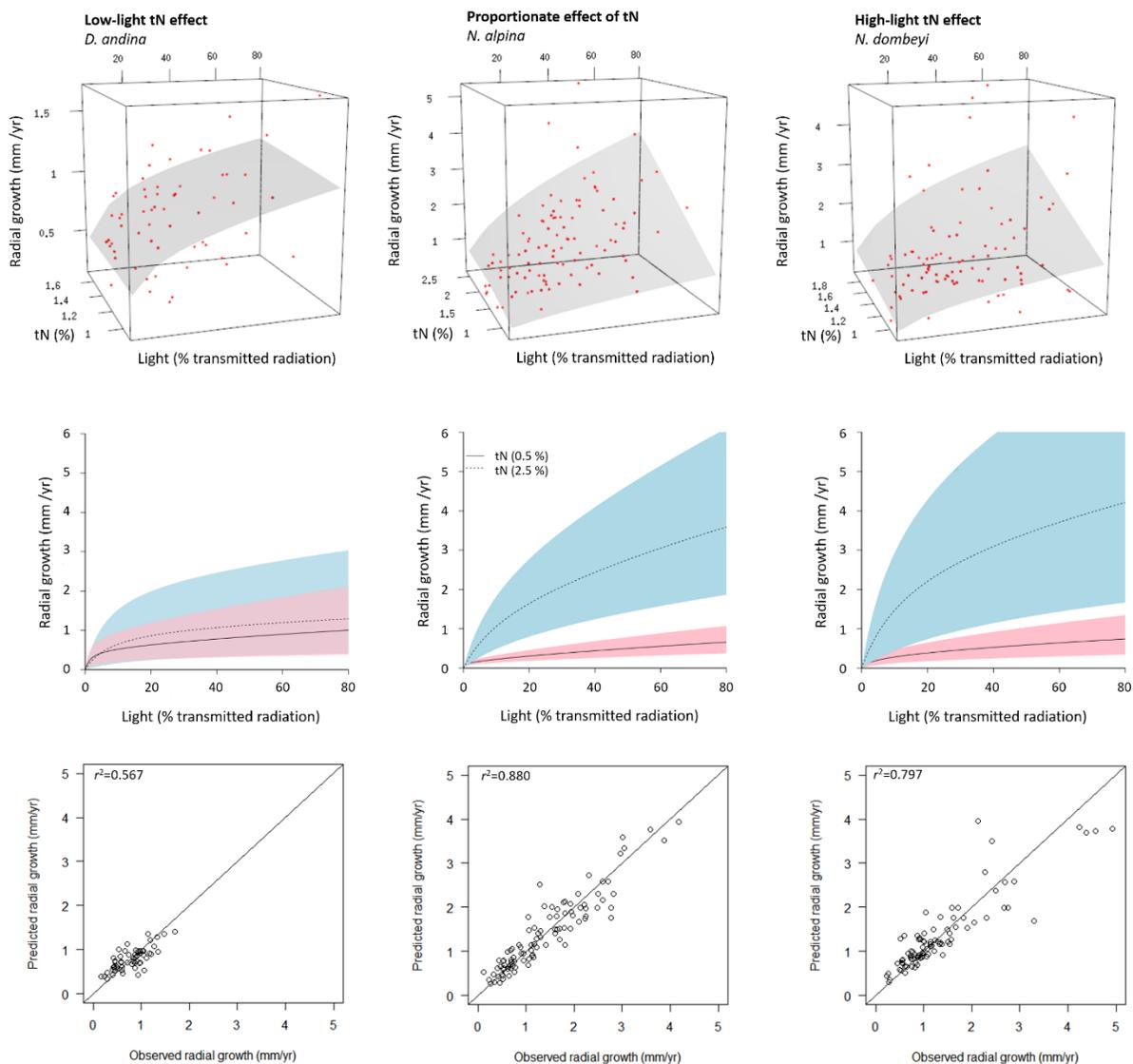


Fig. 2. Best supported models and observed growth values for each studied species (upper row). Middle row shows the effects of high (2.5%)- and low (0.5%)-levels of tN concentrations in leaves, the shaded areas show the Confidence intervals at 95%. Lower row shows the relationship between predicted vs. observed values for the best supported models.

Appendix 1

Estimated parameters (standard error) and confidence intervals at 95% for Michaelis-Menten equation. $\hat{\alpha}$ represents the asymptotic estimated parameter, $\hat{\beta}$ represents the low light parameter and $\hat{\theta}$ represents the parameter of effect of plant size (\emptyset). Bold numbers per species represent the best model estimation (i.e., lowest AICc). Empty spaces are those models without convergence in the estimation.

Model		<i>Drimys andina</i>			<i>Nothofagus dombeyi</i>			<i>Nothofagus alpina</i>		
		$\hat{\alpha}$	$\hat{\beta}$	$\hat{\theta}$	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\theta}$	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\theta}$
1.	Light, \emptyset	0.276***(0.062)	0.069**(0.026)	0.482***(0.072)	0.333***(0.078)	0.036**(0.013)	0.604***(0.051)	0.1814***(0.039)	0.033**(0.012)	0.767***(0.051)
1.	Light, N, \emptyset	0.150-0.402 0.271***(0.073)	0.0163-0.122 0.047**(0.015)	0.336-0.628 0.426***(0.084)	0.176-0.489 0.271***(0.051) .169-0.373	0.009-0.063 0.050***(0.017)	0.501-0.707 0.549***(0.043)	0.103-0.259 0.1611***(0.025) 0.109-0.212	0.008-0.059 0.037***(0.009)	0.664-0.870 0.636***(0.038)
1.	Light, W, \emptyset	0.125-0.418 0.182***(0.056)	0.016-0.078 0.022***(0.006)	0.257-0.595 0.726****(0.096)	-	0.015-0.085	0.464- 0.635	-	0.018-0.057	0.559-0.712
1.	Light, (NxW), \emptyset	0.068-0.296 0.194***(0.056)	(0.008-0.036) 0.026***(0.008)	0.533-0.919 0.621****(0.094)	1.415*(0.584)	0.012****(0.002)	0.482****(0.057)	0.672*(0.259)	0.007****(0.001)	0.641****(0.070)
1.	Light, N, \emptyset	0.076-0.313 0.275***±0.059	0.010-0.043 0.086**±0.030	0.432-0.811 0.486***±0.070	0.254-2.577 0.261***±0.054	0.007-0.017 0.090ns±0.056	0.367-0.596 0.644***±0.050	0.158-1.186 0.139***±0.027	0.003-0.010 0.140ns±0.123	0.502-0.781 0.819***±0.049
1.	Light, W, \emptyset	(0.156-0.395) 0.233***±0.056	(0.024-0.148) 0.158ns±0.122	(0.345-0.627) 0.504***±0.079	(0.152-0.370) 0.362***±0.081	(-0.021-0.203) 0.024***±0.007	(0.544-0.743) 0.587***±0.051	(0.085-0.193) 0.226***±0.043	(-0.105-0.386) 0.031***±0.006	(0.720-0.917) 0.713***±0.048
1.	Light, (NxW), \emptyset	(0.121-0.346) 0.242***±0.056	(-0.087-0.404) 0.150ns±0.150	(0.344-0.664) 0.499***±0.077	(0.201-0.524) 0.281***±0.059	(0.010-0.039) 0.053*±0.024	(0.485-0.688) 0.630***±0.050	(0.139-0.312) 0.181***±0.033	(0.017-0.044) 0.070**±0.021	(0.617-0.810) 0.762***±0.048
1.	Light, N, \emptyset	(0.128-0.356) 0.283***±0.069	(-0.029-0.330) 0.059**±0.017	(0.343-0.654) 0.424***±0.017	(0.163-0.400) 0.234***±0.040	(0.004-0.102) 0.102*±0.046	(0.529-0.731) 0.574***±0.042	(0.114-0.248) 0.141***±0.019	(0.027-0.112) 0.071***±0.019	(0.666-0.858) 0.670***±0.036
1.	Light, W, \emptyset	(0.144-0.421) 0.245***±0.072	(0.024-0.093) 0.025***±0.007	(0.268-0.580) 0.633***±0.092	(0.154-0.314) -	(0.009-0.196) -	(0.490-0.658) -	(0.102-0.180) 0.683***±0.170	(0.034-0.109) 0.009***±0.001	(0.598-0.742) 0.661***±0.060
1.	Light, (NxW), \emptyset	(0.099-0.390) 0.224***±0.064	(0.011-0.039) 0.037**±0.011	(0.447-0.819) 0.572***±0.091	0.742***±0.174	0.016***±0.003	0.530***±0.053	(0.345-1.020) 0.331***±0.071	(0.005-0.012) 0.016***±0.002	(0.540-0.781) 0.685***±0.053
1.	Light, N, \emptyset	(0.095-0.354) 0.028***±0.008	(0.015-0.060) 0.003ns±0.002	(0.390-0.755) 0.420±0.094	(0.395-1.089) 0.0282***±0.007	(0.009-0.022) 0.002ns±0.001	(0.424-0.636) 0.516***±0.043	(0.189-0.473) 0.017***±0.003	(0.010-0.021) 0.001*±0.000	(0.578-0.791) 0.564***±0.041
1.	Light, W, \emptyset	(0.010-0.046) 0.012**±0.003	(-0.001-0.007) 0.001ns±0.001	(0.230-0.610) 0.876***±0.116	(0.013-0.042) -0.011**±0.004	(-0.001-0.006) 0.001*±0.000	(0.429-0.602) 0.944***±0.096	(0.001-0.024) -	(0.000-0.003) -	(0.004-0.647) -
1.	Light, (NxW), \emptyset	(0.004-0.020) -	(-0.000-0.003) -	(0.644-1.108) -	(-0.019-(-0.003)) -	(0.000-0.002) -	(0.752-1.135) -	-	-	-

ns: non-significant, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

RECOVERY OF HIGH-GRADED *NOTHOFAGUS* FORESTS:
BUILDING RESILIENCE THROUGH THEORY AND PRACTICE

Chapter 5

General conclusions

Study synthesis

The motivation of this dissertation was to study how recovery of degraded forests can be explained using an integrative ecological perspective, and how this information can be used to develop efficient restoration treatments. Using degraded *Nothofagus*-dominated forests in south-central Chile as a real-world example also allowed development of a linkage between theoretical concepts and restoration practices.

Chapter two describes a view of ecosystems in the context of properties related to phases of the adaptive cycle (e.g. from exploitation to conservation phases) and ecological traps (poverty, rigidity and lock-in trap) (Gunderson and Holling, 2002; Allison and Hobbs, 2004), specifically in terms of potential (biomass or energy of the system), connectedness (rigidity of internal control to external influences) and resilience (the ability of ecosystems to react to disturbances while staying in the same basin of attraction). This perspective provided important insights for designing restoration strategies to overcome arrested succession, move the ecosystem into a desirable basin of attraction, and encourage successional development. Similarly, viewing basins of attraction (stable states that tend to change toward an attractor) in a dynamic context, e.g.,

viewing how the shape of a basin of attraction changes over time due to changes in properties (e.g. potential and connectedness are built through succession, and resilience is reduced), provided a conceptual linkage between the multiple equilibrium and succession theories. Viewing basins of attraction in such a dynamic way may facilitate the design of restoration activities that re-shape the basin of attraction by altering the species composition (Ghazoul et al., 2015). Next, I illustrated how management activities that reduce undesirable understory vegetation and provide suitable conditions (resources and safe microsites) for regeneration of desirable species may deepen and widen the basin of attraction and thus facilitates provision of desirable ecosystems services associated with advanced successional stages. My review highlighted important connections between succession and multiple equilibrium theories. Contrasting two distinct states in term succession (one dynamic and the other static) provided important ideas to aid in the promotion of efficient restoration efforts based on strong ecological principles.

Chapter three showed that topsoil removal through scarification effectively controlled the recalcitrant understory vegetation and improved regeneration of early-seral tree species as evaluated eight years after application of restoration treatments. These treatments improved the safe site conditions for regeneration of early-seral *Nothofagus* tree species, mostly by reducing interspecific competition from *Chusquea culeou* and the thick litter layer on the forest floor (Veblen, 1982). Also, the likelihood to find desirable early-seral regeneration increased by an interaction of (higher) soil water content and (higher) light availability. This finding appears to be unique to the Andean forests, as other studies in similar settings have suggested a dominant light effect only (Veblen, 1982; González et al., 2002). On the other hand, in undisturbed ground conditions the

combination of high litter cover and high light levels was indicative of higher abundance of *C. culeou*. This study supports earlier findings that *C. culeou* strongly interferes with tree regeneration (Veblen, 1982; González et al., 2002). Among others, high litter cover acts as an ecological filter for tree establishment (George and Bazzaz, 1999). Overall, topsoil removal could be considered an important restoration tool in the studied forests.

Chapter four quantifies how resources levels influence the growth of understory shrub (*Drimys andina*) and other species groups. Mainly, the interaction of higher light availability and higher plant N concentration improves growth of species groups that initiate successional development. Shade intolerant and plastic tree species (*Nothofagus dombeyi*) grew better at high levels of light and N, showing the typical characteristic of light demanding species (Lambers et al., 2008; Harpole et al., 2011). On the other hand, mid-tolerant and resource demanding tree species (*Nothofagus alpina*) grew better along the light gradient (4.5-80.5% of transmitted radiation) when N was highly available at low and high light availability. Contrary to expectations, the shade tolerant and plastic shrub species (*Drimys andina*) reacted positively to the interaction of light and N, showing an adaptation mechanism at the leaf level. This is an important finding because, in general, shrub species have higher water and nutrient conservation strategies than trees, which increase their competitive ability in the understory (Valladares et al., 2000).

Studies integration

This study is an example of how viewing restoration treatments in the context of ecological theories, i.e., integration of succession, properties (potential, connectedness and resilience) of adaptive cycle phases and ecological traps (poverty, rigidity and lock-in trap) into multiple equilibrium model can provide a better understanding of opportunities

for restoring forest ecosystems, using in this context the regeneration as a proxy of engineering resilience; sensu Gunderson and Holling, 2002). Specifically, it provided a conceptual understanding about why topsoil removal through scarification in high-graded *Nothofagus* old-growth forests appears to be an effective and successful restoration practice for controlling *C. culeou* and encouraging early-seral *Nothofagus* species regeneration in these forests.

In the studied forests, one of the main drivers of vegetation development is the presence of native understory shrub *C. culeou*, which is a common component in almost all undisturbed, late-successional, temperate old-growth forests in South America (sensu Veblen 1982; González et al. 2002). High grading, typically lead to increased cover of *C. culeou* in disturbed forests due to its high connectedness and resilience. *C. culeou* arrests successional development by preventing natural regeneration of *Nothofagus* trees and mid- and late-seral tree species, mostly by its high competitive and adaptation (i.e. at leaf level) to new environmental conditions after high-grading (Veblen, 1982; González et al., 2002; Soto et al., 2015). When viewing these forests in the context of the panarchy cycle (sensu Gunderson and Holling, 2002), it is important to consider that late successional forests have high connectedness, high potential (as energy or biomass used to build the system), and low resilience (sensu Gunderson and Holling, 2002; Carpenter and Brock, 2008). The connectedness allows the system to remain stable, as, for example, after small-scale openings are typically filled with late-successional tree species that are already present in the overstory, leading to minor changes in structure and composition. The late successional phase in absence of disturbances can be considered as a stable state, can be viewed as a trap (sensu Carpenter and Brock, 2008), that prevents ecosystems

from adapting to new or altered conditions. In this context, late successional *Nothofagus*-dominated forests can be viewed as being in a rigidity trap in absence of disturbances.

High grading appears to be an anthropogenic disturbance that is typically large and intense enough to move late successional stage out of the stable state by reducing the connectedness and environmental conditions that are not suitable for regeneration of late-seral tree species that would replace the harvested trees and maintain the forest in late-successional conditions. However, rather than following more standard successional development, the environmental conditions after high-grading in *Nothofagus* old-growth forests typically match those conditions of *C. culeou*, rather than those of early (in larger openings)- and late-seral (in smaller openings) trees species. Thus, these conditions in understory lead to an extended dominance of dense thickets of *C. culeou* in many high-graded old-growth *Nothofagus* forests in south-central Chile. One can view such arrested succession conditions in ecosystem as another ecological trap (Allison and Hobbs, 2004). This provides an example of what Allison and Hobbs (2004) labeled a “lock-in trap” pathological state, which is characterized for having high resilience and connectivity, but low potential (e.g. biomass).

Implications for forest management

This study highlights how restoration scientists can take advantage of ecological theories to propose management strategies for a broader set of environmental conditions than tested in experiments, such as topsoil removal by scarification. Utilizing ecological theory to gain a more mechanistic understanding is especially useful when restoration treatments are planned for conditions that have not existed in the past, i.e., when results are extrapolated to novel conditions without an historical equivalent (Hobbs et al., 2009).

I found that the factors indicative for the establishment of regeneration of early-seral *Nothofagus* species included high soil water content and exposed mineral soil, with light availability playing a secondary role during the establishment and early growth of early- and late-seral tree species. The plasticity of *Nothofagus* species in terms of light requirements during early stages of regeneration allows seedlings to establish and persist under deep shade in areas with relatively little competition from understory species (Pollmann and Veblen, 2004; Donoso et al., 2015). However, the radial growth of seedlings established of early-seral *Nothofagus* (*N. dombeyi* and *N. alpina*) species were strongly influenced by the interaction of light availability and total nitrogen concentration in leaves, showing that this interaction plays a pivotal role during early secondary succession after disturbances, such as high-grading. Thus, the differences in resource use at the “establishment” and “growth” stages (sensu Schupp 1995, Young et al. 2005) may be considered carefully in restoration and management practices. For example, the information about which species’ environmental variables are influencing the establishment and growth stages in plant development for different seral species or plant groups may vary in ecosystems, e.g., as influenced by belowground resource conditions (Royo and Carson 2006). Thus, the scope of inference for management practices might be clearly defined in conjunction with key ecological information, such as those gave in this thesis, to avoid inefficient and unexpected management results (e.g. scarify soils in heavier or shallower soils than this thesis).

Thus, the broader ecological framework, based on ecological theories gave important insights for a better and integrated understanding of ecosystem dynamics. This understanding can be useful for the selection of practical and viable solutions for

restoration. Additionally, my thesis showed that viewing plants in terms of their traits appears to be helpful when applying restoration treatments (Pywell et al., 2003; Herault et al., 2005). Knowledge about plant traits allows a better understanding of the ecological processes driving regeneration patterns. For example, grouping species according to their shade tolerance, life span, crown form, and general information about requirements of belowground resources is very useful and also facilitates that our findings can be extrapolated to other forest ecosystems (sensu McGill et al., 2006).

Final thoughts

Restoring a degraded forest may be a hard and costly task, especially if the forest dynamics are not well understood. A comprehensive analysis and integration of theories may lead to a better understanding of ecosystems and thus may help avoid inefficient restoration efforts. In this context, successional theory provides important insights, but by itself is not enough to ensure desirable results of restoration treatments in the long term (Suding et al., 2004; Pickett et al., 2009).

Investigating restoration strategies based on integration of ecological theories may help to restore more efficiently degraded forests, which is globally important since forests are receiving increased pressure to provide ecosystem services, such as clean water, habitat diversity, tourism, carbon sink, among others. At the same time, demand for forest products increases due to increasing population levels, higher demands for forests to provide a basis for a sustainable "green" economy.

Depending on how much the system is degraded, or how many remnant trees provide seeds or propagules, forest restorationists might put more or less efforts on tree

regeneration as a prime outcome of forest restoration (Lamb et al., 2005; Chazdon, 2008; Ghazoul et al., 2015). When propagules are available by succession is stagnant, enhancing or constraining the availability of resources (light, nutrients, and water) and safe sites for regeneration of desirable tree species that re-initiate succession is an imperative task in forest restoration. Tree regeneration that leads succession progression can be viewed as a proxy of ecosystem resilience and the basis to foster succession dynamics that will eventually allow forests to provide the ecosystems services expected from society.

Finally, it is important to mention the need for social and political acceptance and the role that a better integration of basic ecological knowledge can play when defining institutional and community agendas (Chapin et al., 2011). Ecosystems that can provide a variety of goods and services, in addition to timber, are viewed in some discussions as becoming a fundamental human right for societies (Andersson et al., 2015).

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