

Regeneration patterns, environmental filtering and tree species coexistence in a temperate forest

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Summary

- Forest ecologists researching the functional basis of tree regeneration patterns and species coexistence often attempt to correlate traits with light-gradient partitioning. However, an exclusive focus on light can overlook other important drivers of forest dynamics.
- We measured light, temperatures, humidity and sapling densities in each of four phases of a forest dynamic mosaic in New Zealand: shaded understoreys, tree-fall gaps, treefern groves and clearings. We then measured leaf, wood and seed traits, as potential predictors of species' regeneration patterns.
- Saplings of 18 out of 21 species were significantly associated with one or other of the four phases, and associations were best predicted by a two-trait model (leaf size, wood density) explaining 51% of observed variation. Species associated with treefall gaps had traits favouring light pre-emption (large leaves, low-density wood), whereas those establishing in clearings mostly had small leaves and dense wood, traits probably conferring resistance to the frosts and summer water deficits that saplings were exposed to there.
- The dynamics of some forests cannot be explained adequately by light-gradient partitioning through a growth vs shade tolerance tradeoff, underpinned by the leaf economics spectrum. Consideration of multiple environmental filters and multiple traits will enhance understanding of regeneration patterns and species coexistence.

Introduction

Gradients of light availability are widely regarded as the primary ecological template for the evolution of tree life histories in humid forests (e.g. Denslow, 1987; Poorter, 2007). Light gradient partitioning by tree species' juveniles has often been shown to reflect a tradeoff between growth rate in well-lit environments and survival under shade (Hubbell & Foster, 1992; Kobe *et al.*, 1995; Lin *et al.*, 2002; Poorter & Bongers, 2006) and this tradeoff is thought to contribute to species coexistence. Ecologists seeking a general understanding of forest dynamics and species coexistence have usually aimed to identify relationships of seedling or sapling traits with the light environments in which species typically establish, often linking light gradient partitioning to leaf economic traits (Coley, 1988; Poorter, 2007; Lusk *et al.*, 2010; Wright *et al.*, 2010; Laurans *et al.*, 2012), and to wood density (Kitajima, 1994; van Gelder *et al.*, 2006; Wright *et al.*, 2010): fast-growing pioneer trees typically have rapid foliage turnover and soft wood, whereas shade-tolerant species often have tough, long-lived leaves and dense wood. This pattern is consistent with the view that habitat favourability increases monotonically with light availability in humid forests (Coley *et al.*, 1985).

However, an exclusive focus on responses to light will sometimes overlook other important drivers of forest dynamics and

species coexistence. Severe disturbances that destroy both overstorey and understorey vegetation can produce microclimates somewhat removed from those prevailing in forest understoreys or treefall gaps (Fetcher *et al.*, 1985), especially in regions subject to frost and/or significant rainless periods (Groot & Carlson, 1996; Nepstad *et al.*, 1996). In tropical rainforests, fast growth of juvenile pioneer trees suggests that the main threat to survival in large openings is overtopping by competing vegetation. In temperate evergreen forests, frost may be a more important environmental filter on open sites (Lusk *et al.*, 2013, 2015; Richardson *et al.*, 2013). On clear nights, leaf temperatures of plants growing in the open can be as much as 4°C lower than those of shaded plants at the same site (Caramori *et al.*, 1996; Scowcroft *et al.*, 2000). Similarly, sunny rainless periods can pose serious difficulties for tree seedlings on open sites, as leaves are subject to high radiation loads, but shallow root systems limit seedlings' ability to access soil moisture and hence cool their leaves by transpiration (e.g. Padilla & Pugnaire, 2007). Frequent drought or frost can therefore be expected to strongly filter the functional traits of species establishing in large openings (Lohbeck *et al.*, 2013).

Here we document environmental variation across four phases of a forest dynamic mosaic, and identify the functional correlates of tree species regeneration patterns. We measured sapling abundances of 21 common tree species in each phase of the mosaic, and quantified leaf, wood and seed traits of each species. We then

determined the combination of functional traits that best predicted which phase the saplings of each species were most commonly associated with. We also measured temperature and relative humidity in each of the four forest phases, to inform our interpretation of trait–environment relationships. We show that a two-trait model can predict the regeneration patterns of most species (i.e. the forest phase in which a species is most likely to recruit). We also show that, unlike species associated with treefall gaps, the functional traits of species establishing primarily in clearings probably reflect environmental filtering by frost and drought stress, rather than maximization of growth rates.

Materials and Methods

Study area

The study was carried out in warm-temperate forest in the Lake Okataina Scenic Reserve, in the North Island of New Zealand (-38.082°S , 176.422°E). Sampling was carried out in a 300 ha basin lying at 395–425 m above sea level (asl) within the reserve, infilled with tephra (mainly rhyolitic) derived from the Okataina Volcanic Centre (Pullar *et al.*, 1973). The nearest weather station is at Rotorua airport, *c.* 10 km west and 120 m lower in elevation; the mean annual temperature recorded there is 12.7°C and mean annual precipitation is 1359 mm (New Zealand Meteorological Service, 1983). Snowfall is rare, and although ground frosts can occur in any month except January and February, they are frequent only from May to September.

A four-phase forest dynamic mosaic

Beveridge (1973) described a three-phase regeneration cycle in old-growth forests of the central North Island, beginning with the fall of a large canopy or emergent tree. Although this often results in recruitment of small short-lived trees and shrubs as well as release of canopy species' saplings, treefall gaps are also often pre-empted by clonal expansion of the treefern *Dicksonia squarrosa* (Dicksoniaceae). The resulting dense groves of this species form a 5–6 m high closed canopy and impede terrestrial regeneration of most trees and shrubs. Although these groves resemble the low palm canopies that sometimes fill treefall gaps in tropical forest (Schnitzer *et al.*, 2000), an important functional difference is that seedlings of some tree species (especially *Weinmannia racemosa*, Cunoniaceae) are able to establish epiphytically on the treefern trunks, eventually smothering their hosts and reforming a high forest canopy (Beveridge, 1973). This three-phase cycle (treefall gaps, treefern groves, closed-canopy tall forest) is readily apparent in the Lake Okataina Scenic Reserve.

Sawmilling and burning during the mid-20th century left two extensive clearings (>5 ha) in the reserve, as well as several smaller ones. The large clearings were farmed for *c.* 20 yr before being abandoned (Nicholls, 1991); they are now occupied mostly by bracken (*Pteridium esculentum*), Spanish heath (*Erica lusitanica*), blackberry (*Rubus fruticosus*), exotic grasses, and scattered small trees and shrubs; forest encroachment around most of the perimeter is slow. We treated these clearings as a fourth phase

of a dynamic vegetation mosaic, analogous to large openings created at rare intervals by natural disturbances. Such openings could be caused at our site by at least three disturbance agents: volcanic eruptions, fire and blowdown. Although the anthropogenic disturbances responsible for the present clearings are not a perfect analogue of any of these types of natural disturbance, the important commonality is that they expose seedlings to more light, larger water deficits and harder frosts than those encountered in any of the three phases of the old-growth mosaic. The Kaharoa eruption from the Tarawera volcanic complex *c.* 16 km away, dated to AD 1314 ± 12 yr (Hogg *et al.*, 2003), deposited at least 600 mm of rhyolitic tephra on our study site (David J. Lowe, pers. comm.). It is not known how much damage this ash-fall caused to the forest canopy in the basin, but deposits of similar depth killed over 50% of evergreen trees in stands affected by the 2011 eruption of Cordón Caulle in southern Chile (Swanson *et al.*, 2016).

Closed-canopy tall forest stands comprise the greater part of the forest mosaic. The canopy is dominated by *Beilschmiedia tawa* (Lauraceae), reaching heights of up to 30 m and diameters up to *c.* 1 m. Although less abundant, *Knighitia excelsa* (Proteaceae), *Litsea calicularis* (Lauraceae), *Laurelia novae-zelandiae* (Atherospermataceae) and *Elaeocarpus dentatus* (Elaeocarpaceae) are also ubiquitous canopy species. Emergent conifers up to 50 m tall are scattered throughout, mainly *Dacrydium cupressinum* and *Dacrycarpus dacrydioides* (Podocarpaceae). Conifers occurred at higher densities before selective logging during the mid-20th century (Nicholls, 1991). All native tree and shrubs species present are evergreen, except for occasional deciduous *Plagianthus betuloides* (Malvaceae) and semideciduous *Fuchsia excorticata* (Onagraceae).

Sampling design

We measured densities of sapling in 10 replicate plots in each forest phase. Our sampling procedure was centred on treefall gaps, as gaps of standardized size and age were harder to find than any of the other three phases. Gaps were located by reconnaissance from walking tracks, and on transects run through the reserve. We chose discrete canopy gaps around 20–30 m in length, created by low wind-snap or uprooting of overstorey trees >60 cm diameter. Although each gap appeared to have resulted from a single treefall event, in most cases the main gap-maker tree had toppled or snapped at least one other tree in falling. All 10 gap-makers were *B. tawa*, easily the commonest overstorey tree in the reserve.

We sought gaps old enough for the development of saplings of light-demanding species to have occurred, but recent enough to still allow ample light penetration to the forest floor. We found that the condition of logs associated with gaps of this age corresponded well to decay class 2 in Pyle & Brown (1999): a solid log with bark present but not firmly attached, and with branches retaining twigs but not leaves.

All tree and shrub saplings 50–250 cm tall were counted in a 20 m × 5 m plot laid out along the long axis of the gap, centred on the fallen log of the main gap-maker, and encompassing at

least part of the crown of the fallen tree. Occasional resprouts from toppled or snapped trees were counted as saplings, these accounting for *c.* 3% of all stems between 50 and 250 cm tall on our plots.

A randomized procedure was used to establish a plot of the same size in each of the other three forest phases, in close proximity to each treefall gap. An understorey plot was established by walking between 25 and 30 m in a random cardinal direction away from the gap, with the requirement that a closed canopy be present over most of the plot. The same compass bearing was followed until a treefern grove of at least 100 m² area was located; if this compass bearing did not lead to a suitable treefern grove within *c.* 100 m of the gap, a search was begun in a different cardinal direction from the gap. A 20 × 5 m plot was centred on each of these locations. Lastly, a satellite photograph was used to locate the clearing margin nearest to each treefall gap, and another plot laid out along the margin; as forest encroachment along margins was patchy, we stipulated the requirement that at least five tree saplings be present on the plot, rejecting sites that did not meet this criterion. Clearings were sampled only on the margins, because few tree saplings were found more than a few metres outside the forest. Our procedure for sampling the four forest phases was intended to minimize the risk of confounding with unmeasured variation in soil or other environmental factors (Fig. S1). All sampled plots were on flat to near-flat terrain between 395 and 425 m asl, within an area of *c.* 2 km² (Supporting Information Fig. S1).

Microenvironmental measurements

Hemispherical photography was used to quantify light availability above each plot. A Nikon D5100 digital camera and a Sigma 4.5 mm fisheye lens was used to take three digital hemispherical photos at 1.5 m above ground, at 3, 10 and 17 m along the long axis of each plot. The captured images were processed using Gap Light Analyzer (Frazer *et al.*, 1999) to determine mean daily availability of direct and diffuse light at each plot.

Temperature and relative humidity were monitored for 1 yr on a randomly selected subsample of four plots in each forest phase. One DS1923-F5# Hygrochron temperature and humidity sensor (Maxim Integrated, San Jose, CA, USA) was placed 60 cm above ground at a randomly chosen point on the central axis of each chosen plot. Radiation shields, custom-made from stacked plastic plates (Tarara & Hoheisel, 2007), were used to protect sensors against radiative heating and chilling. Sensors were programmed to record relative humidity and air temperatures (to the nearest 0.5°C) every 4 h.

Functional traits

We measured leaf size (area) because of its relevance to leaf energy balance and efficiency of foliage display. The thin boundary layers of small leaves mean they are more closely coupled to air temperatures at low wind speeds (Parkhurst & Loucks, 1972). As a result, small leaves use water more efficiently than large leaves in dry, sunny conditions and are less prone to overheating (Yates

et al., 2010). For the same reason, small leaves should also be less vulnerable to chilling when exposed to a cold, clear night sky (Leuning, 1988). On the other hand, large leaves can enhance the foliage display efficiency of juvenile trees, as a crown with few large leaves usually has less self-shading than one composed of many small leaves (Duursma *et al.*, 2012; Lusk *et al.*, 2012).

The leaf economics spectrum is widely accepted as a major axis of variation relevant to ecological differences between plants (Westoby *et al.*, 2002; Wright *et al.*, 2004). Leaf economic traits usually correlate with juvenile growth rates of rainforest trees and often also with shade tolerance (e.g. Veneklaas & Poorter, 1998; Poorter & Bongers, 2006; Lusk *et al.*, 2010). Leaf dry mass per area (LMA) is the easiest to measure of this suite of traits, but suffers from two important drawbacks. First, the highly plastic response of LMA to light environment (Wilson *et al.*, 1999; Poorter *et al.*, 2009) makes standardization of sampling environments critical, yet it is not always feasible to find all species in a common light environment. Second, LMA is difficult to apply to scale-leaved conifers, two of which were present in our dataset. We therefore opted instead to measure leaf dry matter content (LDMC), which is less sensitive to light environment (Lusk *et al.*, 2010) and readily applicable to nonlaminar leaves.

Wood density is another trait likely to have value in predicting regeneration patterns. High wood density has been linked to both drought tolerance (Hacke *et al.*, 2001; Poorter & Markesteijn, 2008) and shade tolerance (van Gelder *et al.*, 2006; Wright *et al.*, 2010), as well as correlating negatively with growth rates (Chave *et al.*, 2009; Kunstler *et al.*, 2016).

Seed size was included as a trait likely to influence patterns of seed dispersal and seedling establishment. Species establishing in large openings and treefall gaps often have small seeds, whereas those establishing in shaded understoreys are often (but not always) large-seeded (Hewitt, 1998; Coomes & Grubb, 2003). Additionally, small seeds are typical of species that establish epiphytically on treeferns or on other elevated substrates (Newton & Healey, 1989; Lusk & Kelly, 2003; Coomes *et al.*, 2005).

Seed mass data were obtained as average values per species from the literature (Moles & Drake, 1999; Moles *et al.*, 2000), whereas leaf size, LDMC and wood density were measured on saplings growing on our plots. In most cases, we obtained a leaf sample and a wood sample from each species represented by saplings on each plot. Leaves were placed immediately in resealable plastic bags with moist paper and blotted dry before determining FW. A LI-3100C Area Meter (Li-Cor, Lincoln, NE, USA) was used to measure area of leaf samples, which were then oven-dried at 60°C for 3 d (Cornelissen *et al.*, 2003). Petioles were not removed from laminae before determination of area and LDMC. Wood density was estimated from twig sections 60–100 mm long and 5–10 mm in diameter. The volume of a section was estimated by measuring the length and the diameter on two orthogonal axes at three points along the length of the section. Bark was stripped before measuring wood volume, and samples were then oven-dried for 3 d at 60°C before determining DW. In some cases, wood could not be obtained from saplings on our plots because they were unbranched, or had no branches of sufficient diameter; this was usually true of *Elaeocarpus*

dentatus saplings, and occasionally of other species. In these cases, we sought twigs from larger saplings or trees of the same species growing nearby.

Trait measurements were obtained from one sapling of each species present on each plot. The only exception was *Pseudopanax arboreus* (Araliaceae), which was present on only three plots: two saplings of this species were sampled on one of these three plots, giving a total of four replicates. Species present on fewer than three plots being omitted from all analyses, so the number of replicate measurements per species ranged from four to 26,

Statistical analysis

First, we tested for compositional differences of tree regeneration among the four forest phases, including all species present as saplings on three or more of our 40 plots. Nonmetric multidimensional scaling (NMS) was used to illustrate the compositional differences in two dimensions (Clarke, 1993), and permutation-based multivariate analysis of variance (PERMANOVA) was used to test whether forest phase explained significant variation in the composition of tree regeneration (Anderson, 2001). Indicator species analysis (ISA) was used to identify species associated with particular forest phases. Species were considered indicators of a forest phase for which they had their largest indicator value (INDVAL). We restricted our attention to species with $P < 0.05$ (assessed using Monte Carlo randomizations with 10 000 permutations) and $INDVAL > 0.25$ (Dufrene & Legendre, 1997). All analyses were conducted using the 'VEGAN' package of R (Oksanen *et al.*, 2015).

Second, we compared average community-level trait values across the different forest phases in order to determine the potential adaptive value of these traits in each environment. We calculated community-weighted mean (CWM) traits in each of the plots as:

$$\sum_{i=1}^S t_i p_i, \quad \text{Eqn 1}$$

where t_i is the mean trait of tree species i , and p_i is the relative tree density (proportion of total stems) of species i , and S is the number of tree species in the plot. We used ANOVA to test whether forest phase explained significant variation in CWM traits and followed significant overall tests with Bonferonni-adjusted pairwise comparisons.

We also tested for plastic intraspecific responses of functional traits to the four forest phases by using linear mixed effects models (NLME package in R) to partition the variance of individual-level traits into three sources: interspecific, intraspecific and forest phase. Species and forest phase effects were modelled as random intercepts, and the remaining within-level variation accounted for intraspecific variation plus residual error.

Lastly, we used Traitspace, a trait-based predictive model of community assembly (Laughlin *et al.*, 2012; Laughlin & Laughlin, 2013), to determine the most parsimonious combination of traits predicting tree species regeneration patterns. Traitspace is a

Bayesian model whose hierarchical dependence structure can be represented using a directed acyclic graph: $E \rightarrow T \rightarrow S$, where E represents environmental gradients, T represents functional traits, and S is a vector of the probabilities of s species S_1, \dots, S_S . The model quantifies how traits structure species–environment relationships by using traits to predict species abundances along environmental gradients: if the trait-based predictions do not match field observations, then the traits do not explain the species–environment relationships. Furthermore, evaluating predictions from multiple models that use different traits can determine which trait combinations best explain species distributions.

The Traitspace model consists of two stages: a calibration stage, and an inference and validation stage. The calibration stage quantifies two things necessary for inference: the relationships between traits and environment and the multivariate trait distributions of each species. To calibrate the model, we characterize the size and shape of the environmental filter by fitting $T = f(E)$. Generalized linear models (GLMs) were employed to fit individual-level traits as a function of the four forest phase categories, using the 'LM' function in R. This calibrates the conditional distributions of individual-level plant traits given the environmental conditions $\varphi_{T|E}$. Next, we characterized the location and dispersion of species in trait space using semiparametric Gaussian mixture models (Fraleley *et al.*, 2012). This calibrates the conditional distributions of traits given species $\varphi_{T|S_i}$. All the traits are modelled jointly by these mixed models to account for trait covariance. Mixture models are more flexible than parametric density estimations because they do not rely on strict unimodal distributions and allow for multimodal trait distributions.

The inference and validation stage combines these two sources of information to make predictions about the probability that a species will occur in a given environment, which are then compared against observations. First, we simulated community assembly stochastically by sampling a large number ($n = 1000$) of trait values at each site from the distributions $\varphi_{T|E}$ defined by the GLM. For every trait value sampled, the likelihood $P(T|S_i)$ is computed using the conditional distributions $\varphi_{T|S_i}$. In addition, for every trait value sampled, the posterior distribution of species conditioned on both the trait data and the environmental conditions $P(S_i|T, E)$ is computed using Bayes theorem:

$$P(S_i|T, E) = \frac{P(T|S_i)P(S_i)}{\sum_{i=1}^S P(T|S_i)P(S_i)}. \quad \text{Eqn 2}$$

Here, $P(S_i)$ denotes a flat (uniform) prior on the species. Note that Eqn 2 is valid because $P(S_i|T, E) = P(S_i|T)$ is implied by the directed acyclic graph model. The traits are integrated out to obtain the probabilities of species given the forest phase:

$$P(S_i|E) = \int P(S_i|T, E)P(T|E)dT. \quad \text{Eqn 3}$$

Using Monte Carlo integration, the desired conditional distribution is thus approximated as:

$$P(S_i|E) \cong \frac{1}{N} \sum_{k=1}^N P(S_i|T_k, E)P(T_k|E). \quad \text{Eqn 4}$$

Species probability distributions indicate the environment in which a species is most likely to be found. The probability (q_j) of species i in forest phase j is defined as the density (number of stems per plot) of species i in forest phase j divided by the sum total density of species i across all j forest phases, such that:

$$\sum_{j=1}^J q_j = 1. \quad \text{Eqn 5}$$

To evaluate the predictive accuracy of the model, we compared model predictions of these probabilities (\hat{q}_j) with the observed probability distributions (q_j) of species i across each of the j forest phases.

We tested a series of models using forward selection to determine the most parsimonious combination of traits for predicting regeneration patterns. First, we evaluated the predictive accuracy of four-one-trait models individually, each of which used only one of the four traits. These models were then ranked from best to worst according to the R^2 of the relationship between observed and predicted q_{ij} . Second, we fitted three-two-trait models, each of which contained the trait that ranked highest in the single-trait models, in combination with the other three traits. These models were then ranked from best to worst. Third, we fitted two three-trait models, each of which contained the two traits that performed the best of the two-trait models, in combination with the other two traits. Finally, we fitted a four-trait model.

Results

Microenvironmental measurements

Direct and diffuse light availability differed consistently between the forest phases. Light availability was significantly higher on forest margins than in treefall gaps, which in turn consistently received more light than plots located in treefern groves or forest understoreys (Table 1).

Table 1 Quantification of microclimatic variables in four forest phases in Lake Okataina Scenic Reserve

Variable	Clearing margins	Treefall gaps	Treefern groves	Understoreys
Direct light (annual photon flux, %)	31.1 a (± 19.9)	15.5 b (± 8.8)	4.1 c (± 2.0)	3.4 c (± 2.2)
Diffuse light (annual photon flux, %)	32.4 a (± 8.4)	19.6 b (± 11.2)	4.8 c (± 2.6)	3.9 c (± 2.5)
Highest recorded temperature ($^{\circ}\text{C}$)	26.9 a (± 2.1)	24.4 abc (± 2.3)	20.5 b (± 0.2)	21.4 c (± 0.8)
Mean summer daily maximum temperature ($^{\circ}\text{C}$)	22.2 a (± 1.1)	20.1 ab (± 0.4)	18.6 b (± 0.2)	18.4 bc (± 0.3)
Average daily range ($^{\circ}\text{C}$)	8.6 a (± 0.8)	5.2 b (± 0.6)	4.8 b (± 0.2)	4.5 b (± 0.4)
Mean winter daily minimum temperature ($^{\circ}\text{C}$)	3.4 a (± 0.2)	4.4 b (± 0.5)	4.8 b (± 0.3)	4.8 b (± 0.7)
Lowest recorded temperature ($^{\circ}\text{C}$)	-5.1 a (± 1.7)	-2.2 b (± 0.3)	-2.2 bc (± 0.5)	-1.3 c (± 0.6)
Days of frost	24.8 a (± 5.3)	8.3 b (± 4.3)	6.0 b (± 2.6)	5.3 b (± 5.3)
Mean summer daily maximum VPD (kPa)	0.98 a (± 0.34)	0.57 ab (± 0.25)	0.31 b (± 0.09)	0.28 b (± 0.20)
Highest recorded VPD (kPa)	1.95 a (± 0.56)	1.31 ab (± 0.50)	0.65 b (± 0.22)	0.88 b (± 0.16)

VPD, vapour pressure deficit. Temperature and VPD were measured from December 2014 to November 2015 (mean \pm SD). Values followed by the same letter do not differ significantly at $P = 0.05$. $n = 10$ for light environments, and $n = 4$ for temperature and VPD measurements. Summer, the December–February quarter; winter, the June–August quarter.

Among the four forest phases, the most distinctive microclimates were found on the margins of clearings. Clearing margins were significantly hotter in summer and colder in winter than treefern groves or forest understoreys, and experienced wider daily temperature ranges, four to five times more frosts, and larger summer vapour pressure deficits (Table 1).

The microclimates of clearing margins also showed some differences from those of treefall gaps. Margins were exposed to a significantly wider daily temperature range than treefall gaps, were significantly colder on winter nights, and experienced three times as many frosts (Table 1). In summer, margins also tended to reach higher temperatures and larger vapour pressure deficits than treefall gaps, but these differences were not significant (Table 1).

Understoreys and treefern groves did not differ significantly in any environmental variable (Table 1), although the lowest recorded temperatures tended to be milder on understorey plots ($P = 0.07$). Both these phases tended to experience smaller vapour pressure deficits and narrower temperature ranges than treefall gaps, although there were few significant differences (Table 1).

Composition of regeneration

The four forest phases accounted for 42% of the variation in sapling community composition across the 40 plots (PERMANOVA, $F_{3,36} = 8.5$, $P < 0.001$). These compositional differences are illustrated in the NMS diagram, where gaps, understoreys, treefern groves and clearing margins are clearly differentiated in ordination space (Fig. 1). Eighteen of the 21 species were found to be significantly associated with a specific forest phase, indicating preferences for specific environmental conditions (Table 2).

Community-weighted trait variation

Interspecific differences accounted for the greater part of variation in leaf size, LDMC and wood density (Table 3). Although intraspecific variation in wood density was relatively high, little of this variation could be attributed to forest phase, indicating that the variation within species was not strongly determined by the environment.

Community-weighted mean traits differed significantly across the four forest phases (Fig. 2), which accounted for 42–66% of variation in CWM trait values (Table 3). Leaves were largest, on average, in treefall gaps, and smallest on the margins of clearings (Fig. 2). LDMC was lowest in gaps, highest

on margins, and intermediate in understoreys and treefern groves (Fig. 2). Wood density was lowest in gaps, highest in understoreys, and intermediate in treefern groves and on margins (Fig. 2). Species associated with understoreys had the largest seeds, those establishing primarily in gaps were intermediate, and those associated with margins or treefern groves had the smallest seeds (Fig. 2).

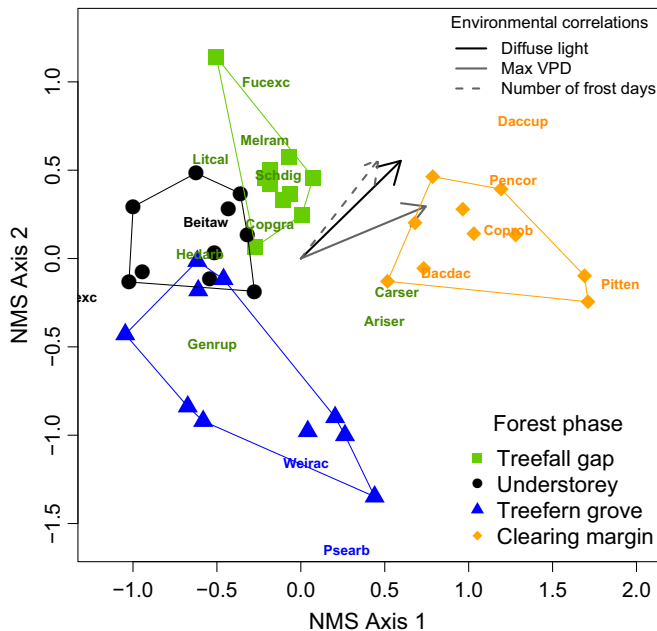


Fig. 1 Nonmetric multidimensional scaling (NMS) ordination diagram illustrating contrasting composition of regenerating trees in four different forest environments. Stress = 0.12; cumulative $R^2 = 0.91$; distance metric = Bray–Curtis. Species shown as six-letter codes (see Table 2) are significant indicators of each environment coded by colour. VPD, vapour pressure deficit.

Traits predicting species regeneration patterns

Forest phase accounted for significant variation in individual-level trait values (Table 3), and these individual-level trait-environment ANOVA models were used to calibrate the Traitspace model. The best-performing one-trait model was the leaf size model ($R^2 = 0.37$), followed by the wood density model ($R^2 = 0.16$) (Table 4). The best-performing two-trait model was the model that included both leaf size and wood density (Table 4). This model predicted species probabilities that were significantly correlated with the observed probabilities ($R^2 = 0.51$, $P < 0.001$, Fig. 3). The best three-trait model included leaf size, wood density and LDMC, but this model was slightly inferior to the more parsimonious two-trait model ($R^2 = 0.50$, Table 4). The four-trait model performed worse ($R^2 = 0.40$) than the best two-trait and the best three-trait models (Table 4).

A two-trait combination of leaf size and wood density was thus the best predictor of sapling distribution patterns across the four forest phases. This combination differentiated well between species associated with understoreys (large leaves, dense wood), those establishing primarily in treefall gaps (large leaves, low-density wood), and most of those associated with clearing margins (generally with small leaves and dense wood) (Fig. 4). Trait

Table 2 Results of indicator species analysis testing for species whose saplings were significantly more abundant in a particular forest phase

Forest phase	Species	Code	Indicator value	<i>P</i> -value	Sample size
Treefall gap	<i>Alectryon excelsus</i>	Aleexc	0.150	0.363	6
	<i>Aristotelia serrata</i>	Ariser	0.405	0.027	34
	<i>Carpodetus serratus</i>	Carser	0.588	0.001	81
	<i>Coprosma grandifolia</i>	Copgra	0.481	0.006	32
	<i>Elaeocarpus dentatus</i>	Eladen	0.171	0.703	14
	<i>Fuchsia excorticata</i>	Fucexc	0.400	0.019	6
	<i>Geniostoma rupestre</i>	Genrup	0.378	0.017	19
	<i>Hedycarya arborea</i>	Hedarb	0.504	0.013	166
	<i>Laurelia novae-zelandiae</i>	Launov	0.405	0.092	304
	<i>Litsea calicularis</i>	Litcal	0.540	0.003	40
	<i>Melicytus ramiflorus</i>	Melram	0.842	0.001	95
	<i>Schefflera digitata</i>	Schdig	0.818	0.001	55
	Clearing margin	<i>Coprosma robusta</i>	Coprob	0.488	0.002
<i>Dacrydium cupressinum</i>		Daccup	0.428	0.008	8
<i>Dacrycarpus dacrydioides</i>		Dacdac	0.825	0.001	107
<i>Pennantia corymbosa</i>		Pencor	0.600	0.001	38
<i>Pittosporum tenuifolium</i>		Pitten	0.400	0.014	10
Treefern grove	<i>Pseudopanax arboreus</i>	Psearb	0.300	0.048	4
	<i>Weinmannia racemosa</i>	Weirac	0.747	0.001	53
Understorey	<i>Beilschmiedia tawa</i>	Beitaw	0.609	0.001	138
	<i>Knightia excelsa</i>	Kniexc	0.456	0.045	107

Species showing significant patterns are in bold. Sample size = total number of saplings recorded on the 40 plots.

Table 3 ANOVA of the effect of forest phase on community-weighted mean (CWM) and individual-level traits, and partitioning of variance

Trait	CWM traits	Individual-level traits	Partitioning of trait variance		
			Forest phase	Interspecific	Intraspecific + error
Leaf size	$R^2 = 0.57, P < 0.0001$	$R^2 = 0.21, P < 0.0001$	< 0.001	0.985	0.015
Leaf dry matter content	$R^2 = 0.43, P = 0.0001$	$R^2 = 0.09, P = 0.0002$	0.081	0.785	0.133
Wood density	$R^2 = 0.42, P < 0.0001$	$R^2 = 0.11, P < 0.0001$	0.035	0.538	0.427
Seed mass	$R^2 = 0.66, P < 0.0001$	$R^2 = 0.12, P < 0.0001$	na ¹	na	na

¹na, not applicable. There are no data on variance partitioning of seed mass data, which were obtained from the literature.

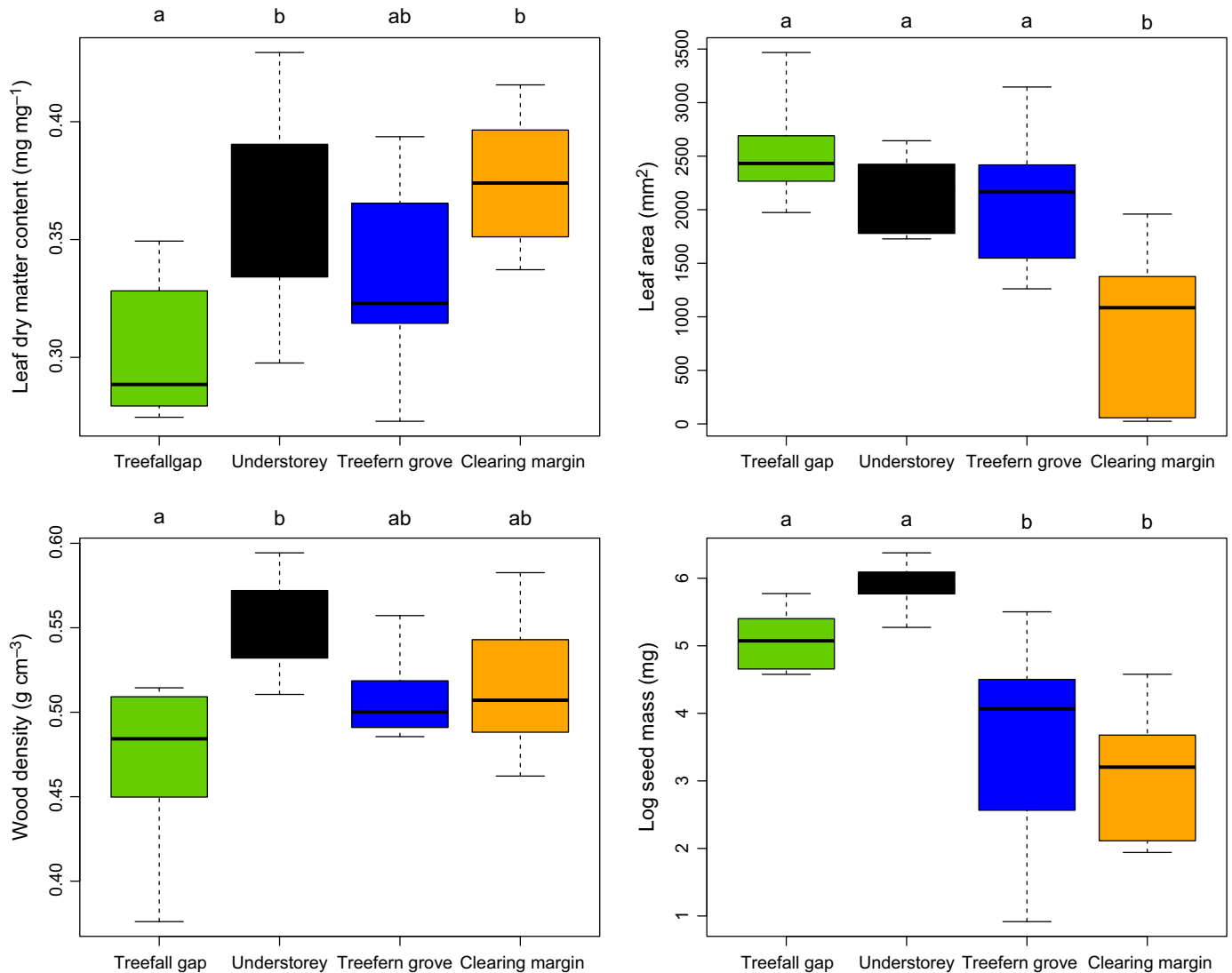


Fig. 2 Community-weighted mean traits of juvenile trees in different forest phases, showing percentiles 0, 25, 50, 75 and 100. ANOVA showed significant variation of all traits across forest phases (all $P < 0.001$). Within each panel, forest phases sharing the same lowercase letter do not differ significantly from one another.

combinations associated with treefern groves were less distinctive, the two species diverging considerably in leaf size. No bivariate relationships of traits with microenvironmental gradients had as much explanatory power as our two-trait predictive models (Table S1, cf. Table 3).

Discussion

Our results show that the dynamics of some forests cannot be adequately explained by a trait-mediated tradeoff between growth rate in well-lit environments and survival under shade (cf. Bazzaz,

Table 4 Traitspace model selection results using different numbers and combinations of traits

Models	R^2	P -value
One-trait models		
Leaf area	0.37	< 0.0001
Wood density	0.16	0.0006
LDMC	0.07	0.0254
Seed mass	0.06	0.0395
Two-trait models		
Leaf area, wood density	0.51	< 0.0001
Leaf area, LDMC	0.42	< 0.0001
Leaf area, seed mass	0.35	< 0.0001
Three-trait models		
Leaf area, wood density, LDMC	0.50	< 0.0001
Leaf area, wood density, seed mass	0.37	< 0.0001
Four-trait models		
Leaf area, wood density, LDMC, seed mass	0.40	< 0.0001

LDMC, leaf dry matter content. Leaf area explained by far the most variance as a single trait, so two-trait models compared the effects of adding each additional trait to a model with leaf area. The two-trait model of leaf area and wood density was selected as the best model. Models with three or four traits performed worse.

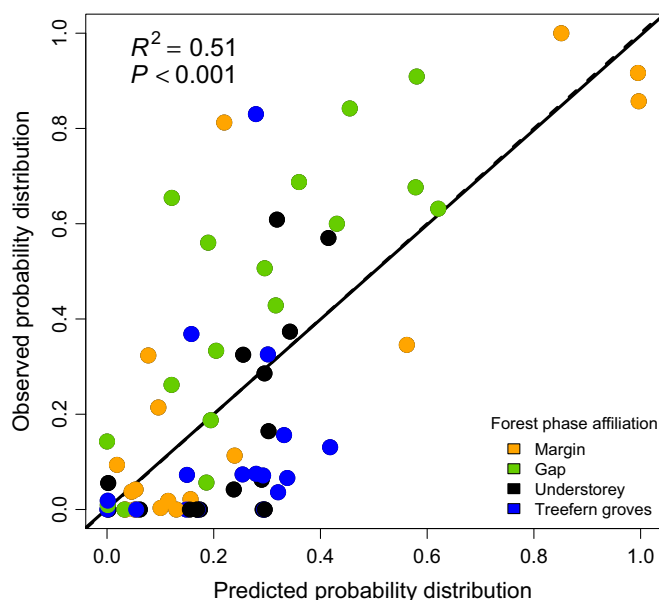


Fig. 3 Traitspace predictions (\hat{q}_j) compared with observations (q_j) for the two-trait model that included leaf area and wood density ($R^2 = 0.51$, $P < 0.001$). Each point represents a species–forest phase combination; the coordinates of each point are determined by the predicted probability of a species in a given forest phase (\hat{q}_j) and the observed probability distribution (q_j) of that species in each forest phase (see the Materials and Methods section for details on how these quantities are computed). We modelled 17 species across four forest phases, totalling 68 species–forest phase combinations. The fitted regression line overlaps the 1 : 1 line (slope = 0.994).

1984; Hubbell & Foster, 1992; Kobe *et al.*, 1995; Poorter & Bongers, 2006; Lusk *et al.*, 2010). As reported elsewhere, species establishing primarily in treefall gaps at our site had traits favouring light pre-emption and rapid growth, that is, large leaves and low-density wood. However, we are not aware of any previous

work showing the trait combinations associated with the microclimates of more extensive openings to be quite distinct from those favoured by treefall gaps (Fig. 4). The dense wood and small leaves of most species establishing on the margins of clearings indicate that the dominant environmental filters there may be frost and summer water deficits, rather than competition for light. Although some of the species associated with clearings were small, short-lived trees (e.g. *Pittosporum tenuifolium*, *Pennantia corymbosa*), most saplings of the long-lived conifers *Dacrydium cupressinum* and *Dacrycarpus dacrydioides* were also found in this forest phase (Fig. 1). Life spans of > 700 yr enable emergent New Zealand podocarps such as *D. cupressinum* and *D. dacrydioides* to coexist with shorter-lived but faster-growing angiosperms that regenerate more readily beneath small openings (Ogden & Stewart, 1995; Lusk & Smith, 1998; Lusk *et al.*, 2015). Differences in longevity and in ability to withstand the microclimates of large openings may therefore be important controls on tree species coexistence in these forests.

Functional traits predicted regeneration patterns of most species, but a two-trait model (leaf size, wood density) performed significantly better than single-trait models (Tables 4, S1). Similarly, Easdale *et al.* (2007) found that consideration of multiple functional dimensions gave an enhanced understanding of tree species coexistence in a montane subtropical forest. Model results did not match our initial expectation that seed size would explain some of the variation in tree regeneration patterns (Table 4); other studies have shown that species establishing on treefern trunks and other elevated substrates are mostly small-seeded (Newton & Healey, 1989; Lusk & Kelly, 2003; Coomes *et al.*, 2005).

Treefall gaps appeared to be very favourable environments for juvenile trees, admitting abundant light without exposing plants to environmental extremes. Light availability in treefall gaps averaged fourfold higher than on plots in the understorey or treefern groves, but the effect of treefalls on temperature regimes and vapour pressure deficit was less marked (Table 1). Similarly modest effects of small canopy gaps on microclimate have been reported in several other humid forests from a wide range of latitudes (Fetcher *et al.*, 1985; Collins & Pickett, 1987; Groot & Carlson, 1996). In a seasonal tropical forest, however, Nepstad *et al.* (1996) found that dry-season maximum air temperatures in treefall gaps climbed 4°C higher than in nearby understoreys. In regions subject to a prolonged dry season, treefall gaps might therefore be less unequivocally favourable for survival and growth of juvenile trees.

Although twice as much light was available on margins of clearings than in treefall gaps, plants growing on margins were also much more exposed to environmental extremes, especially frost. Studies comparing openings of different sizes in some other regions have also reported large microclimatic differences between clearings and treefall gaps (Nepstad *et al.*, 1996), or between clearings and small canopy gaps created by logging (Groot & Carlson, 1996). In our study, margin plots experienced on average *c.* 25 air frosts during the year, three times as many as were recorded in treefall gaps, and minimum air temperatures averaged *c.* 3°C lower (Table 1); these differences were larger

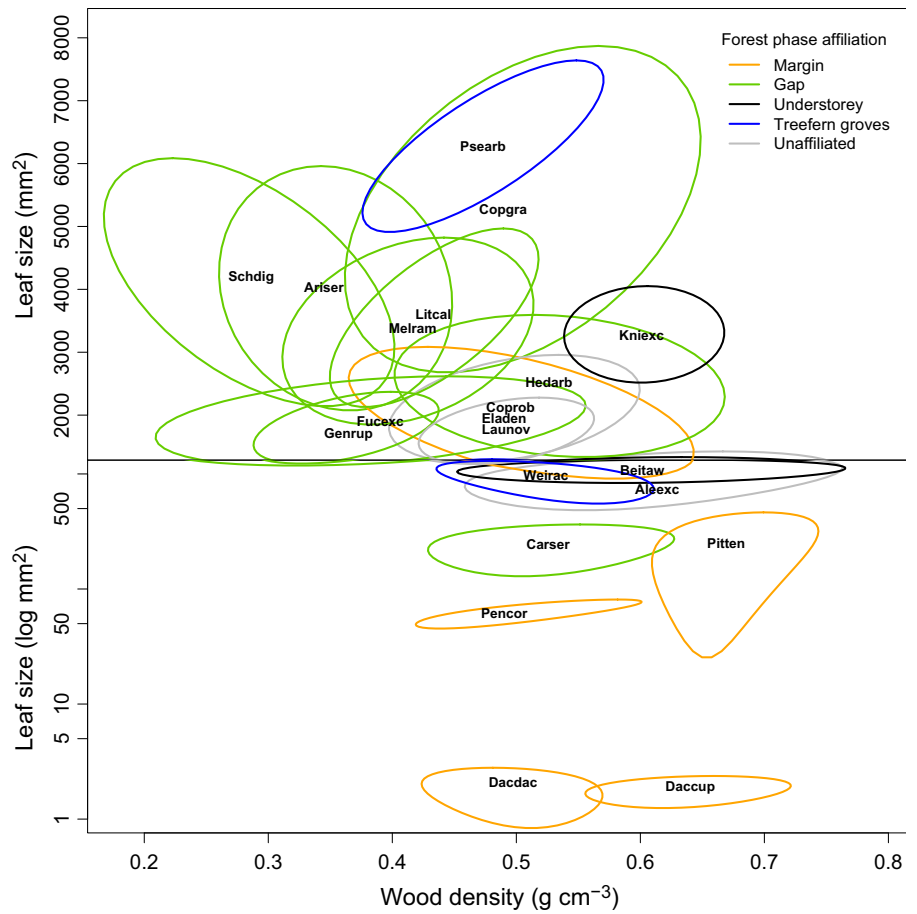


Fig. 4 Two-dimensional ellipses illustrating variation in wood density and leaf size of juvenile trees and their association with treefall gaps (green), treefern groves (blue), understorey (black), and margins of clearings (orange), as well as species showing no significant association (grey). A log scale is used for the lower half of the y-axis, to show small-leaved species more effectively. Species shown as six-letter codes (see Table 2).

than those between treefall gaps and understoreys or treefern groves. Frost tolerance measurements on over half of our study species have been published (reviewed by Bannister, 2007) and these indicate that the average minimum air temperatures recorded on margins (-5.1°C) exceeded the maximum tolerances of winter-hardened foliage of two treefall gap specialists (*Hedycarya arborea* and *Fuchsia excorticata*), but were well within the reported tolerances of all species associated with margins (Table S2). Furthermore, freezing tolerance provides only part of the explanation, as the small leaves of most of the species that establish on margins are also more able to avoid potentially damaging low temperatures as they are less susceptible to radiative cooling on clear nights (Leuning, 1988). Plants were also exposed to larger vapour pressure deficits and higher summer temperatures on margins than in treefall gaps, although differences were not statistically significant (Table 1).

Trait divergences between species associated with treefall gaps and forest margins (Figs 2, 4) confirm that quite distinct environmental filters act on juvenile tree recruitment in these two forest phases. The traits of species associated with treefall gaps (large leaves, low-density wood) often underpin efficient light capture and fast growth (Veneklaas & Poorter, 1998; Wright *et al.*, 2010; Lusk *et al.*, 2012), and experimental data in Kramer-Walter *et al.* (2016) show that the fastest seedling growth rates of New Zealand trees are generally those of short-lived treefall-gap specialists such as *Aristotelia serrata* and *Schefflera digitata*

(Table S3). Treefall gap environments in our study appear to select for traits conferring pre-emptive access to light through rapid height growth and efficient deployment of foliage, as in other humid forests (Falster & Westoby, 2005). In humid tropical forests, some pioneer trees that establish in treefall gaps have even lower wood density than any values reported from humid temperate forests (van Gelder *et al.*, 2006; Lusk *et al.*, 2016), presumably resulting in even faster growth rates. By contrast, species establishing on margins of clearings in this temperate forest mostly had small leaves and dense wood (Figs 2, 4), traits likely to confer resistance to the frosts and vapour pressure deficits to which plants growing there are exposed (Table 1). The dense wood often found in drought-tolerant plants appears to support resistance to xylem implosion under negative pressure (Hacke *et al.*, 2001). Small leaves stay closer to ambient air temperatures than large leaves (Parkhurst & Loucks, 1972), conserving water in hot dry weather and minimizing frost damage on cold, clear nights (Leuning, 1988; Yates *et al.*, 2010). Data in Kramer-Walter *et al.* (2016) show that seedling maximum growth rates of species associated with margins of clearings in our study averaged only about half those of tree-fall gap specialists (Table S3; *T*-test, $P=0.04$), supporting the idea that competition is not the major environmental filter on seedling recruitment on clearing margins.

We expect species establishing in large openings to show similar stress-adapted traits in other evergreen-dominated forests subject to aseasonal frost or significant rainless periods. In New

Zealand's oceanic climate, aseasonal frost is characteristic of inland basins, terraces and valley bottoms (NIWA, 2016), where large openings will inevitably expose seedlings to intermittent subzero temperatures throughout much of the year. The frequent dominance of long-lived, small-leaved conifers on these frost-prone sites has been noted (Norton *et al.*, 1988; Leathwick & Mitchell, 1992). Aseasonal frost is also a feature of similar inland sites in south-central Chile (INIA, 2012), where temperate forests grow in oceanic climates broadly comparable to those of New Zealand (McGlone *et al.*, 2016). Although the species colonizing old-fields and other large openings in south-central Chile encompass a range of leaf sizes and wood densities, the most ubiquitous colonizer of old-fields (*Maytenus boaria*, Celastraceae) has traits closely matching those associated with clearing margins in our study (dense wood and small leaves), as do two *Nothofagus* species with slightly narrower ecological amplitude, *N. dombeyi* and *N. obliqua* (Nothofagaceae) (Donoso, 2006; Lusk *et al.*, 2016). The regeneration of all three of these species in lowland forests is restricted mainly to large openings (Veblen *et al.*, 1996). Small leaves and dense wood are also typical of the *Acacia* spp. that establish on cleared sites in seasonal tropical forest, but show little gap regeneration in old-growth forest (Kennard, 2002; Kalacska *et al.*, 2004); in view of the lack of frost in the lowland tropics, these traits are presumably advantageous in coping with the dry season. However, an important difference from the oceanic temperate climates of New Zealand is the temporal predictability of climatic stress in the seasonal tropics, where many trees avoid drought stress by shedding most or all of their foliage at the start of the dry season (van Schaik *et al.*, 1993; Reich, 1995), reducing the need for drought-tolerant form and function.

A single growth vs shade tolerance tradeoff is not sufficient to explain the regeneration dynamics of some forests (Lusk *et al.*, 2015). Although trait differences between species associated with understoreys and treefall gaps were consistent with prevailing ideas about the basis of light gradient partitioning through a growth vs shade tolerance tradeoff, this framework cannot adequately explain the traits of species establishing in more open environments on the margins of clearings, where filtering may be effected primarily by aseasonal frost and summer drought stress. Consideration of multiple environmental filters and multiple functional traits (Easdale *et al.*, 2007; Laughlin, 2014) will thus enhance our understanding of tree regeneration patterns and species coexistence in regions outside the wet tropics, where seedlings are exposed to climatic stressors in large openings.

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Author contributions

C.H.L. developed the idea, collected the data and wrote most of the manuscript. D.C.L. analysed the data, wrote parts of the Methods and Results sections, and edited the rest of the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Satellite photograph showing spatial arrangement of plots in Lake Okataina Scenic Reserve.

Table S1 Correlations of functional traits with average light environments and microclimates occupied by juvenile trees

Table S2 Freezing tolerance of study species associated with different forest phases at Okataina

Table S3 Seedling relative height growth rates of species associated with different forest phases at Okataina

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