

Regeneration niches in *Nothofagus*-dominated old-growth forests after partial disturbance: Insights to overcome arrested succession

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ABSTRACT

Arrested succession may lead to losses of productivity and biodiversity in forests after disturbance. In this condition, recalcitrant understory vegetation often dominates over long periods of time and delays forest recovery and succession. Arrested succession has been defined as a type of forest degradation because ecosystem processes and functions that underlie successional dynamics are dramatically reduced. We used the Hutchinson' niche concept to understand the relative importance of environmental variables that define niche axes of species leading to arrested succession (recalcitrant understory vegetation) and to identify a shift along niche axes that promote the successional progression of long-lived early- and late-seral tree regeneration after partial disturbance due to restoration treatments. We studied *Nothofagus* old-growth forests in the Chilean Andes, where after selective harvests (i.e., a partial overstory disturbance) the understory is commonly dominated by dense thickets of native bamboo (*Chusquea* spp.), which has been shown to arrest succession by preventing tree regeneration. To overcome this, sites are typically partially scarified (24 to 45% of the area) following harvest to control bamboo and to encourage early-seral tree regeneration. The partial overstory and ground disturbance leaves a wide array of conditions (environmental gradient) that allowed us to investigate the factors under which a given plant group may regenerate, grow, and dominate the forest. Ordination and niche modeling were used to investigate the niche breadths for bamboo and regenerating tree species, as well as the environmental niche axes at this early successional stage, i.e., eight years after disturbance. The results showed different trends in the shift of centroid and extent of realized niches among three plant groups. For instance, performance of the early-seral group was related to litter cover (–), exposed mineral soil (+) and soil water content (+), which resulted in a niche expansion. In contrast, soil water content affected bamboo (–) and may be responsible for the reduction in realized niche space. Light had less influence on defining niches for tree regeneration during early successional stages. Linking the niche concept to succession provided a simple display of multifaceted issues and thus a better understanding of underlying processes and mechanisms. It provides an example of how application of this concept can help to determine situations in which such regeneration can (or cannot) be established successfully and promote the progression of succession following disturbance. This knowledge provides important insights for designing management and restoration practices based on strong ecological foundations.

1. Introduction

Arrested succession occurs due to proliferation of dense thickets of recalcitrant understory vegetation that act as an ecological filter in early successional stages by preventing early- and late-seral tree establishment and growth (Niering and Goodwin, 1974; George and Bazzaz, 1999; Mallik, 2003; Royo and Carson, 2006; Soto and Puettmann, 2018a). This condition stalls and delays forest successional

dynamics over long periods of time (George and Bazzaz, 1999; Royo and Carson, 2006; Soto and Puettmann, 2018a). It is a type of forest degradation because ecosystem processes and functions that underlie successional dynamics are dramatically reduced (sensu Ghazoul et al., 2015).

The *niche* concept is used extensively in ecology to understand the environmental variables and factors that shape performance of species (Hutchinson, 1957; Chase and Leibold, 2003). The *fundamental* niche

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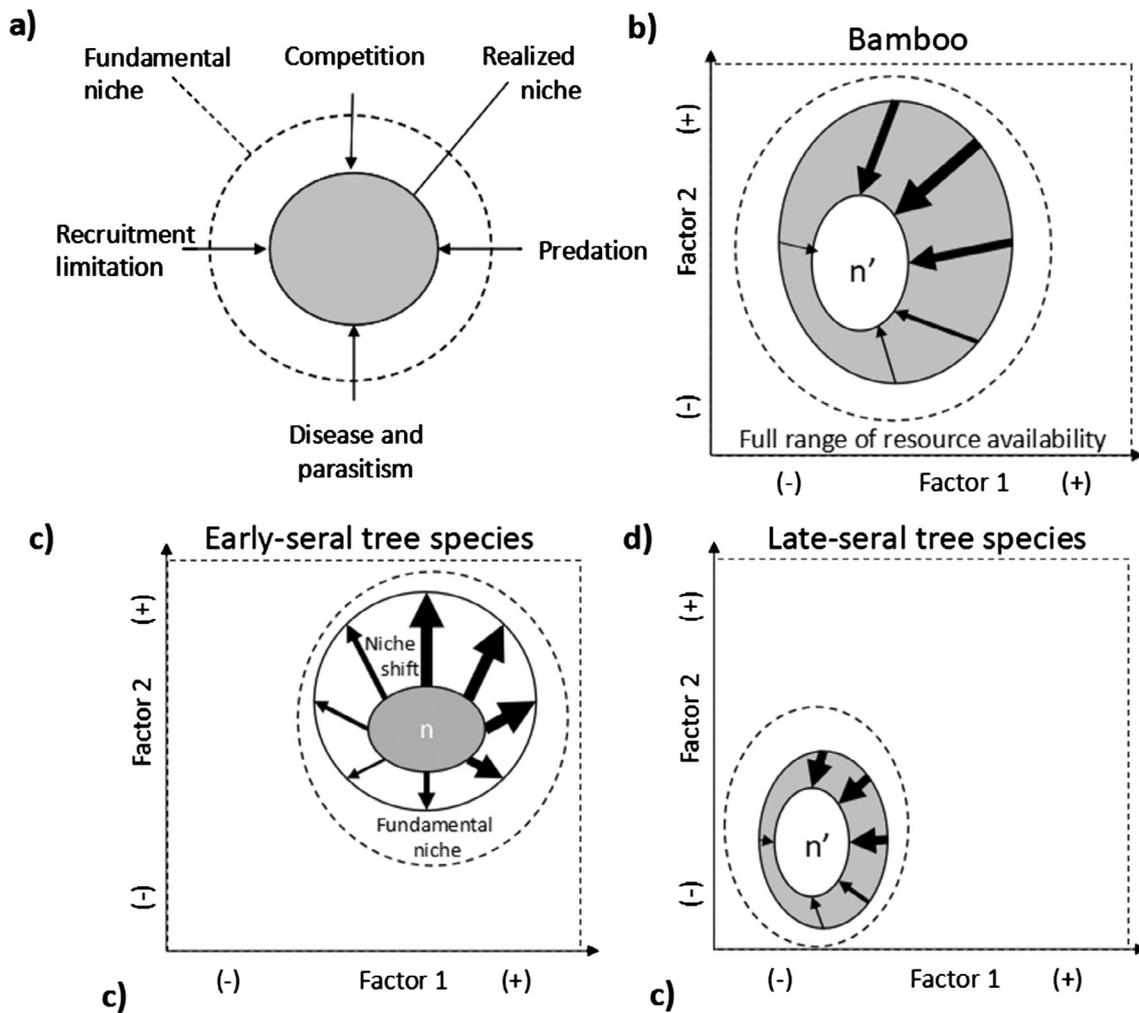


Fig. 1. Conceptual models depicting Hutchinson's fundamental and realized niches modified from Bruno et al. (2003, panel a). Grey color circled by a continuous line represents realized niches for the presence of Bamboo (b), and for early-(c) and late-seral tree (d) species in arrested succession condition. The effect of management (including restoration activities) is shown in white circle and continuous lines, highlighting the niche shift (n') for bamboo (constraint; b) and for early (expansion; c) and late-seral species (constraint; d). Factors 1 and 2 represent the main environmental gradients that shape the niches of different plant groups.

(sensu Hutchinson, 1957) is defined as ranges of resources and environmental dimensions in which species or plant groups can survive and reproduce without competition from other species and predation by natural enemies (Bruno et al., 2003; Chase and Leibold, 2003; Pearman et al., 2008; Soto and Puettmann, 2018b) (Fig. 1a). In contrast, the *realized* niche (sensu Hutchinson, 1957) is smaller than the fundamental niche as it includes the impacts of competitive effects by other species and herbivory (Bruno et al., 2003; Chase and Leibold, 2003) (Fig. 1a). Thus, field studies of forest ecosystems can only quantify the realized niche (Austin et al., 1990; Chase and Leibold, 2003; Soto and Puettmann, 2018b). As part of the debate about the benefit of this concept in ecology (Pianka, 1979; Chase and Leibold, 2003; Pearman et al., 2008), Chase and Leibold (2003) concluded that the niche concept is a powerful tool to unify discrepancies in research and theoretical approaches and can be used to address environmental problems in a practical and precise way.

The niche concept has been used to explain the preferences of different plant groups regenerating in various forest ecosystems; specifically, by using the term "regeneration niche" of Grubb (1977; an extension of Hutchinson' niche concept to explain regeneration as a function of resources). Some worldwide examples include the oak-dominated forests in the northeastern USA (Collins and Good, 1987), the Norway spruce forests in Bavaria (Baier et al., 2007), Canadian temperate forests in British Columbia (Coates, 2002), the north

Patagonian bog forests (Bannister et al., 2017), the temperate forests of South America (Caccia et al., 2009; Soto and Puettmann, 2018b), and the Atlantic forests in Brazil (da Silva and Tabarelli, 2000). These examples highlight how regeneration niches of different plant groups can elucidate variables and conditions needed for successful natural regeneration and thus can provide information to support restoration and management efforts.

In this study, we used the niche theory to identify environmental variables that are responsible for the breadth of realized regeneration niches of contrasting plant groups. Using a field study in recently disturbed *Nothofagus* old-growth forests in south-central Chile, we applied the niche concept after partial overstory and ground disturbance as part of restoration treatments. We investigated which environmental conditions influence the regeneration of species that promote ecological succession (i.e. early- and late-seral plant groups) and recalcitrant understorey species that cause arrested succession (sensu Royo and Carson, 2006; Soto and Puettmann, 2018a). This study provides an opportunity to link ecological theory with restoration issues to gain a better understanding of impacts of natural disturbances and management practices on ecological processes and mechanisms (Fig. 1; Bradshaw, 1987; Falk et al., 2006). We addressed the following questions:

1. Which environmental variables are responsible for shaping the realized niche after recent partial disturbance due to restoration

Table 1
Description of study sites.

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 ha ⁻¹)	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 ha ⁻¹)	13	25	13	20
Dead tree basal area dead trees (m ² ha ⁻¹)	13.9	19.7	7.5	20.9
Scarified area** (%)	45.8	32.5	33.8	24.1
Light availability (%)	8.3–78.0	3.9–73.6	2.2–69.7	4.1–73.2
Soil water content (%)	8.5–46.2	4.8–43.9	4.2–45.0	4.3–41.2
Litter cover (%)	0–100	2–100	0–100	0–100
Bamboo cover (%)	0–100	0–100	0–87	0–100
Coarse-woody debris (%)	0–100	0–90	0–100	0–90
Slope (%)	0–15	0–20	0–15	0–20
Aspect	SE	SW	E	SE
Resistance to penetration (kPa)	292–2237	142–2340	93–2736	142–2511
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.

treatments for different plant groups, especially bamboo (a species leading to arrested succession) and early- and late-seral tree species (indicators of successional processes)?

2. Is there a realized niche shift for the different plant groups after applied restoration treatments?

2. Methods

2.1. Study sites

Four selectively harvested stands within the Coihue-Rauli-Tepa forest type in Huilo-Huilo biological reserve were randomly selected and the soil was partially treated through topsoil scarification on 25 to 45% of the area (Table 1). Huilo-Huilo biological reserve comprises around 100,000 ha of continuous land in the Andes of south-central Chile. Stands are separated by 10 to 20 km from each other and had 8 years of understory and regeneration responses under a wide range of environmental conditions (Table 1) after disturbance. The restoration treatments resulted in overstory conditions ranging from large canopy openings to untouched, dense patches of trees. Soil conditions varied from severely disturbed patches with exposed mineral soil to undisturbed patches with dense carpets of litter and deadwood on the forest floor (details in Soto et al., 2017; Soto and Puettmann, 2018a). The stands were at least 10 ha in size with slopes < 20%. Further details about the study settings are described in Soto et al. (2017) and Soto and Puettmann (2018b), and the effects of topsoil removal through scarification on soil structure and nutrition is reported in Reyes et al. (2014).

The study conditions are representative of the zone where *Nothofagus* spp. are most productive, growing on recent volcanic ashes (the Andisol and Inceptisol soil complex). In the study forests, *N. dombeyi* and *N. alpina* are the dominant species with *Saxegothaea conspicua*, *Laureliopsis philippiana*, and *Dasyphyllum diacantoides*, which are considered shade tolerant (Donoso, 2006). In this region, *Nothofagus* species establish most successfully in environments created by infrequent large scale and intense stand replacing disturbances, such as landslides and fire (Pollmann and Veblen, 2004). At the same time,

partial overstory disturbances such as treefall gaps are typical (Pollmann and Veblen, 2004). These result in intense competition between relatively shade intolerant *Nothofagus* spp. and mid to late successional trees species (e.g., Asteraceae, Atherospermateaceae, Podocarpaceae families). After partial overstory disturbance, however, bamboo species (*Chusquea* spp.) often rapidly proliferate in dense thickets (Veblen, 1982; González et al., 2002) and prevent establishment of shade-intolerant and shade-tolerant tree species for extended periods (Veblen, 1982; González et al., 2002). The conditions created by bamboo after partial overstory disturbance are an example of arrested succession that results in forests that are considered “degraded” and are of regional environmental and social concerns (Lara et al., 2003; Bahamondez et al., 2009).

The climate in Huilo-Huilo is Andean polar, with short, dry summers (December-March) and humid winters (June-September). Annual precipitation reaches 3500 mm (Reyes et al., 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 month (February), respectively. Extreme temperatures can range from -10 °C to 30 °C; 30 to 50 annual frost events are common at 550 m.a.s.l., typically in August and September, (Reyes et al., 2014; Soto et al., 2015).

Soils on the study sites are a transition between Andisol (Acruodisol Hapludand) and Inceptisol (Andic Dystrudepts); both coarse mixed and mesic soils (CIREN, 2001; Reyes et al., 2014) with stratified structure and medium texture occur throughout the profile. The soil consists of different layers of volcanic materials, such as slag and sand, with a medium coarse texture (CIREN, 2001) and pH from 5.3 to 5.7 (Reyes et al., 2014).

2.2. Forest structure and regeneration sampling, and data management

Eight years after ground and overstory disturbances, permanent rectangular plots of 1 ha (plus a buffer of 10 m on each side) were located randomly in the four different sites within the Coihue-Rauli-Tepa forest type (Table 1). Each 1-ha plot was broken down into a grid of 10 × 10 m, and 2 m² (radii of 0.8 m) permanent regeneration plots were centered on all grid intersections (121 regeneration plots in each 1-ha plot). In these plots, the occurrence of all vascular plants (species richness, S) were documented (0 = not present, 1 = present). Plant species were divided into three plant categories used previously by Soto and Puettmann (2018a) as follows:

- (1) Bamboo—dominant and aggressive shrub species that can dominate the understory after partial and small overstory disturbances and latent during the late successional stages (Veblen, 1982).
- (2) Early-seral trees—long-lived early-seral tree species (*Nothofagus dombeyi*, *N. alpina*, *N. pumilio*), lifespan > 500 years, shade-intolerant and pioneer tree species, tall, small crown depths, expansive and shallow root system, and small seeds dispersed by wind (Donoso, 2006). These species typically initiate succession after large-scale disturbances (Veblen et al., 1980) and sometimes in canopy gaps above 1000 m² (Donoso, 1993).
- (3) Late-seral trees—long-lived late-seral tree species (*Laureliopsis philippiana* and *Dasyphyllum diacantoides*), lifespan > 500 years, shade-tolerant and late successional tree species, intermediate stature, profound tree crowns, deep root system, and seed dispersed by wind (Donoso, 2006). These species typically dominate the secondary succession after small-scale disturbances, e.g., small canopy gaps (Veblen et al., 1980).

2.3. Niche space as defined by environmental and resource variables

We measured the following variables in each regeneration plot: (1) exposed mineral soil (MS, % as indicator of ground disturbance); (2) litter cover (litter: % as indicator of untreated soils); (3) coarse woody debris (CWD: woody debris above 10 cm in diameter, %); (4)

Table 2
Descriptive statistics of the predictor variables (mean (SD), maximum-minimum) used in this study.

Plant groups	Light	SWC	MS	RP	S	Litter	CWD	MT
Early-seral trees	31.4 (16.2)	25.8 (11.5)	18.6 (24.5)	1,020.2 (490.6)	4.6 (2.5)	38.6 (30.8)	8.1 (20.6)	2.3 (1.3)
	3.9–73.6	4.2–46.2	0–95	93.0–2,736.3	1–20	0–100	0–100	1–4
Late-seral trees	21.9 (14.9)	17.4 (9.2)	4.5 (10.8)	906.6 (544.6)	4.5 (3.0)	44.1 (27.3)	12.7 (21.3)	3.0 (1.2)
	4.1–69.7	4.3–45.8	0–55	142.8–2,212.7	1–20	2–100	0–90	1–4
Bamboo	26.1 (17.6)	20.6 (9.6)	5.9 (15.4)	796.3 (431.0)	3.0 (1.5)	52.8 (31.3)	13.1 (22.8)	2.6 (1.4)
	2.2–73.6	4.4–45.8	0–90	93.0–2,312.4	1–10	0–100	0–100	1–4

Light: light availability (% total transmitted radiation), SWC: soil water content (%), MS: exposed mineral soil (% cover), RP: resistance to penetration (kPa), S: species richness (n), Litter: litter cover (%), CWD: cover of coarse woody debris (%), MT: microtopography (1, flat, 2, convex, 3: concave, and 4: mixed).

microtopography (MT: flat, convex, concave, and mixed); (5) soil resistance to penetration (RP) in kPa; (6) soil volumetric water content (SWC); and (7) light availability (light). Specifically, the soil resistance to penetration was used as an integrated measure of soil disturbance (Berger et al. 2004; Soto et al., 2015). We used a cone soil compaction meter (Fieldscout SC 900, Spectrum instruments, Inc.) with a resolution of 35 kPa and an accuracy of ± 103 kPa. Resistance to penetration was measured in five random points in each regeneration plot by inserting the meter with a uniform speed of ~ 3 cm s⁻¹. Measurements were obtained using a cone with a base area of 1.25 cm²; readings were taken once the cone reached soil depth of 20 cm. Thus, we covered the 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 et al., 2004; Puettmann et al., 2008; Soto et al., 2015).

Soil volumetric water content (SWC) was measured in five random points 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 dS m⁻¹, and range of from 0% to 50% of volumetric SWC, where 50% is typically the 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 (sensu Soto et al., 2015).

At the center of the regeneration plots, we took a hemispherical photograph at 1.5 m above ground. Light conditions in the understory (total transmitted radiation; %) was estimated using WinSCANOPY Pro 2013c software (Regent instruments). The setup consisted of a 24 MP DSLR compact camera with a self-leveling O-Mount system, a calibrated fisheye lens, and an automatic north finder. Light availability was estimated as total radiation (a combination of direct beam and diffuse radiation) and calculated as a percentage of growing-season incident radiation (Canham, 1988). Photographs were taken under homogeneous diffuse skylight conditions during March, i.e., late summer in the southern hemisphere.

2.4. Statistical analysis

To determine the community gradients between occurrence of (1) bamboo, (2) regeneration of early-seral trees, and (3) regeneration of late-seral trees in understory with the associated gradient of environmental predictors (i.e., species groups \times regeneration plot matrix of 3×484), we used canonical correspondence analysis (CCA; ter Braak, 1986) performed in PAST 3.04 software (<https://folk.uio.no/ohammer/past/>). CCA has proven to be a robust approach (Palmer, 1993; Zuur et al. 2017) that succinctly describes the differential niche preferences by plant groups through ordination biplots (ter Braak, 1986; Legendre and Legendre, 2012). As the selection of proper sets of variables plays an important role in the performance of CCA and to decrease the data noise (McCune, 1997; McCune et al., 2002), we first ran a correlation

analysis on these environmental variables to reduce the number of environmental predictors used in the model and help to reduce effects of collinearity (McCune et al., 2002). In addition, we chose CCA instead of other ordination techniques because (1) we could assume unimodal responses (McCune et al., 2002), (2) this allowed us to visualize the place of plant groups in the canonical space constrained by environmental predictors using the explained inertia (i.e., the variance) of the major axes (Jongman et al., 1995; McCune et al., 2002), and (3) we had a wide range of predictor values that may create problems when applying more constraint ordination tools, such as Redundancy Analysis (Palmer, 1993; Jongman et al., 1995; Legendre and Legendre, 2012). The potential predictors with strong ecological meaning were light availability, species richness (S), soil resistance to penetration (RP), volumetric soil water content (SWC), coarse-woody debris (CWD), exposed mineral soil (MS), litter cover (litter), and microtopography (MT). The descriptive statistics of the predictor variables are shown in Table 2. In our study, the ordination axes were implemented using a linear combination of environmental predictors, and the CCA's implementation follows the eigen analysis algorithm given by Legendre and Legendre (2012). To assess the statistical significance of axes was used a Monte Carlo permutation test (with 10 K iterations) and using a significant level of 0.05. Finally, to determine potential relationships between plant groups, environmental variables, and axes scores, we looked at the corresponding Pearson's correlation coefficients (r).

To predict the occurrence (binary response variable) of the three species plant groups (early-seral trees, late-seral trees and bamboo) per regeneration plot, we used non-parametric multiplicative regression (NPMR) and Gaussian weighting kernel local mean estimator (LM-NPMR) procedures using HyperNiche 2.22 (McCune, 2006; McCune and Mefford, 2009). This approach avoids strict distributional assumptions and can accommodate a wide range of response surface shapes when searching for the best predictor combination (McCune, 2006). We used as predictors the values from both axes of the CCA, which represent an integrated measure of community gradient constrained by environmental variables (sensu Jovan and McCune, 2005; Reisner et al., 2013). To accommodate the nested structure of the experiment (regeneration plots within sites), we tested the potential effect of the four sites (block effect represented by 4 sites) as a random variable by running generalized linear mixed model (GLMM) in the package 'nlme' in R (Pinheiro et al., 2017) prior to conducting NPMR. We used the binomial distribution and the link function for the predictor was gaussian. We found that addition of random intercepts to account for the intraclass correlation was weak for early-seral trees and bamboo (10%), and relatively higher only for the late-seral tree model the intraclass correlation (59%). Even in this case, there were no significant differences between the results obtained for the mixed effect models and for the fixed effect models (Appendix 1). Based on these findings, we concluded that in this study concerns due to spatial pseudoreplication (Zuur et al., 2017) were negligible and using NPMR will provide a statistically valid approach to address our questions of interest (McCune, 2006).

To evaluate the quality of the models obtained for the occurrence (and select the best ones), we computed the Bayes factors (BF) of each

model under consideration (M_1) against an alternative model (M_2). Typically, the alternative model is taken to be a “naïve model”, that does not include any information contained in the covariates and is simply given by the average frequency of occurrences of a seral group of species in the data (McCune, 2006). Then, assuming *a priori* that the two competing models are equally likely (i.e., $P(M_1) = P(M_2) = 0.5$), Bayes factors are obtained as likelihood ratios for comparing occurrence and no occurrence of seral groups in a given plot. For a vector of observed occurrences $\mathbf{y} = (y_1, y_2, \dots, y_i)$, the Bayes factor comparing models M_1, M_2 , is given by

$$BF_{12} = \frac{l(\mathbf{y}|M_2)}{l(\mathbf{y}|M_1)}$$

where

$$l(\mathbf{y}|M) = \prod_{i=1}^n \hat{y}_i^{y_i} (1 - \hat{y}_i)^{1-y_i}$$

is the fitted likelihood of the occurrence for each model. Interpretation of the Bayes factors can be accomplished in different ways. Here, we considered the log-scale interpretation of Bayes factors, where $\log B_{12}$ values between 0 and 0.5 can be viewed as minor, 0.5–1 substantial, 1–2 strong, and > 2 decisive support of the model M_1 (Kass and Raftery, 1995; McCune, 2006). Similarly, negative values of the $\log B_{12}$ are interpreted as degrees of supporting evidence for model 2. Finally, we conducted sensitivity analyses in HyperNiche to evaluate the relative contribution of predictors (i.e., axes obtained in CCA) for the candidate model (McCune, 2006).

To visualize the shift in realized niches for the presence of species groups and bamboo as consequence of restoration treatment, as hypothesized in Fig. 1, we plotted the 95% confidence ellipses with centroids of each seral tree groups and bamboo separated in areas with and without restoration treatments (i.e., ground and overstory disturbances). This analysis was performed in PAST 3.04 software.

3. Results

3.1. Factors influencing niches of species groups

The presence of different seral species groups was related to selected environmental conditions (Fig. 2). Axes 1 and 2 of the canonical correspondence analysis (CCA) contributed 79.8% and 16.1% to the explained inertia, respectively. Axis 1 values were negatively correlated with exposed mineral soil (MS), soil volumetric water content (SWC), and soil resistance to penetration (RP) (Table 3), which are related to ground disturbance (Fig. 2). Axis 1 was also negatively correlated with the presence of early-seral species and species richness (S) (Table 2). In contrast, axis 2 values were positively correlated with presence of early-seral tree species, bamboo, litter cover, and light availability (Table 3), which suggested that overstory removal impacts were the major factors associated with axis 2 (Fig. 2). The negative relationship between late-seral tree species and axis 2 further supported this interpretation (Fig. 2). The plot-species matrix is presented in Appendix 2.

3.2. Niche conditions as defined by environmental variables

Relatively strong correlations were found between species groups and environmental variables (Table 3). Bamboo presence was positively correlated with litter and negatively associated with MS, SWC and RP and the presence of all other species groups. Accordingly, bamboo presence was also negatively related to species richness. Positive correlations were detected between both early-seral tree species and MS, SWC, and RP. In contrast, late-seral tree species were negatively associated with SWC and light, and positively associated with S.

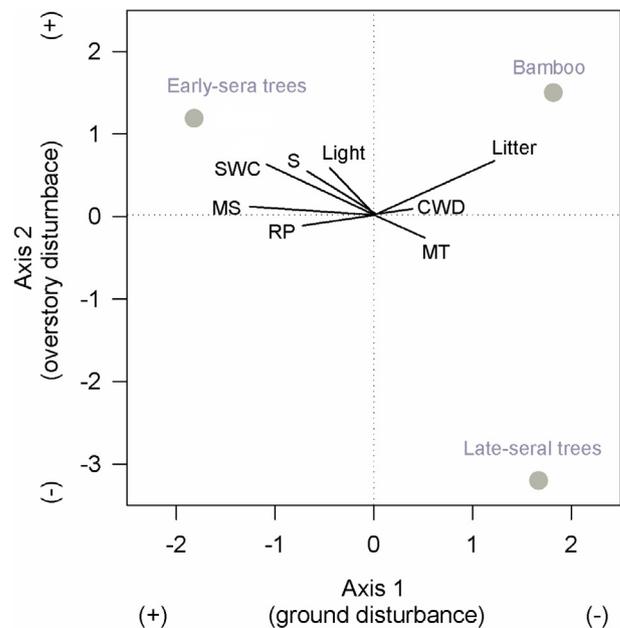


Fig. 2. CCA biplot results of ordinations for the seral plant groups and environmental and resource variables. CWD: % of coarse woody debris cover, litter: % of litter cover, RP: resistance to penetration (KPa), S: species richness, SWC: volumetric soil water (%), SM: % of exposed mineral soil cover, light: light availability (% of total transmitted radiation), and MT: microtopography (flat, convex, concave, mixed).

3.3. Niche modeling

Table 4 shows the results for the Bayes factors (in log scale) when comparing these against the naïve model M_2 with no predictors. Specifically, the best fitted models were those that used both axes (Table 4). The probability of presence of early-seral ($\log BF_{12} = 48.7$) and late-seral tree seedlings ($\log BF_{12} = 44.7$) had decisive support. However, the sensitivity analysis showed that for the probability of the presence of late-seral tree seedlings, the more influential predictor was axis 2, and for early-seral tree seedling was axis 1 (Table 4); Fig. 3 highlights this interpretation. Similarly, the probability of the presence of bamboo had decisive support ($\log BF_{12} = 80.7$) and better fit when both axes were used as predictors (Table 4). The sensitivity analyses showed that bamboo presence was strongly related to axis 2 than to axis 1 (Table 4, Fig. 3).

Finally, we observed that the models that use both axes seem to be appropriated in all groups. This is corroborated in Table 5, which summarizes the comparisons of the different models using axis 1, axis 2 or both as predictors for each one of the three groups. Each one of the comparisons using both axes show strong to decisive support when compared to the models based on one single axis.

3.4. Niche shifts as consequence of restoration treatment

The restoration treatment appeared to move the centroid and shrink the realized niche of bamboo, especially in the region with higher axis 1 (ground disturbance) and lower axis 2 (overstory disturbance) scores (Fig. 4). In contrast, the centroids of realized niches of regenerating tree groups moved and the niches expanded to include areas with higher axis 1 (ground disturbance) and both higher axis 1 and 2 (ground and overstory disturbance) scores for early- and late-seral trees respectively (Fig. 4).

Table 3

Correlation matrix between CCA's axes, environmental variables, seral groups and bamboo cover. In parenthesis, the *p*-values for each possible combination.

	Light	RP	SWC	MS	litter	CWD	MT	S	LLES	LLS	Bamboo	Axis 1	Axis 2
Light													
RP	0.024 (0.620)												
SWC	0.391 (0.000)	0.012 (0.803)											
MS	0.130 (0.006)	0.066 (0.168)	0.230 (0.000)										
Litter	-0.072 (0.132)	0.160 (0.001)	-0.264 (0.000)	-0.219 (0.000)									
CWD	0.015 (0.760)	-0.192 (0.000)	-0.186 (0.000)	-0.212 (0.000)	-0.243 (0.000)								
MT	-0.047 (0.348)	-0.188 (0.000)	-0.145 (0.002)	-0.069 (0.147)	-0.088 (0.065)	0.051 (0.283)							
S	-0.045 (0.348)	0.285 (0.000)	0.071 (0.137)	0.060 (0.208)	0.023 (0.622)	-0.237 (0.000)	0.006 (0.898)						
LLES	0.150 (0.001)	0.302 (0.000)	0.278 (0.000)	0.365 (0.000)	-0.103 (0.030)	-0.163 (0.001)	-0.115 (0.015)	0.420 (0.000)					
LLS	-0.194 (0.000)	0.010 (0.827)	-0.233 (0.000)	-0.145 (0.002)	0.025 (0.605)	-0.003 (0.942)	0.168 (0.000)	0.255 (0.000)	-0.060 (0.208)				
Bamboo	-0.127 (0.007)	-0.187 (0.000)	-0.179 (0.000)	-0.254 (0.000)	0.317 (0.000)	-0.006 (0.901)	0.077 (0.107)	-0.322 (0.000)	-0.425 (0.000)	-0.227 (0.007)			
Axis 1	-0.154 (0.001)	-0.198 (0.000)	-0.280 (0.000)	-0.353 (0.000)	0.291 (0.000)	0.091 (0.057)	0.133 (0.005)	-0.343 (0.000)	-0.680 (0.000)	0.212 (0.000)	0.779 (0.000)		
Axis 2	0.162 (0.001)	-0.055 (0.249)	-0.240 (0.003)	0.041 (0.391)	0.140 (0.003)	0.012 (0.807)	-0.095 (0.046)	-0.226 (0.000)	0.043 (0.367)	-0.710 (0.000)	0.576 (0.000)	0.156 (0.001)	

Light: light availability (% total transmitted radiation), RP: resistance to penetration (KPa), SWC: soil water content (%), MS: exposed mineral soil (% cover), Litter: litter cover (%), CWD: cover of coarse woody debris (%), MT: microtopography (1, flat, 2, convex, 3: concave, and 4: mixed), S: species richness, LLES: presence of early-seral tree, LLS: presence of late-seral tree, and Bamboo: presence of bamboo.

Table 4

NPMR results for occurrence of bamboo and seral plant groups in the studied forests.

Species group	Model	log <i>BF</i> ₁₂	N [*]	Predictors	Tolerance	Sensitivity
Bamboo	Axis1	54.2	200.6	Axis 1	0.536	0.996
	Axis2	17.8	286.5	Axis 2	0.429	1.224
	Both	80.7	144.7	Axis 1	0.536	0.756
				Axis 2	0.429	1.086
Early-seral trees	Axis1	47.2	206.4	Axis 1	0.429	1.253
	Axis2	3.6	286.5	Axis 2	0.536	0.462
	Both	48.7	144.7	Axis 1	0.429	1.287
				Axis 2	0.536	0.262
Late-seral trees	Axis1	5.6	206.4	Axis 1	0.429	0.845
	Axis2	36.3	248.9	Axis 2	0.536	1.316
	Both	44.7	144.7	Axis 1	0.429	0.949
				Axis 2	0.536	1.135

Table 5

Bayes factors comparing different models for each one of the species groups.

M1 vs M2	Bamboo log <i>BF</i> ₁₂	Early-seral trees log <i>BF</i> ₁₂	Late-seral trees log <i>BF</i> ₁₂
Axis1 vs. Axis2	36.4	43.6	-30.7
Axis1 vs Both	-26.5	-1.5	-39.1
Ax2 vs Both	-62.9	-45.1	-8.4

4. Discussion

4.1. Environmental conditions shaping realized niches as influenced by disturbances

Our study confirmed that bamboo “excludes” early- and late-seral tree groups, which has been amply discussed in southern temperate forests (Veblen et al., 1980; Veblen, 1982; González et al., 2002; Muñoz and González, 2009; Soto and Puettmann, 2018a,b). Past studies

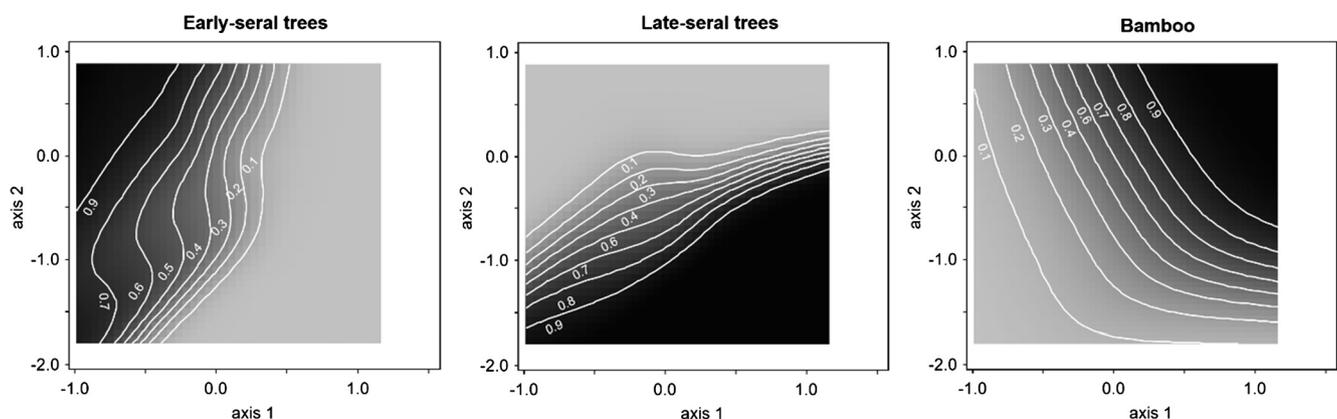


Fig. 3. NPMR-LM contour probability plots of the presence of bamboo and tree regeneration of early- and late-seral tree group as a function of canonical axes scores from CCA ordinations. Axis 1 represents the gradient of ground disturbance and axis 2 the overstory removal.

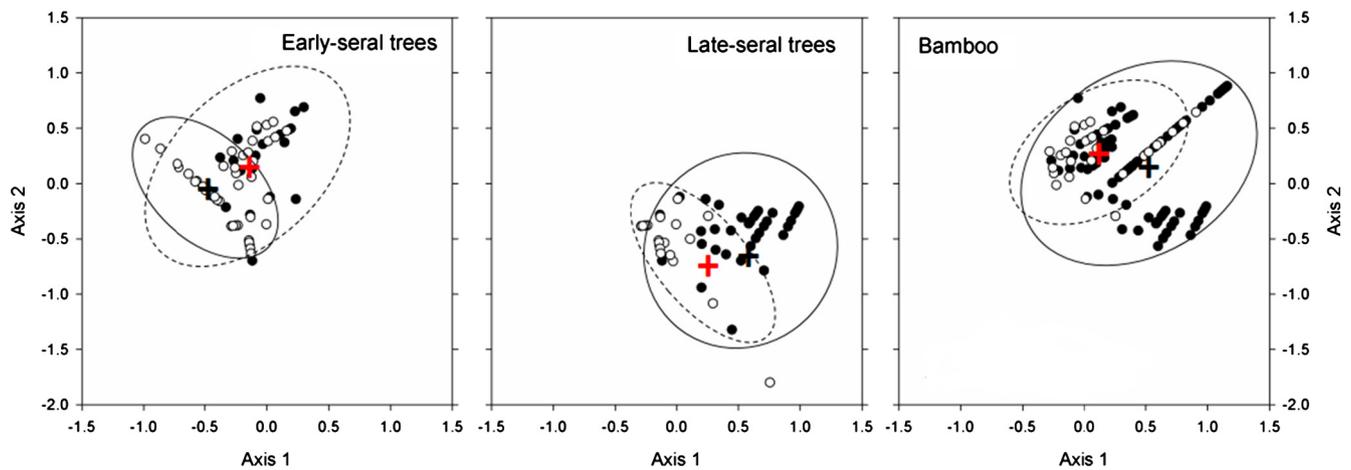


Fig. 4. The realized niche shifts for different seral tree groups and bamboo after restoration treatments as depicted using 95% confidence ellipses. White open circles surrounded by ellipses with continuous lines represent conditions after overstory removal without restoration treatment. In contrast, black circles surrounded by dashed lines indicate realized niches after overstory disturbance and restoration treatment. Black crosses show the centroid of the ellipse area with only overstory disturbance and red crosses represent the change in the centroid after applied restoration treatment.

suggest that partial overstory disturbance allows the expansion of the realized niche for bamboo during the first few years after disturbances. This has been attributed mainly to increases in light availability (Veblen, 1982; González et al., 2002; Caccia et al., 2015), with less attention paid to other environmental conditions (Royo and Carson, 2006; Muñoz and González, 2009; Soto and Puettmann, 2018a). In addition to light effects, our results suggest that the dense cover of leaf litter and low soil water content typically found in late successional forests in the study region (Donoso, 1993; González and Donoso, 1999; Soto and Puettmann, 2018a) enabled the expansion of the realized niche of bamboo. This expansion was likely facilitated by low competitiveness of early-seral tree species in low light understory environments (Veblen, 1982; Donoso, 1993, 2006; Muñoz and González, 2009; Caccia et al., 2015). Furthermore, the dense bamboo thickets resulted in production and accumulation of ground litter—a positive feedback loop that further reduces the likelihood of overcoming the ecological trap (sensu Allison and Hobbs, 2004) through early-seral *Nothofagus* spp. regeneration (González and Donoso, 1999; Muñoz and González, 2009; Caccia et al., 2015; Soto and Puettmann, 2018a,b).

In contrast, our study pointed out that after recent disturbances high soil water content and exposed mineral soil were most indicative of the realized niche of regenerating early-seral tree species, with light availability playing a secondary role. It appears that water and soil conditions in conjunction with the plasticity of early-seral *Nothofagus* spp., in terms of light requirements during early stages of regeneration, allowed seedlings to establish and persist under deep shade (Pollmann and Veblen, 2004; Coopman et al., 2008; Donoso et al., 2015; Soto et al., 2015; Soto and Puettmann, 2018a). Thus, our study provided a direct quantification and visualization of safe sites (Fowler, 1988) suitable for the regeneration of seral tree species groups.

4.2. Disturbance and regeneration ecology studies in *Nothofagus* old-growth forests

The dominance of understories by bamboo species after partial overstory disturbances, such as selective harvestings or treefall gaps or death of individual trees, appears to be a widespread phenomenon and can be found in various biomes in the world. Similar patterns have been documented for bamboo species in Japan (Taylor and Qin, 1992; Yoshida et al., 2005), the tropical Peruvian Andes (Griscom and Ashton, 2003), and rainforests in Brazil (Campanello et al., 2007; de Carvalho et al., 2013). Insights from Schupp (1995) can be helpful in understanding the regeneration process in these settings. He showed that seed storage and germination may require different environmental and

resource conditions than necessary for growth and survival of seedlings, saplings, and mature trees. Thus, it may be necessary to distinguish niche conditions for the different stages of plant development (Schupp, 1995). In the context of our study, microsite conditions (e.g., exposed mineral soil, soil water content) are especially important axes (sensu Silvertown, 2004) of the germination niche, suggesting that small-scale factors may play an important role in this phase of regeneration for early-seral trees (Gray and Spies, 1997; Fahey and Puettmann, 2007; Dodson et al., 2014; Soto and Puettmann, 2018a). In contrast, late-seral tree species have a different niche during this stage; they are better able to tolerate the low soil water content and high litter cover typically found in old-growth *Nothofagus* forests (Veblen et al., 1980; González and Donoso, 1999; Christie and Armesto, 2003; Soto and Puettmann, 2018a). Several studies have confirmed that germination niches are not only defined by resource axes, but that other axes reflecting physical damage, e.g., through litter, negatively influences the establishment of different seral groups in understory settings (Facelli and Pickett, 1991). These niche axes are especially important for trees with small seeds (Sydes and Grime, 1981; Molofsky and Augspurger, 1992; Christie and Armesto, 2003), such as *Nothofagus* spp. However, such niche conditions typically vary at extremely small spatial scales, e.g., as a function of microtopography (Gray and Spies, 1997; Cornett et al., 2000). In contrast, resource and microclimate niches act at slightly larger scales and climate niches are defined from microclimate to global scales. The variability in these niche conditions across scales, in conjunction with other conditions in safe sites (Cornett et al., 2000), such as the quantity and condition of downed wood, is often responsible for the differential establishment of most tree- and especially late-seral species (Spies et al., 1988; Harmon and Franklin, 1989; Gray and Spies, 1997; Carmona et al., 2002; Christie and Armesto, 2003; Schlegel and Donoso, 2008).

In the field, we observed that downed wood had not decayed sufficiently to allow the establishment of seedlings on logs (D. Soto, personal observation). Thus, we hypothesize that in the future, further decay of the logs will lead to the expansion of realized niches for all seral tree species groups, especially for late-seral trees (Veblen et al., 1981; Donoso, 1993; Christie and Armesto, 2003). Our hypothesis is based on widespread trends as these patterns have been found in different temperate old-growth forest ecosystems, including the Pacific Northwest of the USA (Spies et al., 1988; Harmon and Franklin, 1989; Gray and Spies, 1997), New Zealand (Lusk and Ogden, 1992), temperate rainforests in south-central Chile (Schlegel and Donoso, 2008), and the northern Patagonia region (Carmona et al., 2002; Christie and Armesto, 2003). Decaying logs may be an especially important niche for regeneration in *Nothofagus*-dominated old-growth forests, where Veblen

et al. (1981) found that > 90% of tree regeneration occurred on logs in advanced decay stages.

4.3. Realized niche shifts after restoration treatments

The shift in realized niches, as visualized in Fig. 4, provides an example of how theoretical concepts can help to simplify a complicated story; in this case it highlights how factors leading to the realized niche only occupy a portion of the fundamental niche (Rehfeldt et al., 1999). As changing of niches (sensu Pearman et al., 2008) can be ruled out, differences in realized niches are due to overstory and understory disturbance and associated shifts in resource levels and vegetation. The shift in centroid and shrinkage of the realized niche (sensu Guisan et al., 2014) for bamboo in regards to axes and associated environmental factors suggested that the impact of the ground disturbance itself, rather than canopy opening, is the main factor contributing to the altered dynamics after the restoration treatments. The late-seral tree species showed a shift in niche limits reflecting a similar trend in niche shift, but in the opposite direction, i.e., the niche expanded after ground disturbance. In contrast, the niche limit of early-seral tree species expanded in the direction of both axes, suggesting that overstory openings and ground disturbance may be responsible for niche expansion of these species.

4.4. Implications for management

Arrested succession after recent partial overstory disturbances is an increasingly important ecological and social issue because it stalls the essential processes and functions underlying successional dynamics and thereby affects the provision of forest ecosystems services (Ghazoul et al., 2015). The regeneration niche of early-seral trees is defined by exposed mineral soil and soil water content, suggesting that ground disturbance after partial overstory removal can be applied to accommodate this niche. Application of niche theory thereby provides a means to manage and restore regeneration processes and thus the resilience of those forests by overcoming arrested succession (Soto and Puettmann, 2018a,b). Partial overstory removal without sufficient soil disturbance was inadequate to allow the establishment of early-seral tree species, as their realized niche was restricted by bamboo through competition and litterfall. In a nutshell, the aboveground resources released by overstory disturbance and associated physical hindrance through litter were insufficient to guarantee the natural regeneration of early-seral tree species in temperate mesic stands (Nakashizuka, 1989; Royo and Carson, 2006; Soto and Puettmann, 2018a). Alternatively, low intensity overstory removal with the presence of adequate coarse-woody debris can improve the likelihood for seedling establishment of late-seral trees that can use downed wood as safe sites (Spies et al., 1988; Fahey and Puettmann, 2007).

In many settings, studies have shown that light plays the most important role in shaping forest ecosystems dynamics (Canham et al., 1990; Pacala et al., 1996). Consequently, silviculturists and restoration ecologists have based forest treatments on ecological principles driven by light availability (e.g., BC Ministry of Forestry, 1995). A broader view of changes in niche spaces and breadths through ontogeny (Young et al., 2005) may be helpful or even crucial in such settings (Boyden et al., 2009). The differences between niche spaces during the “establishment” and “growth” stages may have been misunderstood or not given enough credit (Schupp, 1995; Young et al., 2005). Our study is an example that highlights the dynamics of niche conditions associated with plasticity of tree development (Poorter et al., 2005); light conditions may not be as influential during the germination and early establishment phase (Kyereh et al., 1999), but will impact growth of early- and late-seral species differentially during later stages (Shatford

et al., 2009). This distinction is especially important as the regeneration niche appears to be to have a long-lasting effect on plant species (Poorter, 2007). Also, information on which species’ environmental variables are influencing realized niches for different seral groups may vary in ecosystems, e.g., as influenced by soil conditions (Royo and Carson, 2006; Soto and Puettmann, 2018a).

Thus, the broader ecological framework, based on niche theory, disturbance ecology and regeneration dynamics, provides a better and integrated understanding of ecosystem dynamics, especially in forests with arrested succession. Basic principles and theories may be applied in this context for the selection of practical and viable solutions for designing management and restoration approaches (e.g., topsoil removal through scarification; Örländer et al., 1996; Berger et al., 2004; Yoshida et al., 2005; Löf et al., 2012; Soto and Puettmann, 2018a). Additionally, viewing plants in terms of their functional traits may be helpful when using the niche concept (Kraft et al., 2008; Kearney et al., 2010) to apply active management (McGill et al., 2006; Poorter, 2007). Relying on theoretical frameworks provides a better basic understanding of the ecological principles driving vegetation dynamics and also facilitates extrapolation of study findings to other forest ecosystems (Pywell et al. 2003; McGill et al. 2006).

5. Conclusions

Arrested succession is an ecological issue because it stalls and prevents successional development in some forests following disturbance (i.e., endogenic and/or anthropogenic). Our study highlights how a broader ecological framework, based on niche theory, succession, and regeneration dynamics provides a deeper and integrated understanding of ecosystem dynamics and gives important insights for forest restoration and management. The realized niches varied for the vegetation groups analyzed in this study. Specifically, after recent partial overstory disturbance, recalcitrant understory vegetation (bamboo) was commonly released under conditions whereby its realized niche was expanded as a consequence of low soil water content and high litter cover. During the initial stages of succession, regeneration of early-seral trees was positively related to high soil water content and exposed mineral soil, while development of late-seral trees was negatively related to soil water content under overstory conditions characterized by low disturbance. Light availability for all plant groups played a secondary role, at least during early successional stages (8 years for this study). Thus, after partial overstory disturbance without sufficient ground disturbance to enhance soil water content and expose mineral soil, resultant conditions match the expansion of the realized niche of recalcitrant understory vegetation that increases the likelihood of an arrested succession condition. This knowledge can provide important insights in designing restoration and management practices to avoid or/and overcome an arrested succession condition, and promote succession after partial overstory disturbances to maintain, improve, or restore essential processes and functions in forests ecosystems.

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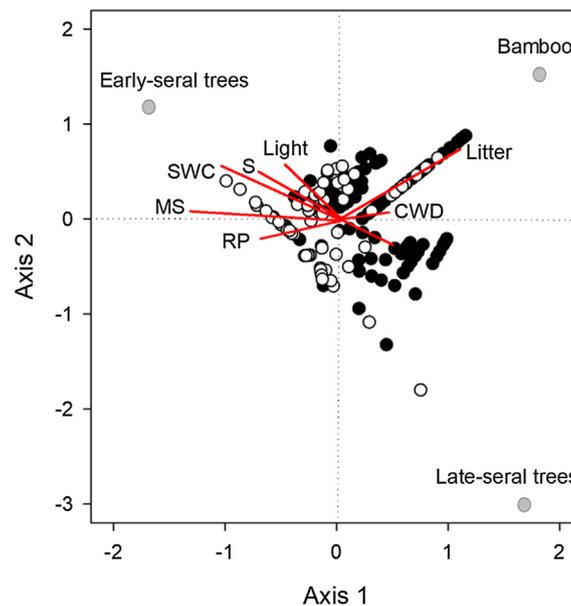
Appendix 1

Comparison between fixed and mixed effect models using GLMM. ICC is the interclass correlation (sites).

Early-seral trees	Mixed effects		Fixed effects	
	Estimate (Std Error)	p-value	Estimate (Std Error)	p-value
Intercept	-0.851 (0.342)	0.013	-0.714 (0.138)	0.000
Axis 1	-4.090 (0.409)	0.000	-3.894 (0.371)	0.000
Axis 2	1.126 (0.4628)	0.014	1.041 (0.395)	0.008
ICC (Site)	0.102			
Late-seral trees	Mixed effects		Fixed effects	
	Estimate (Std Error)	p-value	Estimate (Std Error)	p-value
Intercept	-6.937 (1.721)	0.000	-4.293 (0.748)	0.000
Axis 1	7.492 (2.124)	0.000	5.570 (1.524)	0.000
Axis 2	-19.731 (3.802)	0.000	-14.426 (2.419)	0.000
ICC (Site)	0.593			
Bamboo	Mixed effects		Fixed effects	
	Estimate (Std Error)	p-value	Estimate (Std Error)	p-value
Intercept	0.738 (0.432)	0.087	0.708 (0.313)	0.023
Axis 1	10.023 (1.370)	0.000	9.528 (1.179)	0.000
Axis 2	10.087 (1.518)	0.000	9.808 (1.396)	0.000
ICC (Site)	0.089			

Appendix 2

CCA biplot showing the species groups × regeneration plot matrix of ordinations for the seral plant groups and environmental variables. White and black circles represent disturbed and undisturbed soil conditions, respectively. CWD: % of coarse woody debris cover, litter: % of litter cover, RP: resistance to penetration (kPa), S: species richness, SWC: volumetric soil water (%), SM: % of exposed mineral soil cover, light: light availability (% of total transmitted radiation), and MT: microtopography (flat, convex, concave, mixed).



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