Simulating long-term vegetation dynamics using a forest landscape model: the post-Taupo succession on Mt Hauhungatahi, North Island, New Zealand

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Abstract: Forest dynamics in New Zealand are shaped by catastrophic, landscape-level disturbances (e.g. volcanic eruptions, windstorms and fires). The long return-intervals of these disturbances, combined with the longevity of many of New Zealand's tree species, restrict empirical investigations of forest dynamics. In combination with empirical data (e.g. palaeoecological reconstructions), simulation modelling provides a way to address these limitations and to unravel complex ecological interactions. Here we adapt the forest landscape model LandClim to simulate dynamics across the large spatio-temporal scales relevant for New Zealand's forests. Using the western slope of Mt Hauhungatahi in the central North Island as a case study, we examine forest succession following the Taupo eruption (c. 1700 cal. years BP), and the subsequent emergence of elevational species zonation. Focusing on maximum growth rate and shade tolerance we used a pattern-oriented parameterisation approach to derive a set of life-history parameters that agree with those described in the ecological literature. With this parameter set, LandClim was able to reproduce similar spatio-temporal patterns in vegetation structure to those seen in pollen reconstructions and contemporary vegetation studies. The modelled successional sequence displayed a major shift in forest composition between simulation years 400 to 700, when the dense initial stands of conifers (dominated mainly by *Libocedrus bidwillii*) were progressively replaced by the angiosperm *Weinmannia racemosa* in the montane forest. From around year 1000, the contemporary elevational species zonation was attained. Competition for light controlled the major successional trends and, together with temperature-limitation, explained the observed elevational species zonation. Although originally designed for European temperate forests, LandClim can simulate New Zealand landscape dynamics and forest response to catastrophic disturbances such as the Taupo eruption. We suggest that LandClim provides a suitable framework for investigating the role of spatial processes, in particular disturbance, in New Zealand's forest landscapes.

Keywords: disturbance regime; gap model; inverse modelling; LandClim; long-lived tree species

Introduction

Climate, soil, relief and exogenous disturbance are important abiotic drivers of the spatial distribution of forest types (Leathwick & Mitchell 1992). Along elevational gradients, temperature and other parameters of climate are the primary controls of species' distributions, in particular their upper limits (Wardle 1964; Druitt et al. 1990). Large-scale disturbances are another key driver of the long-term dynamics of forests in New Zealand (Ogden & Stewart 1995). A number of studies have demonstrated the long-lasting impact of large, infrequent disturbances – such as earthquakes, landslides, volcanic eruptions and windstorms – on New Zealand's forests (Clarkson 1990; Wells et al. 2001; Lecointre et al. 2004; Martin & Ogden 2006). Disturbances and their effects are also central to long-standing questions about the nature of conifer–angiosperm interactions in New Zealand's mixed forests (Veblen & Stewart 1982; Wells et al. 2001; Ogden et al. 2005). Contrasting traits of conifers and angiosperms are considered key in structuring forest communities over time (McKelvey 1963; Ogden & Stewart 1995; Coomes et al. 2005; Kunstler et al. 2009). Conifers are generally slower

growing than angiosperms on productive sites (i.e. those rich in nutrients and water, and/or with warmer temperatures) and therefore tend to be outcompeted by angiosperms over the long term (Bond 1989; Becker 2000; Coomes et al. 2005; Brodribb et al. 2012). However, in New Zealand, and other parts of the Southern Hemisphere, 'long lived pioneer' conifers (e.g. *Agathis australis, Dacrydium cupressinum, Libocedrus bidwillii*) persist alongside angiosperm competitors (Ogden and Stewart 1995). Large, infrequent disturbances are considered key to mediating the competition between both groups (Ogden & Stewart 1995).

The dynamics of forests dominated by long-lived tree species and shaped by the infrequent occurrence of large disturbances are particularly intractable to study (Enright et al. 1999) as timescales up to the millennial need to be considered (Ogden & Stewart 1995). Palaeoecological reconstructions, for example via fossil pollen records, provide descriptions of long-term successions after large disturbances (McGlone et al. 1988; Horrocks & Ogden 1998). However, palaeoecological records are challenging to interpret due to the influence of a multitude of confounding factors such as climate, disturbance, dispersal lags, and biotic interactions (Anderson et al. 2006;

Brewer et al. 2012). Therefore, while such records provide invaluable descriptions of temporal dynamics, they are by themselves seldom sufficient to draw general conclusions about the processes that underlie the patterns they show.

Process-based simulation models are well suited for the exploration of forest dynamics over extended spatio-temporal scales and provide a valuable complement to empirical studies (Henne et al. 2011). So-called 'forest gap models' are widely used to address diverse questions regarding global-change impacts on long-term forest dynamics (Bugmann 2001; Perry and Millington 2008), but have received surprisingly little application in New Zealand. In an early attempt to implement a forest gap model, DeVelice (1988) developed the non-spatial FORENZ model for Fiordland, South Island. Currently, LINKNZ (Hall & Hollinger 2000; Hall & McGlone 2006) and SORTIE/NZ (Kunstler et al. 2009) are the forest gap models best established for New Zealand's forests. For example, McGlone et al. (2011) used the forest gap model LINKNZ to explore how decreased seasonality in the early Holocene might account for the patterns found in pollen records.

Traditional forest gap models are not designed to represent large and heterogeneous landscapes with areas of differing climate, topography and soils (Mladenoff 2004). Rather, they simulate successional processes in small gap-sized (< 1 ha) forest patches, often without interactions between the patches (Bugmann 2001). At the landscape level, however, interactions between patches are important, in particular with respect to seed dispersal and larger disturbance events. Since traditional gap models focus on tracking the development of individual trees in a complex representation of their physical competitive environment, they are computationally expensive (Mladenoff 2004). Therefore individual- to stand-scale gap models tend to consider spatial extents of a few tens of hectares. Furthermore, highly mechanistic, spatially explicit gap models such as SORTIE require considerable parameterisation effort (Uriarte et al. 2009).

While promising approaches have been developed to overcome these computational limits, such as the PPA model for SORTIE (Strigul et al. 2008) and upscaling approaches (Hartig et al. 2012), these remain in their infancy. Forest models suitable for investigating interacting processes across large landscapes need to fulfil three important prerequisites: (1) reduced complexity in the representation of stand-scale processes, while retaining structural realism, (2) an ability to represent spatio-temporally heterogeneous landscapes at extents of up to 1000s of hectares over centuries to millennia, (3) the incorporation of ecological processes important at larger scales (e.g. landscape-level disturbance) (Mladenoff 2004; Schumacher et al. 2004).

LandClim (Schumacher et al. 2004, 2006; Schumacher & Bugmann 2006), as a landscape simulation model, meets these three requirements and can help in the assessment of processes at larger scales. In LandClim individual species are represented in terms of their ecological traits (among them longevity, growth rate, temperature requirements, shade tolerance), which determine the species' ability to establish, grow and survive. Due to its structural realism, simulation outcomes of LandClim can be evaluated against various empirical patterns of forest composition and age structure, thereby facilitating pattern-oriented modelling (POM; Grimm et al. 2005; Hartig et al. 2011; Jakoby 2011; Grimm & Railsback 2012). Pattern-oriented parameterisation, a subset of the broader POM framework, infers realistic parameter ranges from observed system behaviour by comparing model outputs with multiple observed patterns and thereby filtering the parameter space. Pattern-oriented parameterisation therefore provides a promising approach to overcome the difficulties and limitations of direct parameterisation (Jakoby 2011). LandClim, along with most other forest gap models, contains species parameters that are difficult to quantify directly, in particular the crucial species traits of 'shade tolerance' and 'maximum growth-rate' (relative biomass growth rate per year). Growth rates measured in the field are always influenced by the abiotic environment and biotic interactions, and cannot therefore be assumed to be equivalent to the growth potential of a species. Shade tolerance is similarly difficult to quantify in the field due to interactions with other growth-limiting factors and its dependency on ontogeny (Valladares & Niinemets 2008).

Here we make use of the rich spatio-temporal dataset describing forest structure and dynamics on the western slope of Mt Hauhungatahi to apply LandClim to a New Zealand situation for the first time and parameterise the traits 'shade tolerance' and 'maximum growth-rate' of dominant canopy species by means of a pattern-oriented parameterisation approach. The location of Mt Hauhungatahi in the volcanic area of Tongariro National Park offers an ideal study site to investigate the effects of landscape-level disturbance on forest succession following the cataclysmic Taupo eruption of c. 1700 cal. years BP (Wilmshurst & McGlone 1996; Horrocks & Ogden 1998). High-resolution pollen data collected along an elevational transect at Mt Hauhungatahi by Horrocks and Ogden (1998), together with contemporary vegetation studies (Druitt et al. 1990; Ogden et al. 2005), provide key patterns describing the dynamics and structure of the forest ecosystem. The integration of both spatial and temporal data describing long-term forest dynamics allows us to improve the robustness of the species parameterisation and strengthens the reliability of the model. We consider our approach as complementary to previously established forest gap models such as LINKNZ and SORTIE/NZ. No single model can entirely represent reality, therefore using multiple models enables us to explore the significance of different system representations and so increase the robustness of model-based inferences.

Besides being the first adaption of LandClim to New Zealand´s forests, this study aims to increase our understanding of drivers of species organisation following a catastrophic disturbance event and to contribute to the ongoing discussion about the long-term dynamics of mixed angiosperm–conifer forests. Our expectations are that: (1) species' current elevational distribution will emerge from climatic preferences, in particular temperature requirements, and (2) the post-Taupo-eruption forest succession can be explained by trade-offs and interactions between species' shade tolerance, growth rate and longevity.

Methods

LandClim

LandClim is a spatially explicit forest landscape model that was originally developed to investigate the importance of climatic effects and disturbance processes for forest dynamics in the European Alps (Schumacher et al. 2004, 2006; Schumacher & Bugmann 2006). The LandClim model is comprised of two main parts: one tracks stand-structure processes, such as establishment, growth and death, at annual time steps; the other is concerned with landscape-level dynamics at a decadal time step. LandClim tracks individual trees in the aggregated form

of cohorts. Cohorts are groups of same-aged trees within a grid cell (25 × 25 m), and all individuals in a given cohort are assumed to have the same biomass. Trees may establish in grid cells if propagules are available and environmental conditions are suitable. Tree growth is represented by a maximum growth rate (representing growth under optimum conditions), which is reduced as a function of limiting environmental factors and biotic interactions. Despite the problem of determining the maximum potential growth rate (parameter 'R_{max}', see Table 1), this approach is found in most forest gap models, such as JABOWA (Bugmann 2001). Tree mortality is a function of three factors: growth-dependent stress, density-dependent stress, and an intrinsic, age-related component. Detailed descriptions of the formulation of stand-scale processes in LandClim are given in Appendix S1 of the online Supplementary Information.

LandClim represents the effects of disturbance on forest composition and structure reciprocally, which, in turn, allows studies of past and future changing environments (Schumacher & Bugmann 2006; Henne et al. 2011). Environmental input variables are topography, soil water capacity, and 'land-type' (a user-defined map assigning specific establishment rates and disturbance regimes to distinct areas), as well as temperature and precipitation at monthly resolution. Species' environmental responses are defined by traits such as drought tolerance, shade tolerance and temperature requirements. LandClim operates over long timescales (100s to 1000s of years) and large spatial extents (100s to 10 000s of hectares) at a relatively fine scale (grid cells of 25 × 25 m). It has previously been tested in and adapted to the European Alps, the North American Rocky Mountains, and Mediterranean forests (Schumacher et al. 2006; Colombaroli et al. 2010; Henne et al. 2011, 2012; Briner et al. 2012; Elkin et al. 2012).

This study is the first application of LandClim to a forest system in the Southern Hemisphere. The model structure of LandClim was kept unchanged; the only differences from the previous studies were a new allometric relationship for calculation of New Zealand species' biomass to diameter at breast height (dbh), an increase in the maximum stand biomass from 300 t ha^{-1} to 1000 t ha^{-1} (see Appendix S1 for details) and the parameterisation of tree species.

Study site

Our simulations focused on the western slope of Mt Hauhungatahi, which has been intensively studied previously (Druitt et al. 1990; Horrocks & Ogden 1998; Ogden et al. 2005). Mt Hauhungatahi is in Tongariro National Park in the central North Island of New Zealand (Fig. 1) where forests have been subject to recurrent volcanic events throughout the Quaternary, with the rhyolitic Taupo eruption of 1718 ± 5 cal. years BP (Hogg et al. 2012) particularly significant (Horrocks & Ogden 1998).

Druitt et al. (1990), using the importance value as a measure of species dominance, distinguished three main belts of forest[1]:

(1) A montane forest from 850 to 1000 m elevation with the canopy dominated by angiosperms, in particular *Weinmannia racemosa* (kāmahi). Scattered old conifer individuals (e.g. *Dacrydium cupressinum* – rimu) are present and constitute an important part of the total basal area, but younger conifer individuals are mostly absent. Tree ferns (e.g. *Cyathea smithii* – katote) are important components of the subcanopy layer.

(2) A transitional zone ranging from 1000 to 1050 m elevation, where several species (including *Weinmannia racemosa, Dacrydium cupressinum* and tree ferns) reach their upper limit. Conifers, and in particular *Podocarpus cunninghamii* (formerly *P. hallii*, Hall's tōtara)*,* are prominent in this belt.

(3) A subalpine zone (from 1050 m to the treeline), which is largely dominated by the conifer *Libocedrus bidwillii* (pāhautea). The treeline (formed by *L. bidwillii*, together with *Halocarpus biformis*) is highly discontinuous, varying between elevational limits of 1100–1250 m.

Ogden et al. (2005) reported the highest densities and most vigorous regeneration of *Libocedrus bidwillii* in the subalpine zone, with densities and regeneration declining towards the transition zone at around 1050 m. This decline coincided with an increase in angiosperm densities, with *Weinmannia racemosa* becoming dominant in the upper montane zone.

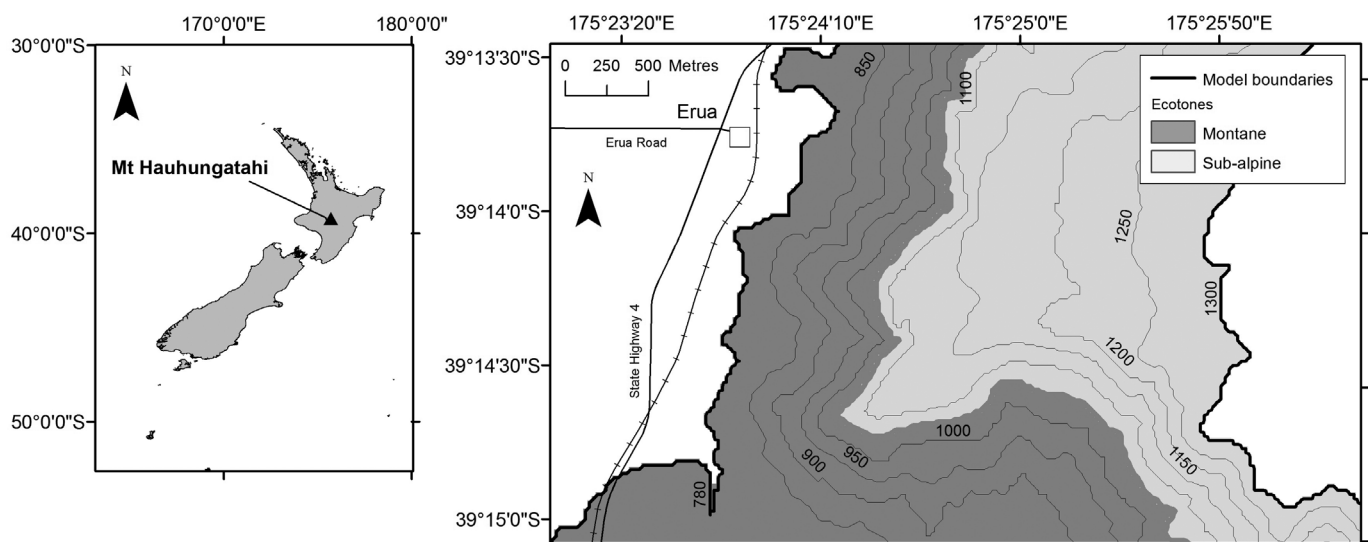[1] Species nomenclature follows Allan Herbarium (2002-2013).

Figure 1. Map of study area on the western slope of Mt Hauhungatahi in Tongariro National Park, New Zealand.

To outline the effect of the Taupo eruption on forest succession at Mt Hauhungatahi, Horrocks and Ogden (1998) used detailed pollen diagrams collected along the elevational transect described by Druitt et al. (1990). The two dominant patterns seen in Horrocks and Ogden's pollen diagrams are: (1) the initial increase and spread of *Libocedrus bidwillii* immediately following the eruption, and (2) the progressive spread of the angiosperm *Weinmannia racemosa* in the montane forest in the centuries following the eruption, resulting in the present vegetation zonation.

Simulation experiments

The western slope of Mt Hauhungatahi was represented in LandClim on a grid of cells (25×25 m) describing topography and soils. Topographic parameters (elevation, aspect and slope) were derived from a digital elevation map of the area (DEM25; Land Information New Zealand 2011). Areas below 780 m were excluded since they are currently deforested and therefore could not be compared with empirical data. The widespread peatland area above the treeline (> 1300 m) was also excluded.

Soil characteristics on the slopes of Mt Hauhungatahi are spatially heterogeneous and are a function of volcanic activity and a suite of secondary processes (Druitt et al. 1990). Due to the generally high water-holding capacity of volcanic soils (Scheffer & Schachtschabel 2002), a high soil water-holding capacity (bucket size of 200 mm) was assigned uniformly to all grid cells (the model was not sensitive to this assumption; results not shown). The climate record (AD 1930–2000) from the nearby Chateau climate station at Mt Ruapehu (12 km east of Mt Hauhungatahi, 1097 m elevation) was used as the climatic input data for the model (data source: NIWA 1850–2013). Because the temperature reconstructions available for the site (Palmer & Xiong 2004) do not span the full 1700-year succession that we consider, the simulation was carried out under a present climate to provide a parsimonious baseline scenario. While climate reconstructions suggest the existence of some warmer and colder periods in past centuries, these are only of the order of less than 0.5°C (Palmer & Xiong 2004).

Since climate change is generally considered to be small in the post-Taupo period compared with the millennium before the eruption (McGlone 1989; Rogers & McGlone 1989) and the fossil pollen data do not show evidence of climate-related vegetation change after the eruption (Horrocks & Ogden 1998), we considered our assumption as reasonably realistic. The 70-year climate record was resampled (with replacement) to generate a 1700-year climate sequence; this randomisation was repeated for every simulation.

The four dominant canopy species that characterise the elevational belts on Mt Hauhungatahi were represented in the model: the angiosperm *W. racemosa* (kāmahī) and the conifers *D. cupressinum* (rimu), *P. cunninghamii* (Hall's totara) and *L. bidwillii* (pāhautea). A tree-fern life form was included due to their high abundance in the montane forest (especially *Cyathea smithii*; Druitt et al. 1990) and their structural importance for forest dynamics (Coomes et al. 2005). The tree-fern life form was implemented as a shade-tolerant understorey species (resembling the behaviour of *Cyathea smithii* as reported by Bystriakova et al. (2011)) and treated by the model in the same way as the other tree species.

Species life-history traits were assigned from the ecological traits database (Landcare Research 1996–2005), the ecological literature, including the *Flora of New Zealand* (Landcare Research no date), and expert-knowledge. Details about the life-history traits and reasoning for the choice of parameters are provided in Appendix S2. The parameter 'minDD' (minimum degree days) was calibrated to fit the upper elevational limits described in Druitt et al. (1990), assuming that the species upper elevation limit is controlled by temperature (see Appendix S2 for further information). The parameters 'shade tolerance' and 'R_{max}' (maximum relative biomass growth rate per year) were determined in a pattern-oriented parameterisation approach, described in the following section.

It was assumed that the Taupo eruption removed all vegetation from the study area, since the actual degree of forest destruction remains unknown. Horrocks and Ogden (1998) noted that the effect of the Taupo eruption (including the shockwave, airfall of tephra and subsequent fires) was

Table 1. Species life-history parameters. Tolerance-classes range from 1 (lowest) to 5 (highest tolerance). Abbreviations: EG: Evergreen, BL-EG: Broadleaved-evergreen. A brief explanation, as well as references and basis for the parameter choice, is given in online Appendices 2 and 3. The parameters 'shade tolerance' and 'R_{max}' were determined via a pattern-oriented parameterisation. The parameter 'minDD' was calibrated to fit species' upper elevational limits described in Druitt et al. (1990); see Appendix S2 for further details. Drought-, fire- and browsing-tolerance were not relevant in the present study, therefore, a default value of 3 was assigned to all species. Parameters are discussed in more detail in Schumacher (2004).

Parameter name	Parameter description	*Dacrydium cupressinum*	*Libocedrus bidwillii*	*Podocarpus cunninghamii*	Tree fern	*Weinmannia racemosa*
maxAge	Maximum age (years) that an individual can reach	800	1000	650	150	400
K_{max}	Maximum above-ground tree biomass (t) a species can reach	12	8	7.73	0.5	6.32
leafHabit	Leaf habit (form)	EG	EG	EG	BL-EG	BL-EG
foliageType	Shading potential of a species' canopy	3	3	4	5	5
minTemperature	Minimum temperature (°C) for establishment	−8	−13	−13	−8	−8
shadeTolerance	Species' shade tolerance	4	2	2	5	4
minDD	Minimum annual degree day sum	1400	1200	1280	1550	1300
R_{max}	Maximum above-ground biomass growth rate (per year)	0.07	0.12	0.11	0.10	0.13

presumably considerable at Mt Hauhungatahi (c. 75 km distance from the vent), although fossil pollen indicates some surviving forest in the area. The simulations started from 'bare ground', initiated by a spatially homogeneous seed rain with the same amount of seed across all species, as is often assumed in forest landscape and gap models, particularly in the absence of detailed species-specific empirical data describing the seed rain. Although this approach neglects the possible influences of prior vegetation and heterogeneous seed rain, it provides a baseline assumption to cope with complex and unknown initial conditions. For the same reason, global seed dispersal was assumed. Succession was simulated and tracked over 1700 years, representing the time since the Taupo eruption. No further disturbance events were simulated over this succession. To ensure direct comparability with the measurements of forest structure by Ogden et al. (2005), only individuals with a dbh larger than 10 cm were considered in the analyses of the simulated elevational transect (although LandClim is capable of tracking smaller individuals).

Pattern-oriented parameterisation

In order to identify plausible parameter combinations for 'maximum growth-rate' (R_{max}) and 'shade tolerance' that reproduce the expected system behaviour, a pattern-oriented parameterisation approach was chosen.

First, a complete parameter space with both traits for all five species was created. Each parameter was given five possible values (for shade tolerance from 1 (low) to 5 (high) and 'R_{max}' from 0.03 to 0.15 (in steps of 0.03)). This parameter space was reduced by discarding ecologically unreasonable parameter combinations a priori from the analysis, using the following criteria: (1) Maximum growth rates of angiosperms (*W. racemosa*) should be higher than those of conifers (Ogden & Stewart 1995). (2) Shade tolerance of conifers *L. bidwillii* and *P. cunninghamii* should be in the range from low to intermediate due to their characterisation as light-demanding pioneer species (Clayton-Greene 1977; Ebbett & Ogden 1998). (3) Shade tolerance of *D. cupressinum* and *W. racemosa* should range between intermediate and high (Lusk & Ogden 1992; Lusk et al. 2009). (4) Shade tolerance of the tree-fern life form (resembling the ecology of *Cyathea smithii*) was defined as high (see Appendix S3 for further details about the tree-fern life form).

The model was run for all possible parameter combinations that fulfilled these criteria (in total 23 364 scenarios). The simulations for the pattern-oriented parameterisation were performed on a small area (covering the length of the entire elevational gradient but reducing the width to only four cells, i.e. 100 m) in order to reduce computation time for each simulation, under a randomised present climate scenario in the absence of further disturbance events.

The simulation outputs were filtered according to spatio-temporal patterns described in the pollen records of Horrocks and Ogden (1998), using a Boolean filter. These patterns were (1) an initial dominance of conifers (in particular *L. bidwillii*) in the first centuries after the Taupo eruption, which was defined as the criterion that conifer species should reach >60% of total forest biomass in the first 300 years of succession; (2) a progressive spread of *W. racemosa* in the montane area during later stages of succession, represented by the criterion that *W. racemosa* should reach >60% of total forest biomass during the years 1000–1700 in the area up to 1050 m elevation. Additionally, parameter combinations resulting in unreasonably low total stand biomass were discarded. Based on the carbon

stock estimates for podocarp–hardwood forests in New Zealand (Hall et al. 2001), a minimum biomass of 100 t ha^{-1} was estimated (under the assumption that biomass consists of 50% carbon). Further parameter combinations for which tree species had disappeared at the end of succession (i.e. species biomass dropped below 1% of total biomass) were also discarded. These criteria narrowed down the parameter space substantially.

Finally, a refined sensitivity analysis was performed to determine optimised 'R_{max}' values for each species. 'R_{max}' values were assigned from within the range determined by the previous analyses and sampled in steps of 0.01. Shade-tolerance values were assigned according to the results of the previous analysis. For the filtering of these results, stronger criteria were applied: *L. bidwillii* should dominate the early successional stage with >75% of total standing biomass, and *W. racemosa* should dominate the late successional stage in the montane forest with >75% biomass. Furthermore, simulated mean annual dbh-growth of species (at year 1700) should be in the range of mean annual growth rates reported by Ogden et al. (2005) for *L. bidwillii*, Smale and Smale (2003) for *P. cunninghamii*, and Lusk and Ogden (1992) for *D. cupressinum* and *W. racemosa* (see Appendix S2). For the tree-fern life form, height-growth estimates from Ogden et al. (1997a) were used (see Appendix S3).

The final parameter set was used to simulate the spatio-temporal forest dynamics of Mt Hauhungatahi (Table 1). Simulations were repeated 50 times with a randomised present climate to account for stochastic variation between model realisations under the same parameter conditions.

Analyses and visualisation of model results were conducted using R, version 2.15.2 (R Development Core Team 2012). The pattern-oriented parameterisation was carried out on a high-performance computer cluster at the University of Bayreuth, Germany.

Results

Species traits

In the pattern-oriented parameterisation, the application of the filter criteria (see previous section) narrowed down the parameter space from 23 364 to 129 possible combinations. The shade-tolerance ranges defined a priori proved suitable, as most model results from the given range were accepted by the filter criteria (Fig. 2, bars). The specific R_{max} values substantially influenced the successional sequence and the biomass of individual species. R_{max} values below 0.06 typically resulted in low species biomass and therefore tended to be discarded by the filter criteria. The refined sensitivity analysis showed that the observed successional dynamic was reproduced within a rather narrow constellation of R_{max} values. *L. bidwillii* and *W. racemosa* (as the main components of the simulated forest ecosystem) displayed a strong successional differentiation between pioneer and later successional species once the parameter constellation was set as shown in Fig. 2. With increasing advantage in growth rate of *W. racemosa* over *L. bidwillii*, the pattern still prevailed but the initial dominance of *L. bidwillii* became less pronounced at the expense of *W. racemosa* in the lower montane forest.

Within the parameter ranges explored, *P. cunninghamii* and *D. cupressinum* were present with only low biomass. Variations in their parameter sets consequently had a minimal effect on the gross successional trends.

Species zonation

LandClim reproduced the actual species zonations described by Druitt et al. (1990) at the end of succession (year 1700) once all species (with traits as in Table 1) were included in competition with each other. The species' upper elevational limits were controlled by their specific temperature ('minimum degree day') requirements. Notably, the observations of Druitt et al. (1990) were used in the calibration of the 'minimum degree day' parameter, therefore they cannot be considered as independent data for model evaluation. In simulations of monocultures each species occurred across the elevational transect from the lower boundary (780 m) to its specific upper elevational limit. Once all species were included (and thus interspecific competition occurred), conifer species largely disappeared from lower elevations.

The lower-elevation forest band (780–950 m) was dominated by *W. racemosa*. Tree-ferns occurred up to 880–900 m, but with a low basal area (< 1 m² ha⁻¹) and density (< 50 stems ha⁻¹; data not shown). *D. cupressinum* occurred up to 1000 m, but only as a very few, scattered individuals. Above 950 m, the basal area of *W. racemosa* steadily declined to its upper elevational limit at around 1050 m. As *W. racemosa* declined, the forest gradually shifted in composition with the conifer species becoming increasingly important. *P. cunninghamii* reached its maximum basal area and stem density between elevations of 950–1050 m. Elevations above 1000 m were dominated by *L. bidwillii* in terms of basal area and stem density until the treeline at around 1220 m.

The simulated basal area and stem density of the species peaked at the same elevations as those described by Ogden et al. (2005), but the model underrepresented basal area for all species and overrepresented stem density for *L. bidwillii* (see Fig. 3). The deviation between observed and simulated forest structure was particularly evident for *D. cupressinum* and *P. cunninghamii*, which achieved only very low values of basal area and stem density in the simulated year 1700.

Forest succession

The simulated post-Taupo succession resembled the general patterns described by Horrocks and Ogden (1998) once species life-history traits were assigned following a rigorous and thorough pattern-oriented parameterisation process (Table 1). The succession was characterised by three main stages, one from simulation years 0 to 400, a second from years 400 to 700, and a third from year 700 onwards. During the early phase of the succession (simulation years 0 to 400), *L. bidwillii* dominated the study area in terms of biomass (Fig. 4). In the following centuries (simulation years 400 to 700; Fig. 4), the biomass of *L. bidwillii* declined, whereas that of *W. racemosa* steadily increased. From around simulation year 1000 onwards, conditions were generally stable and similar to the contemporary composition on Mt Hauhungatahi. Both *D. cupressinum* and *P. cunninghamii* were only present with low biomass throughout the succession. The tree-fern life form occurred across the entire succession, but at lower biomasses than the other four tree species.

The spatial distribution of the tree species shifted over time such that there was a progressive upward expansion of *W. racemosa* in the montane forest, accompanied by a retraction of *L. bidwillii* and *P. cunninghamii* into the higher subalpine forest. The early-successional stage (simulation years 0 to 400) was characterised by the widespread dominance of *L. bidwillii* (Fig. 4). In the montane forest, the dominance of *L. bidwillii* was associated with occasional occurrence of *P. cunninghamii* and *D. cupressinum*. *W. racemosa* occurred only in a few scattered grid cells during the early succession. During the mid-succession (simulation years 400 to 700) *W. racemosa* began to increase in abundance, starting from the lowest elevations and spreading upslope over the following centuries. *W. racemosa* prevailed in most parts of the montane forest below 1000 m by the simulation year 700 and attained dominance in almost all of the montane forest around the simulation year 1000. The later stages of succession (simulation years 700 to 1700)
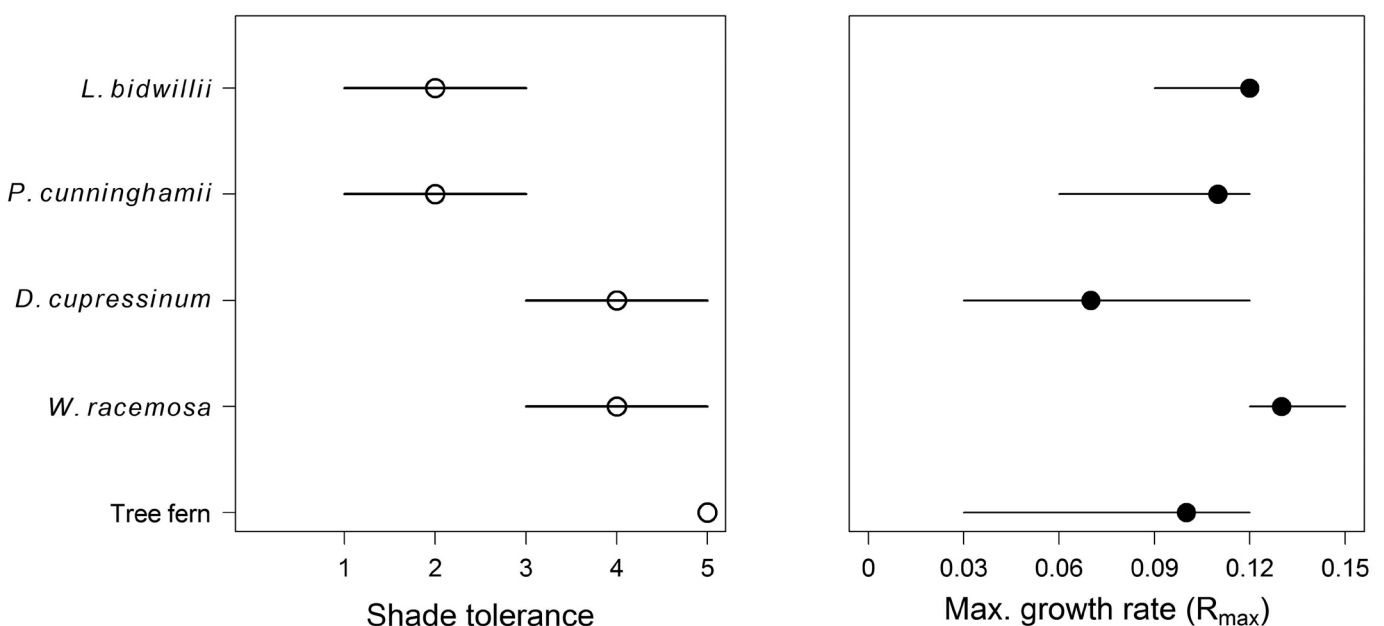

Figure 2. Results of the pattern-oriented parameterisation for the parameters 'shade tolerance' (left) and maximum growth rate – 'R_max' (right). The range of accepted parameters is indicated by the line, parameter values occurring with highest frequencies are indicated by a circle (filled circle indicates result of refined sensitivity analysis of 'R_max'). Species are *Libocedrus bidwillii*, *Podocarpus cunninghamii*, *Dacrydium cupressinum* and *Weinmannia racemosa*.
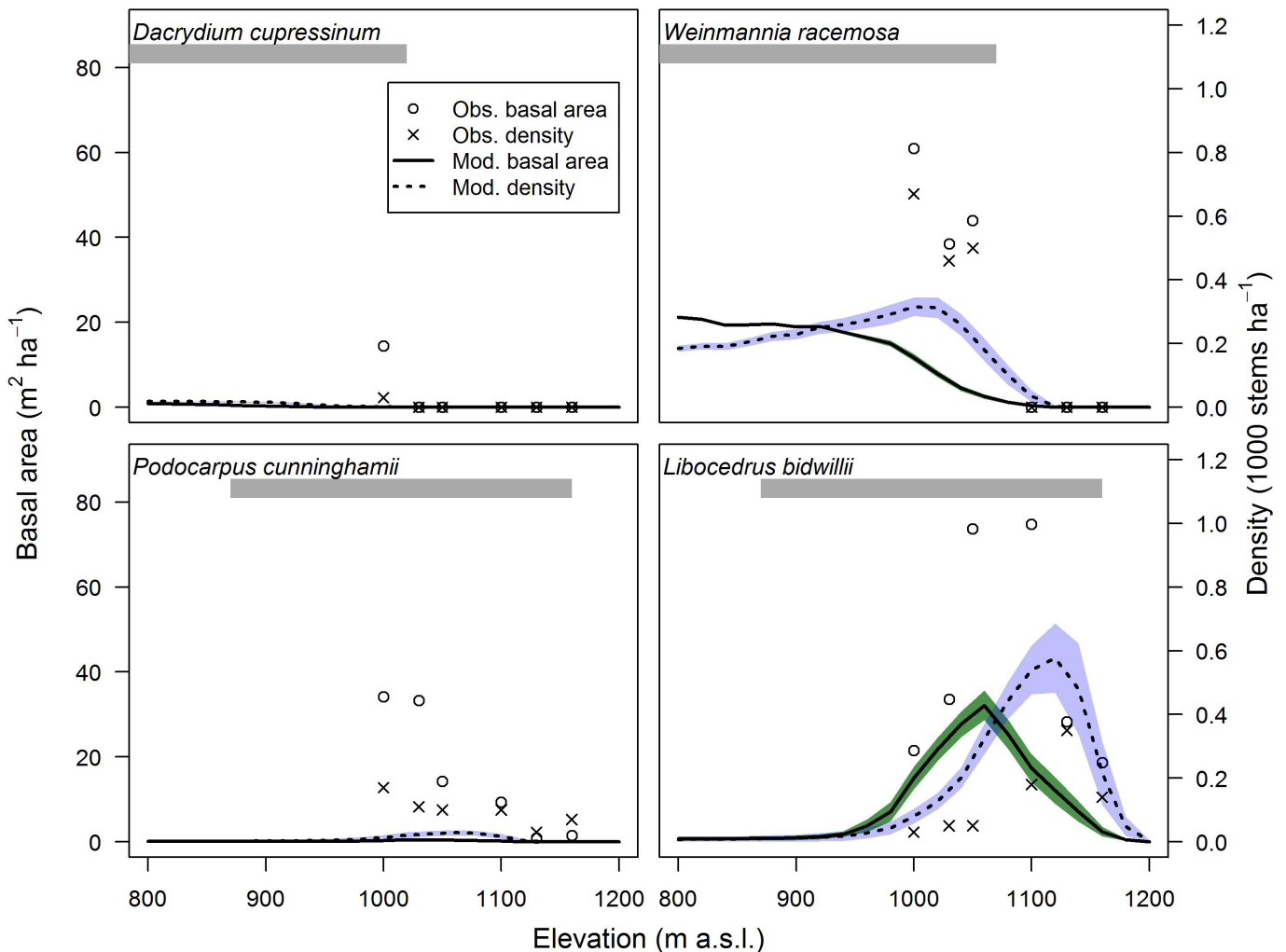
Figure 3. Elevational distribution of species as described by Druitt et al. (1990) (shown as grey bar) and forest structure (basal area and density) as reported by Ogden et al. (2005) (shown as observation points) alongside model outcomes after 1700 simulation years. For model outcomes, the mean of 50 model realisations is shown together with the standard error of the mean. Only individuals with diameter at breast height (dbh) > 10 cm were considered in the model in order to assure comparability with the empirical data. On the basis of their low abundance and the lack of empirical data reporting their stand structure, tree ferns were excluded.

were characterised by the decay of old, scattered stands of *L. bidwillii* in the montane forest and the development of the elevational vegetation zonation described above.

While general temporal patterns of an initial spread of *L. bidwillii* and a subsequent spread of *W. racemosa* in the montane forest coincided with the palynological findings of Horrocks and Ogden (1998), patterns for *D. cupressinum* did not match well. Fossil pollen records show that *D. cupressinum* was continuously present at Mt Hauhungatahi throughout the post-Taupo succession constituting a substantial fraction to the amount of pollen. In the simulation, *D. cupressinum* was present at all times, but with generally very low biomass. According to Horrocks and Ogden (1994), the pollen abundance of *Dacrydium* is, however, not a good predictor for basal area, which prohibits a direct comparison between model results and observation.

Discussion

LandClim proved capable of reproducing the general patterns of species zonation and successional patterns by parameterisation of species traits only. The model structure itself was left unchanged. This finding is of particular interest, as New Zealand's temperate forests are considered to differ from their Northern Hemisphere counterparts in several aspects (McGlone et al. 2010; Wilson & Lee 2012). The reproduction of key patterns by a northern-temperate forest model may, therefore, point towards a generality of underlying mechanisms that structure temperate forest landscapes worldwide.

Species' upper elevational limits resulted from the species' temperature requirements (through calibration of the 'minimum degree days' parameter), whereas biotic interactions (competition for light determined by the species' shade tolerance, temperature requirements and potential growth rate) were important for species' lower elevational limits and for structuring succession. The outcome of interspecific competition therefore varied both spatially and temporally,
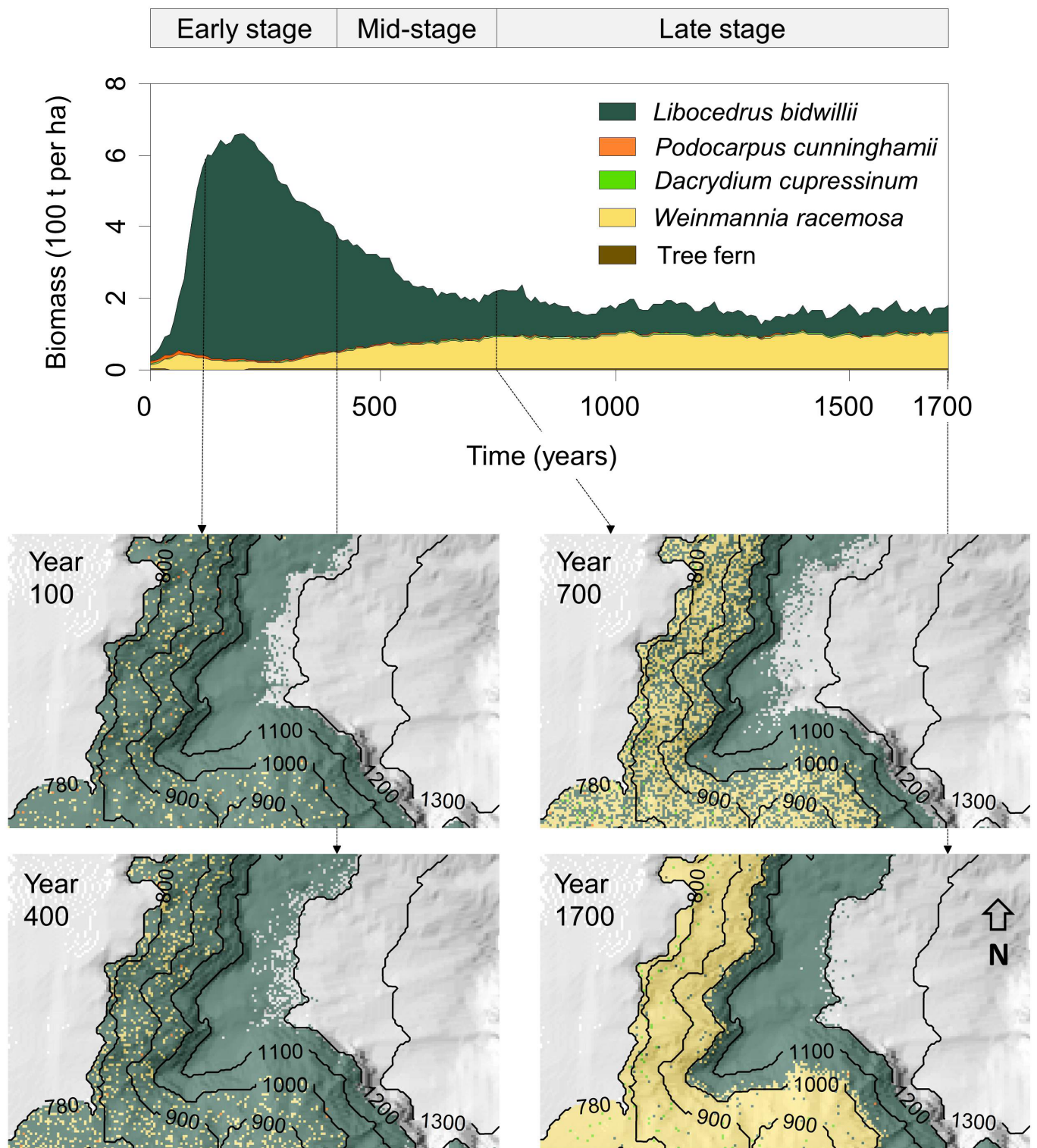
Figure 4. Simulated succession of tree species following the Taupo eruption (c. 1700 cal. years BP) on the western slope of Mt Hauhungatahi. For the spatial distribution of vegetation, dominant tree species (in terms of biomass) of each grid cell are displayed.

since environmental conditions changed with elevation (temperature) and over time (light-transmission to the forest floor). The landscape approach presented here highlights how gradual changes in the environmental conditions affect the competitive balance between species, and results in a differentiated picture of spatio-temporal forest dynamics.

Species traits

In the trait space (Table 1), *L. bidwillii* and *W. racemosa* occupy different positions reflecting a trade-off in their capacity to cope with stress induced by shade and low temperatures. It has frequently been observed that adaptation to a certain climatic environment often comes at the cost of adaptation to other

conditions (Hereford 2009). Similar trade-offs have been described for adaptions to shade, drought and waterlogging (e.g. Niinemets & Valladares 2006) as well as for the relationship between growth rate and survival under limited light (e.g. Lusk & Pozo 2002; Kunstler et al. 2009), cold (e.g. Loehle 1998) or nutrient conditions (e.g. Chapin et al. 1986; Lusk & Matus 2000). In respect to a trade-off underlying spatio-temporal vegetation dynamics, our model results are similar to the study of Smith and Huston (1989), who found that the temporal and spatial shift in species dominance can be explained by different adaptions of plants for two or more resources (in their case light and water use).

In LandClim, the traits shown by *L. bidwillii* enable it to take advantage of well-lit, open sites at higher elevations, where low temperature impedes the growth of its competitors (such as *W. racemosa*). An increase in shading of the forest floor in turn results in a decrease of the regeneration success of *L. bidwillii*. Under these conditions, the more shade-tolerant species *W. racemosa* can outcompete the shade-intolerant conifer and progressively take over its sites. Here, *L. bidwillii* loses its initial advantage (in terms of better growth performance under cooler conditions) since shade becomes the main limiting factor for growth. The strategy of *W. racemosa* proves to be more successful at this point, at least up to a certain elevation (in the model at around 1000 m) where temperature limitations turn the competition-balance again.

The evaluation of the trait shade tolerance was not, however, straightforward for all species. The results of the pattern-oriented parameterisation imply that *D. cupressinum* and *W. racemosa* are both moderately shade tolerant (shade tolerance class 4, implying a minimum requirement of 5% light availability; see also Schumacher 2004, table B.3). This appears to be reasonable for *W. racemosa*, which is usually regarded as a species of intermediate shade tolerance with some evidence for continuous regeneration under closed canopy (e.g. all-aged populations found by Lusk and Ogden (1992) in Horopito, near Mt Hauhungatahi). *D. cupressinum,* by contrast, is often described as a species with pioneer behaviour on open sites (e.g. Beveridge 1973), displaying a restricted age-range, which points towards a regeneration after exogenous disturbances (Lusk & Ogden 1992). However, Lusk et al. (2009) found that seedlings of *D. cupressinum* could tolerate lower levels of diffuse light availability than *W. racemosa*. The result of the pattern-oriented parameterisation (shade tolerance value 4, both species) therefore only reflects partly the ecology and the expected behaviour of both species.

Valladares and Niinemets (2008) reviewed the nature of shade tolerance and pointed out that it is a much more complex trait than it is often considered to be. In particular, they noted that a species' shade tolerance is influenced by numerous biotic and abiotic factors and, furthermore, can vary with plant ontogeny. In New Zealand, Kunstler et al. (2009) investigated the growth and mortality of a range of podocarp–hardwood species (including *W. racemosa* and *D. cupressinum*) and found that several species changed their strategy in respect to the growth – shade tolerance trade-off between sapling, seedling and mature life stages. In particular *D. cupressinum* displayed this phenomenon, commonly referred to as 'ontogenetic trade-off'.

Regeneration of some of New Zealand's tree species (and hence species position during succession) may therefore likely be influenced by more complex processes than those represented in LandClim. A closer consideration of the representation of regeneration (e.g. in respect to the ontogenetic

trade-off) may be beneficial for further studies using LandClim in New Zealand.

Finally, for the incorporation of further New Zealand species it may be necessary to represent more shade-tolerance classes (as per Henne et al. (2012) in Mediterranean forests who considered six) to account for the possibility of species to regenerate and grow in deep shade under light levels below 1% (e.g. as reported for *Beilschmiedia tawa* by Lusk et al. (2009)).

Species zonation

The simulated species zonation was the outcome of temperature requirements (i.e. by the species-specific requirements for minimum degree days – minDD) controlling species' upper elevational limits, and competition determining their lower limits. It is important, however, to note that the observations of Druitt et al. (1990) were used in the calibration of the minDD parameter and are not, therefore, an independent dataset for the purposes of model evaluation. The species' ranking in minimum degree days is supported by Leathwick (1995), who found *D. cupressinum* and *W. racemosa* biased towards warmer habitats (in terms of mean annual temperature), *P. cunninghamii* growing under cooler and *L. bidwillii* under the coldest conditions. Druitt et al. (1990) discussed the effects of climate, competition, soil (and nutrient status), as well as slope steepness, in controlling the vegetation distribution on Mt Hauhungatahi, and suggested competitive exclusion as a potentially important mechanism for the current restriction of *P. cunninghamii* to the 'transition zone' (1000–1050 m elevation). Our model-based experiments support this argument by showing a virtual exclusion of conifers from the montane forest during the late stage of succession (Figs. 3 & 4) in comparison to monocultural simulations, where conifers were abundantly present in lower elevations as well (results not shown). While temperature is an important control on the upper elevational limit of *L. bidwillii*, the variable nature of the treeline at Mt Hauhungatahi suggests that other processes, such as disturbance and previous environmental fluctuations, can also have significant and potentially long-lasting effects (Ogden et al. 1997b; Horrocks & Ogden 1998).

LandClim was able to reproduce the broad spatial patterns of basal area and stem density reported by Ogden et al. (2005). A zone with abundant *W. racemosa* at lower elevations (resembling the montane forest of Druitt et al. (1990) was followed by a belt of *P. cunninghamii* (i.e. the transition zone) and finally *L. bidwillii* dominating the highest elevations (i.e. the subalpine zone). Basal area was, however, systematically underestimated and density of *L. bidwillii* slightly overpredicted, implying that the model produces stands with too many, too-small individuals.

A notable discrepancy between model and empirical observations was found for *D. cupressinum* and *P. cunninghamii*. Conifers, including *D. cupressinum*, currently occur at low densities, and as scattered individuals, at the lower elevations of Mt Hauhungatahi (Druitt et al. 1990). Although some individuals of *D. cupressinum* appeared in the model, the species' basal area was extremely low compared with that described by Ogden et al. (2005) (see Fig. 3). Both species, *D. cupressinum* and *P. cunninghamii*, are long-lived pioneer species (Ogden & Stewart 1995; Ebbett & Ogden 1998) and could therefore be expected to display similar behaviour to *L. bidwillii*. This was not the case in the final model scenarios. Neither species was able to compete effectively with *L. bidwillii* or *W. racemosa*, which implies that important mechanisms in the species' establishment and competition

were not well represented. Horrocks and Ogden (1998) note the potentially important effect of further disturbance events at Mt Hauhungatahi after the 1700 BP Taupo eruption (although their effect on the forest was probably far less severe). Mild volcanic activity in the post-Taupo period (around 660–600 BP; Horrocks & Ogden 1998) and increased storminess in the 1740s may have caused substantial canopy openings and thereby facilitated the establishment of secondary conifer recruits. Lusk and Ogden (1992) found a similar structure of *D. cupressinum* to that at Hauhungatahi at Horopito (15 km further to the south), with a predominance of old individuals and an absence of cohorts younger than 550 years that can likely be attributed to the same disturbance events that affected the forest of Mt Hauhungatahi.

These observations point towards the importance of considering secondary, patchy disturbances (as caused by severe windstorms) in simulation experiments. LandClim contains a disturbance module explicitly designed to represent disturbances by windstorms. Although beyond the scope of the present study, this disturbance module offers further possibilities for exploration of the effect of various patchy disturbance regimes on the forest structure and composition.

Succession of tree species following Taupo eruption

According to Horrocks and Ogden (1998), *L. bidwillii* was dominant in the montane forest until a progressive invasion of *W. racemosa* commenced at 900–850 BP and culminated c. 650 BP. In the model, the initial dense *L. bidwillii* stand persisted in the montane forest for several centuries by virtue of the species' extreme longevity. The disintegration of this cohort was accompanied by the upward spread of *W. racemosa*, which reached the upper montane forest c. 1000 BP and became fully established from c. 700 BP onward (Fig. 4). Therefore the model results imply that the dense stands formed by the initial *L. bidwillii* cohort could have inhibited the spread of *W. racemosa* during the first centuries after the eruption.

Legacy effects from prior vegetation composition, climatic fluctuations and further (natural and anthropogenic) disturbances will all have influenced the forest succession since the Taupo eruption. A shift towards cooler, drier conditions c. 3000–2000 BP (McGlone & Moar 1977; Rogers & McGlone 1989) may have meant that *L. bidwillii* was expanding at the time of the eruption. According to Horrocks and Ogden (1998), the effects of the Taupo eruption on Mt Hauhungatahi were patchy, with some areas of forest escaping damage. Surviving patches of forest could have had a substantial impact on the vegetation composition immediately after the eruption, similar to contemporary post-disturbance succession at Mt St Helens in North America (Dale et al. 2005). Despite its simplified assumptions (succession starting from bare ground with global and uniform seed dispersal), the model results agree with the key patterns seen in the palynological record. The model analysis therefore highlights the profound and sustained effect of a catastrophic disturbance event such as the Taupo eruption for long-lived pioneer conifer species such as *L. bidwillii* (see also Ogden et al. 2005).

More differentiated patterns in the elevational series of pollen assemblages are, however, difficult to compare with the model results. First, the model represented only the main canopy species and did not account for other understorey species, some of which make substantial contributions to the relative abundance of pollen. Second, differences in pollen preservation and dispersal between species mean that there is not a consistent relationship between modern pollen abundance and basal area

for all simulated species at Mt Hauhungatahi (Horrocks & Ogden 1994), which, in turn, makes it challenging to directly relate pollen assemblages to the simulated forest structure.

Application of LandClim for the New Zealand context

LandClim's ability to represent disturbance processes (e.g. fires and stand-replacing windstorms) makes it particularly well-suited for exploring questions about vegetation dynamics across broad scales in space and time. This, in turn, means that LandClim can help address the long-standing questions surrounding the role of disturbance processes in angiosperm–conifer coexistence in New Zealand forests (as suggested by a number of empirical studies, e.g. Lusk & Ogden 1992; Wells et al. 2001; Ogden et al. 2005). On the basis of a pattern-oriented parameterisation of species traits and no other structural changes, LandClim proved capable of reproducing the elevational distribution of species on Mt Hauhungatahi described by Druitt et al. (1990) and, to some extent, the patterns observed in forest structure by Ogden et al. (2005). Furthermore, the model experiments demonstrate how tree species' life-history traits may explain the patterns of succession seen in the palynological record (Horrocks & Ogden 1998). On the other hand, relative to the data of Ogden et al. (2005), LandClim systematically underestimates basal area and tends to overestimate stem density for some species (Fig. 3). This mismatch suggests that the regeneration and mortality of New Zealand's long-lived trees are not represented adequately in LandClim. A more thorough consideration of how regeneration is represented in the model will be an important component of LandClim's development for future application in New Zealand.

Tree ferns constitute a distinctive feature of New Zealand's forests that have no direct equivalent in European and North American forest ecosystems. Our study provides a first attempt to incorporate these into a forest landscape model, but a more adequate representation will need to account for their distinctive growth behaviour.

Conclusion

Our approach highlights the potential for combining forest–landscape modelling with palaeoecological reconstructions in spatially complex environments. The use of simulation models to explore drivers underlying long-term dynamics observed in palaeoecological reconstructions is an area of considerable current interest. Whereas previous such studies using LandClim (Henne et al. 2011) have focused on cumulative pollen abundances over entire catchments, our study shows the model's suitability for use with locally and regionally distinct pollen assemblages. In the forest landscapes we consider, vegetation dynamics are controlled by interactions between biotic and abiotic drivers, but because they play out over long timescales they are challenging to resolve empirically. Process-based simulation models such as LandClim, when informed and supported by empirical data, have the potential to generate and evaluate hypotheses about the long-term trajectories of such forest systems.

Acknowledgements

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Supplementary Material

Additional supporting information may be found in the online version of this article:

Appendix 1. LandClim – model description

Appendix 2. Parameterisation of tree species life-history traits

Appendix 3. Parameterisation of the tree-fern life form

The *New Zealand Journal of Ecology* provides online supporting information supplied by the authors where this may assist readers. Such materials are peer-reviewed and copy-edited but any issues relating to this information (other than missing files) should be addressed to the authors.