



A spatial simulation model to explore the long-term dynamics of podocarp-tawa forest fragments, northern New Zealand



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ABSTRACT

Understanding the interactive effects of fragmentation and invasive species on forest dynamics requires a long-term perspective because they are difficult to assess in the medium- to long-term using observational or experimental data alone. In such settings ecological models have an important role to play. Here we describe the implementation of a spatially explicit individual-based model (SEIBM) representing the dynamics of small forest fragments in northern New Zealand based on empirical data collected in the region. In addition, we performed a baseline analysis to determine how well the model captured podocarp-tawa forest dynamics, and compared its performance with stand structure data obtained from an unfragmented forest in northern New Zealand. We used sensitivity analysis to determine how sensitive the model was to changes in the input parameters. In addition, we simulated different scenarios under diverse management conditions to explore the model's potential as a management tool. The model captures the stand structural characteristics of the fragments reasonably well but under-predicts stand basal area, suggesting that it does not represent the long-term suppression of some canopy tree species adequately. Although some refinement is needed to improve its performance, we believe that the model presented here is a useful tool for management purposes and for the assessment of the long term viability of forest fragments. The model can help inform managers and decision-makers regarding the long-term persistence of podocarp-tawa forest patches.

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1. Introduction

Fragmented ecosystems arise from anthropic actions such as agricultural clearing and timber extraction (Primack et al., 2001) and have resulted in the reduction of many forest ecosystems to isolated clusters of remnant habitat surrounded by a productive matrix (Santo-Silva et al., 2016; Echeverria et al., 2006). The remnant forest fragments experience changes in abiotic and biotic conditions that can have a profound influence on population and community processes such as seed dispersal, seedling establishment and ultimately species composition (Herrera and Garcia, 2010; Broadbent et al., 2008). Understanding how human activities such as fragmentation affect forest ecosystems and how these effects might be passively or actively mitigated is challenging because the processes being considered occur over large extents in space and time and decisions are often made under high epistemic uncertainty (Messier et al., 2015). Furthermore, ecosystem

response to the changes induced by humans (e.g. shifts in disturbance regime) may not be immediate and/or linear, but rather be lagged and/or non-linear (Johnstone et al., 2016), which makes predicting them even more challenging. In such settings it is difficult to design, implement and conduct classical experiments – rather a pluralistic approach, in which empirically grounded modelling plays important heuristic and predictive roles, is required (see Bowman et al., 2015).

The podocarp-tawa forests of Northern New Zealand typify the stresses that fragmented forests suffer from and the challenges involved in understanding how to forecast and mitigate their long-term effects. This forest type is highly fragmented, under pressure from exotic herbivores and suffering invasion by exotic weeds (Ewers et al., 2006; Smale et al., 2008; Innes et al., 2010; Burns et al., 2012). Tawa (*Beilschmiedia tawa*; Lauraceae), a major component of the canopy of this forest type, is a long-lived (up to c. 450 y; West, 1986) endemic native tree species that is showing signs of recruitment failure (Morales, 2015; Morales et al., 2016). In response to these and other pressures, various management strategies have been applied to remnant podocarp-tawa forests. One of the most common management practices in New Zealand is the fencing of

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forest fragments to exclude large herbivores, often followed by the control of small mammalian pests (Dodd et al., 2011; Burns et al., 2012). Passive activities, such as fencing, are globally the most frequently adopted restoration approach (Melo et al., 2013) and encompass a series of activities that do not require constant, active human involvement. To be successful passive approaches do, however, require the removal of activities negatively impacting the ecosystem (e.g. exclusion of large herbivores by fencing) followed by ongoing monitoring to evaluate ecosystem recovery. However, the benefits of passive restoration activities on forest fragments are difficult to assess in the medium- to long-term. In such settings ecological models can help to focus limited resources and guide management actions (Honrado et al., 2016). Ecological models are of particular value in developing and evaluating effective restoration strategies for long-lived taxa such as tree species (Anand and Desrochers, 2004).

Many types of ecological models have been developed to represent vegetation dynamics across a wide range of different ecosystems (Scheller and Mladenoff, 2007; Perry and Millington, 2008). Individual-based models, or IBMs, have become one of the most widely employed types of forest model (Grimm and Railsback, 2005). An IBM represents a collection of single organisms, sometimes known as agents (e.g. a tree), their environment and the interactions between them (Reuter et al., 2011). Forest gap models, a type of IBM, were first developed in the late 1960s to study forest succession (Botkin et al., 1972; Shugart, 1984). Many existing individual-based forest gap models are derived from the JABOWA model, which was designed as a community-level forest dynamics simulator by Botkin et al. (1972). A second gap model called FORET (Shugart, 1984) was developed based on JABOWA and is the basis for 80% of gap models developed prior to 1995 (Liu and Ashton, 1995); widely used contemporary gap models derived from FORET include LINKAGES, SORTIE and FORMIND (Liu and Ashton, 1995; Deutschman et al., 1997; Dislich et al., 2009).

In New Zealand, several gap model derivatives have been developed. For example, Develice (1988) developed a model called FORENZ, derived from JABOWA-FORET, but without including temperature and light limitation on growth, to predict forest dynamics on slip-faces in Fiordland. Hall and Hollinger (2000) used a model called LINKNZ, adapted from LINKAGES, to simulate conifer-hardwood and beech species forest succession. LINKNZ has also successfully been used to explore vegetation and climate shifts in the early Holocene (McGlone et al., 2011). Kunstler et al. (2009, 2013) used a model derived from SORTIE, SORTIE-NZ, to simulate the dynamics of lowland temperate rain forests on the South Island. Thrippleton et al. (2014) used a model called LANDCLIM (Schumacher et al., 2004), based on FORCLIM (Bugmann, 1994) (a descendant of the FORECE model by Kienast (1987)), to simulate long-term ecological dynamics across the large spatio-temporal scales relevant for New Zealand's forests. However, when compared to other regions, such as North America, the use of individual-based forest models in New Zealand has been limited due to the difficulty of collecting parameterization data and the presence of unusual functional types such as long-lived pioneers (Shugart and Smith, 1996).

Here we describe the implementation of a spatially explicit individually-based model (SEIBM) designed to represent the long-term dynamics and viability of podocarp-tawa forest fragments in New Zealand. Our main purpose was to design and implement a model that could simulate the fate of forest fragments across a range of management contexts, representing the effects of both fragmentation and fencing. Also, as a proof-of-concept we simulated different scenarios under diverse management conditions to explore the model's potential usefulness as a management tool.

2. Methods

2.1. Model description

The model described in this section is a spatially explicit individually-based model (SEIBM) designed to represent the long-term dynamics and viability of podocarp-tawa forest fragments under different types of management (unfragmented forest, fenced and unfenced fragments) of a forest of 16 ha (i.e. a 100×100 grid of 4×4 m cells) (Fig. 1). The model design is, by intention, reasonably generic and could be adapted to model other types of forests if needed. The model was essentially manually calibrated but wherever possible we drew on empirical estimates in its parameterization and we evaluated the model's outcomes against forest stand structures described in the NZ literature (although such information was not available for all parameters or outcomes). The information provided in this section is a summary of the Overview, Design concepts, and Details (ODD) protocol described by Grimm et al. (2006, 2010) as presented in Appendix A in Supplementary material 1. The model was implemented using NetLogo 5.3.1 (Wilensky, 1999); a free and open source software tool, available under a GPL license.

The model considers three forest canopy species – *Beilschmiedia tawa*, *Laurelia novae-zelandiae* and *Dacrydium cupressinum* – and three sub-canopy species that typify these forest ecosystems: *Hedycarya arborea*, *Piper excelsum* and *Meliclytus ramiflorus*. In each time-step or tick (one year) the model sequentially processes a series of ecological routines as follows: restoration planting, seed dispersal (both from within and beyond the fragment), herbivory, mortality, gap formation, regeneration (recruitment), growth and seedling/sapling demography (Fig. 1)

The model was initialized with a spatially random pattern (there are not data describing individual-level spatial pattern in these forests) and parameterized using data collected from unfragmented podocarp-tawa forest (continuous fenced forest) and from previously published literature. The study area for data collection was located near Cambridge in the Waikato region, North Island, New Zealand. The unfragmented forests were located at Te Miro Scenic Reserve, Maungatautari Ecological Island North and Maungatautari Ecological Island South (Morales et al., 2016). The Maungatautari Ecological Island is surrounded by a predator-proof fence (Burns et al., 2012) (Fig. 2).

At initialization the species abundances, and the size (diameter at breast height; dbh) and the age of each individual adult tree will depend on the scenario being considered (unfragmented forest, fenced and unfenced fragment). Regardless of the scenario, the model starts with the same number of seedlings of each species (10 seedlings [individuals < approximately 50 cm in height]) regardless of the scenario and saplings (one sapling [individuals > approximately 50 cm in height]) in each grid cell. When simulated, restoration activities (i.e. planting) are represented by adding a species-specific amount of saplings to the sapling bank at a specific frequency.

Each time-step, adult trees produce a number of seedlings following a Poisson deviate specified by a seed production parameter (*seed-prod*). We distinguish between three types of dispersal (Fig. 3): under individual trees ('neighbourhood dispersal'), within the fragment ('local dispersal') and from beyond the fragment ('long-distance dispersal'; by, for example, frugivorous birds). Neighbourhood dispersal represents the dispersal that occurs under parent trees. The area within which this occurs depends on the size of the individual tree's crown. Local dispersal represents those seedlings that establish within the fragment but at some distance from their parent. The process of long-distance seed dispersal is intended to give a chance for all the species to invade and establish a patch during the succession via movement of seeds

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