Disturbance affects short-term facilitation, but not long-term saturation, of exotic plant invasion in New Zealand forest

Laura A. Spence1,*,†, Joshua V. Ross2,*,†, Susan K. Wiser3, Robert B. Allen3 and David A. Coomes1,3,*

1Forest Ecology and Conservation Group, Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EA, UK
2Operations Research and Statistics Group, School of Mathematical Sciences, University of Adelaide, Adelaide, SA 5005, Australia
3Landcare Research, PO Box 40, Lincoln 7640, New Zealand

We investigate the spread of an exotic herb, \textit{Hieracium lepidulum}, into a New Zealand \textit{Nothofagus} forest with the aim of understanding how stand-development of tree populations, propagule pressure and invader persistence, affect invasion across the landscape and within communities. Using data repeatedly collected over 35 years, from 250 locations, we parametrize continuous-time Markov chain models and use these models to examine future projections of the invasion under a range of hypothetical scenarios. We found that the probability of invasion into a stand was relatively high following canopy disturbance and that local abundance of \textit{Hieracium} was promoted by minor disturbances. However, model predictions extrapolated 45 years into the future show that neither the rate of landscape-level invasion, nor local population growth of \textit{Hieracium}, was affected much by changing the frequency of canopy disturbance events. Instead, invasion levels were strongly affected by the ability of \textit{Hieracium} to persist in the understory following forest canopy closure, and by propagule supply from streams, forest edges and plants already established within the stand. Our results show that disturbance frequency has surprisingly little influence on the long-term trajectory of invasion, while invader persistence strongly determines invasion patterns.

Keywords: \textit{Hieracium}; invader persistence; Markov chain models; \textit{Nothofagus}; propagule pressure; stand-development

1. INTRODUCTION
Exotic plant invasions pose a serious threat to native biodiversity and ecosystem functioning, and the development of models predicting the spread of an exotic species, as well as its persistence once established, is important for effective conservation management [1]. Disturbance of grassland communities (e.g. fire, grazing) is recognized to accelerate the establishment and invasion of exotic plants [2,3], but less is known about the influence of disturbance of tree structure and dynamics on the invasion of forests by herbaceous plants [4,5]. The death of established trees allows light and precipitation to penetrate forest floors and increases the availability of below-ground resources to plants [6–8], changes that strongly influence the composition of woodland herb communities [9,10]. Exotic species are also likely to benefit from the extra resources available in tree-fall gaps, but the degree to which they can use this ‘invasion window’ is constrained by propagule availability at the time of disturbance [11,12], especially during the early stages of a species’ invasion into a region [13]. Many native herbs persist for decades in forest understories until the creation of canopy gaps provides opportunities for flowering, reproduction and population growth [10,14]. Similarly, in the long term, the success of invasive herbs is likely to be driven by their persistence in the shaded understorey that develops subsequent to disturbance [15]. However, the importance of persistence rates, rather than colonization rates, for the long-term success and distribution patterns of exotic herbs is largely unknown [5,16].

Here we quantify the effects of stand-development and propagule supply on the spread of an exotic plant, \textit{Hieracium lepidulum}, into a New Zealand forest understorey, testing whether canopy disturbance increases the probability of invasion and whether canopy closure increases the probability of local extinction. We use data from 250 permanent plots, repeatedly collected over 35 years, to understand the spread of \textit{Hieracium} in natural forests of mountain beech (\textit{Nothofagus solandri} var. \textit{cliffortioides}). These plots are distributed across 9000 ha of the Southern Alps and differ greatly in stand-development stage ([17,18]; figure 1) and distance from \textit{Hieracium} seed sources [19]. The dataset is notable in recording the invasion process from its beginning; research is therefore not biased towards a system heavily impacted by invasion [20].

We used continuous-time Markov chains (CTMCs) to model the rate at which forest stands change from one...
stand-development stage to another and then, within the context of these dynamics, model the invasion of *Hieracium* into stands, and its persistence and abundance within-stands. CTMCs are useful for modelling such data because: (i) allow for events to occur at any point in time; (ii) explicitly model the dynamic transitions between discrete entities (e.g. change in stand-development stage, or the absence to presence of *Hieracium* in a stand); (iii) account for randomness in the type and timing of events that occur; and (iv) provide a rigorous framework in which to model long-term data. We used the parametrized models to predict *Hieracium* invasion under different hypothetical scenarios, investigating whether altering the frequency of canopy disturbance or propagule supply influenced invasion and persistence of *Hieracium*. Specifically, we used the parameter estimates and subsequent model predictions to answer the following questions: (i) Does disturbance of tree structure and dynamics promote the initial invasion of *Hieracium*? (ii) Do such disturbances affect the long-term trajectory of *Hieracium* invasion? (iii) Do different intensities of canopy disturbance differ in their effect on *Hieracium* spread? (iv) What are the relative effects of disturbance, propagule pressure and invader persistence, on the long-term trajectory of *Hieracium* invasion?

2. MATERIAL AND METHODS

(a) Study site and species

Our study was conducted across 9000 ha of forest within a 200 km² tract of land in the eastern ranges of the Southern Alps, Canterbury, New Zealand (43° 8′ S, 172° 42′ E). The forest forms a belt from the valley bottoms at 600 m elevation to the tree-line at about 1400 m [23] and is composed solely of mountain beech. A sequence of large-scale disturbances of tree structure and dynamics have affected this forest over the past 40 years. Extensive damage was caused by wind-throw and snowstorms in 1968 [24], followed by heavy snowfall in 1973 [17,24], then extensive low-intensity disturbance up to 1987 caused by a fungal pathogen spread by pinhole beetles *Platypus* spp., Platypodidae, Coleoptera [17,24] and finally an earthquake in 1995 [25]. These disturbances were unpredictable and spatially patchy and have created a patchwork of stands at different stages of structural development [17,18]. The stages of stand-development range from rocky slopes devoid of vegetation, through dense stands of saplings and poles, to patches of large trees with open understories, and have strong corresponding gradients in light and nutrient availability (e.g. [26,27]). The forest understorey is sparse, and comprises woody shrubs, ferns, herbs and graminoids. The most abundant understorey species are the shrubs *Podocarpus nivalis* (Podocarpaceae), *Coprosma depressa* and *Podocarpus nivalis* (Podocarpaceae), *Coprosma depressa* and *Podocarpus nivalis* (Podocarpaceae), *Coprosma depressa* and *Podocarpus nivalis* (Podocarpaceae), *Coprosma depressa* and *Podocarpus nivalis* (Podocarpaceae), *Coprosma depressa* and

![Figure 1. (a) Schematic of our model of forest stand structure and development; arrows denote feasible transitions, each labelled with the corresponding parameter; (b) criteria used to determine stand structure from observed tree growth measurements; (c,d) observed (solid lines) and fitted (dashed lines) proportion of stands in each development stage, 1985–2004: (c) model fit when conditioned only on initial 1985 values, and (d) model fit when re-conditioned at each observation in time. Open circles, regenerating (R); open diamonds, competitive (C); crosses, mature (M); filled circles, major-disturbed (D); filled squares, minor-disturbed.](http://rspb.royalsocietypublishing.org/Downloaded from http://rspb.royalsocietypublishing.org/ on April 7, 2017)
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C. pseudoeucatea (Rubiaceae), and a sedge, Uncinia angustifolia (Cyperaceae). Total understory species richness ranges from 1 to 63 (mean = 14.0) per 400 m², while exotic species richness ranges from 0 to 16 (mean = 1.7). There are currently no serious invaders at our study site, other than Hieracium lepidulum, although invasive species do exist at high abundances in surrounding tussock grassland [28]. In 2004, only seven exotic species occurred in more than 10 per cent of plots (400 m²) in the forest, and Hieracium lepidulum was over three times more abundant than the next commonest exotic—Mycelis muralis (mean of 10.5% versus 2.9% seedling plots occupied per plot).

Hieracium lepidulum is a broad-leaved, basalt rosette-forming, perennial herb, with flowering stems up to 80 cm tall. Reproduction is predominantly by apomictic, asexual seeds [29,30] in the form of wind-dispersed achenes [31]. Hieracium lepidulum is one of several Hieracium species introduced to New Zealand [32], but as no other species within the genus are considered in this study, we refer to it as Hieracium. The earliest record of its occurrence in New Zealand is from 1941, along a stream margin within the very area of this study [33]. This site may have acted as a centre of subsequent spread, and now H. lepidulum occurs widely in a range of different natural habitats in the region [33].

(b) Data collection

The 250 permanently marked forest plots were established along 98 transects in the study area in the austral summers starting in 1970 and 1972. Transects start from random locations along streams (30–1000 m apart), and are aligned along random compass bearings; plots are positioned systematically at 200 m intervals along each transect from stream to tree-line, starting from random distances at least 20 m into the forest (one to eight plots per transect, mean = 2.6; electronic supplementary material, S1). Each plot is 0.04 ha (20 × 20 m), and has within it twenty-four 0.75 m² subplots arranged systematically and marked permanently with metal pegs. After the initial establishment, plots were measured again in the austral summers starting in 1985, 1993, 1999 and 2004.

In 1972, the presence or absence of Hieracium was recorded on 217 plots, and from 1985 on all plots and subplots. Diameter at breast height (dbh) for all trees over 25 mm dbh was recorded in each measurement and also in the interim years of 1974, 1983 and 1987. Recruits were tagged and deaths recorded at each census. Dense populations of Hieracium, which act as propagule sources, are found in the tussock grasslands surrounding the forest [28] and along streams [34]. We assumed that Hieracium is present along all streams and edges, basing this assumption on extensive observations made in the study area [34], and the proximity of plots to these propagule sources was measured off topographic maps using forest boundaries measured in 1988 (1:25 000 New Zealand Map Series, cf. [19]).

(c) Classification of stand-development stages

Mountain beech is a relatively light-demanding species that fails to regenerate under the shade of its own canopy. Carpets of seedlings form in tree-fall gaps, which develop over time, while separated them from regenerating and disturbed stands. Regenerating stands were defined as those that gained stems over time (through the recruitment of new stems), whereas stands lost stems. Thinning stands were separated into competitive or mature stands by a logistic regression model for each stand predicting the probability of individual tree death from its dbh: stands on which smaller trees were significantly more likely to die (at the 95% level) over the preceding years were classified as competitive-thinning, whereas stands on which tree mortality was unrelated to size were classed as mature stands. Finally, we distinguished between two magnitudes of disturbance (minor- and major-) because some stands jumped from disturbed to mature categories in adjacent time steps, effectively bypassing the regeneration and thinning stages. The explanation for this observation is that populations respond to low-intensity disturbance, such as one or two tree-falls, by lateral branch growth of existing trees and without recruitment from the seedling layer [17,35]. These stands were observed to have a significantly lower reduction in mean diameter in the process of disturbance than those stands which proceeded to the regenerating stage, so a stand was categorized as minor-disturbed if the mean diameter change was smaller than the 5 per cent quantile of change observed in all disturbed plots. There was no significant relationship between forest stand structure and proximity to the main sources of propagules (forest edge and stream habitats) in any of the measurement years.

(d) Model specification and calibration

In modelling using CTMCs, you first define the set of possible states that the process can adopt, which for our forest stand dynamics model comprises our five stand-development stages. Next, you must specify the rate at which the stands make a transition between each of the possible states; the rate of transition from state X to state Y is denoted as $a_{XY}$, where $X$ and $Y$ are one of R (regenerating), C (competitive), M (mature), N (minor-disturbed) or D (major-disturbed; figure 1a). There are nine rates of transition, as some transitions are excluded from the model because they are not ecologically feasible; for example, transition from a mature-thinning stand to a regenerating cannot happen, because that mature stand must first experience a disturbance. These rates are specified as parameters in our forest dynamics model (table 1) and provide information of both the time until a transition occurs and the nature of that transition. A stand remains in its initial state for an exponentially distributed time, with mean equal to one divided by the sum of the rates of feasible transitions out of that initial state. For example, a regenerating stand will remain such for an exponentially distributed period of time with mean $1/(a_{RR} + a_{RN} + a_{RC})$ because it could move either to a major-disturbed or competitive-thinning state. The probability of the stand undergoing a particular feasible transition is given by the ratio of the rate of moving to that state divided by the sum of all the possible rates out of that initial forest stand state.
Table 1. Parameter estimates and bootstrap results for best-supported models of (i) forest stand structure dynamics; (ii) *Hieracium* invasion into stands across the landscape; and (iii) *Hieracium* invasion within occupied stands. Those parameters estimated at each stage of the model that are required in the subsequent stages are assumed fixed. The mean, median and standard error values are evaluated from 100 parametric bootstrap simulations (see electronic supplementary material, figure S2).

<table>
<thead>
<tr>
<th>parameter</th>
<th>definition</th>
<th>estimate</th>
<th>mean</th>
<th>median</th>
<th>s.e.</th>
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<td>(i) forest stand dynamics model</td>
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<td></td>
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<td></td>
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<tr>
<td>$a_{DR}$</td>
<td>major-disturbed to regenerating stands</td>
<td>0.5139</td>
<td>0.4629</td>
<td>0.4470</td>
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<td>$a_{RD}$</td>
<td>regenerating to major-disturbed stands</td>
<td>0.0093</td>
<td>0.0113</td>
<td>0.0098</td>
<td>0.0092</td>
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<tr>
<td>$a_{RC}$</td>
<td>regenerating to competitive thinning stands</td>
<td>0.0140</td>
<td>0.0139</td>
<td>0.0135</td>
<td>0.0040</td>
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<td>$a_{CD}$</td>
<td>competitive thinning to major-disturbed stands</td>
<td>$\leq 10^{-8}$</td>
<td>0.0006</td>
<td>$\leq 10^{-5}$</td>
<td>0.0009</td>
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<tr>
<td>$a_{CM}$</td>
<td>competitive thinning to mature thinning stands</td>
<td>0.0533</td>
<td>0.0520</td>
<td>0.0521</td>
<td>0.0063</td>
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<tr>
<td>$a_{MD}$</td>
<td>mature thinning to major-disturbed stands</td>
<td>0.0261</td>
<td>0.0235</td>
<td>0.0247</td>
<td>0.0083</td>
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<tr>
<td>$a_{MN}$</td>
<td>mature thinning to minor-disturbed stands</td>
<td>0.0219</td>
<td>0.0434</td>
<td>0.0243</td>
<td>0.0733</td>
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<td>$a_{NM}$</td>
<td>minor-disturbed to mature thinning stands</td>
<td>0.2747</td>
<td>0.6622</td>
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<td>$a_{ND}$</td>
<td>minor-disturbed to major-disturbed stands</td>
<td>0.1290</td>
<td>0.1905</td>
<td>0.1364</td>
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<td>(ii) stand-level invasion model</td>
<td></td>
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<td></td>
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<tr>
<td>$I_{DN}$</td>
<td>probability of successful invasion of (major- and minor-) disturbed stands</td>
<td>0.4626</td>
<td>0.4805</td>
<td>0.4529</td>
<td>0.1733</td>
</tr>
<tr>
<td>$I_{RCM}$</td>
<td>probability of successful invasion of non-disturbed stands (regenerating, competitive thinning and mature thinning)</td>
<td>0.0502</td>
<td>0.0530</td>
<td>0.0505</td>
<td>0.0127</td>
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<tr>
<td>$E_{stoch}$</td>
<td>extinction rate from occupied stands</td>
<td>0.0080</td>
<td>0.0078</td>
<td>0.0074</td>
<td>0.0024</td>
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<td>$E_{dis}$</td>
<td>probability of disturbance (major- and minor-) removing <em>Hieracium</em> from stand</td>
<td>0.0384</td>
<td>0.0404</td>
<td>0.0229</td>
<td>0.0490</td>
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<tr>
<td>$\alpha$</td>
<td>(exponential) decay rate of propagules with distance from source</td>
<td>0.0099</td>
<td>0.0101</td>
<td>0.0102</td>
<td>0.0026</td>
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<tr>
<td>$P_{e}$</td>
<td>rate of propagule supply from stream</td>
<td>1.1527</td>
<td>1.1786</td>
<td>1.1457</td>
<td>0.3362</td>
</tr>
<tr>
<td>$P_{c}$</td>
<td>rate of propagule supply from forest edge</td>
<td>0.8151</td>
<td>0.7844</td>
<td>0.7491</td>
<td>0.3453</td>
</tr>
<tr>
<td>(iii) within-stand invasion model</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>$i_{D}$</td>
<td>rate of successful spread on subplots within major-disturbed stands</td>
<td>0.1993</td>
<td>0.2111</td>
<td>0.2026</td>
<td>0.0822</td>
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<td>$i_{N}$</td>
<td>rate of successful spread on subplots within minor-disturbed stands</td>
<td>0.4816</td>
<td>0.4908</td>
<td>0.4881</td>
<td>0.1066</td>
</tr>
<tr>
<td>$i_{RCM}$</td>
<td>rate of successful spread on non-disturbed stands (regenerating, competitive thinning and mature thinning)</td>
<td>0.1434</td>
<td>0.1418</td>
<td>0.14</td>
<td>0.0155</td>
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<tr>
<td>$e_{stoch,DN}$</td>
<td>extinction rate from subplots on major- and minor-disturbed stands</td>
<td>$\leq 10^{-8}$</td>
<td>0.0158</td>
<td>$\leq 10^{-8}$</td>
<td>0.0314</td>
</tr>
<tr>
<td>$e_{stoch,RCM}$</td>
<td>extinction rate from subplots on non-disturbed stands</td>
<td>0.0647</td>
<td>0.0645</td>
<td>0.0648</td>
<td>0.0087</td>
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<tr>
<td>$e_{dis}$</td>
<td>probability of disturbance (major- or minor-) removing <em>Hieracium</em> from subplot</td>
<td>0.0731</td>
<td>0.0593</td>
<td>0.0466</td>
<td>0.0602</td>
</tr>
</tbody>
</table>

For example, a regenerating stand will change to major-disturbed with probability $a_{RD} (a_{DR} + a_{RD})$, or to competitive-thinning with probability $a_{RC} (a_{RD} + a_{RC})$. The rates of each transition are assumed constant through time, an assumption we believe logical for a first analysis, and likely to be reasonably accurate for most rates such as transitions between forest types and invasive species persistence upon a given stand type.

We use standard CTMC techniques to evaluate the (computationally-) exact distribution of the process and, given the specified parameter structure, search for the parameter set that maximizes the likelihood of our data, using EXPOKIT [36] and MATLAB (see electronic supplementary material, S2 for full details of the modelling methods). The likelihood of our observed forest stand data, given a set of parameter values, is simply the product of the probabilities of moving between the configurations in our data over the time elapsed between re-measurements [37]. Details of these techniques are described more fully in the electronic supplementary material, S2.

The parameter values estimated for the forest stand dynamics are assumed known and then used in modelling the *Hieracium* invasion dynamics at two spatial scales, stand and within-stand. We assume that stand dynamics are independent of *Hieracium* occupancy state. The stand-level model uses the *Hieracium* presence/absence data for each stand, and we allow the following dynamics to alter stand-level *Hieracium* occupancy: rate of *Hieracium* invasion of unoccupied stands ($i_{D}$); rate of stochastic *Hieracium* extinction on occupied stands ($E_{stoch}$); and probability of *Hieracium* extinction on occupied stands subjected to a major or minor disturbance ($E_{dis}$). In addition, stands are modelled with different rates of attempted invasion (i.e. propagule supply) relating to the distance from two measured sources of propagules, forest edge ($P_{e}$) and stream ($P_{c}$), and a third unmeasured potential source ($P_{u}$). The latter source is included to allow for any other source of propagules that may have been overlooked, and is assumed to be a constant rate of propagule supply per unit time to every stand. We assume exponential decay (parameter $\alpha$) of propagules with distance from each source, but allow for different dispersal rates between sources. We evaluate the parameter set for the stand-level invasion model using the combination of observed forest stand state and *Hieracium* presence/absence data using the maximum-likelihood technique described above.

The within-stand invasion model uses *Hieracium* presence/absence data upon subplots to provide a measure of *Hieracium* abundance, specified as the proportion of subplots, out of 24, occupied in a stand. We allow similar dynamics of *Hieracium* occupancy of individual subplots to those of stand-level occupancy: invasion into unoccupied...
subplots from an external source ($I_1$; decreased by a factor $\rho = 4.5/100$ as subplots only cover 4.5% of the stand area); invasion into unoccupied subplots from a within-stand source ($I_2$); stochastic *Hieracium* extinction from occupied subplots ($\varepsilon_{\text{stoch}}$); and *Hieracium* extinction from occupied subplots due to a major or minor disturbance ($\varepsilon_{\text{dis}}$). When evaluating the parameters for the within-stand model, the parameters that are required from the forest stand dynamics model, and (best-fitting) stand-level model are assumed known.

In order to find the optimal parameter structure, we create alternative stand- and within-stand level models with permutations of different parameter structures. We find the best-fitting alternative model by using the sum of ranks from each of three model selection criteria: Akaike Information Criterion (AIC), Schwarz (BIC) and Hannan-Quinn (HQ). The parameter structures of the alternative models differ as follows: for each of the *Hieracium* dynamics modelled ($I_1$, $I_2$, $E_{\text{dist}}$, $E_{\text{intra}}$, $E_{\text{stoch}}$, and $\varepsilon_{\text{stoch}}$), we include either a constant rate for all forest stand stages (one parameter), different rates for disturbed (major and minor) versus non-disturbed stands (two parameters); different rates for major-disturbed and non-disturbed stands (three parameters); or different rates for each stand stage (five parameters). For propagule supply, we test alternative structures including with and without the unmeasured source ($P_5$); with both stream and edge sources ($P_6$ and $P_7$); and with stream only ($P_7$). Permutations of these parameter structures lead to 54 and 11 alternative models at the stand- and within-stand level, respectively (see electronic supplementary material, S4 for parameter structure of maximal and best-fitting models).

Our approach produces only ‘approximate’ maximum-likelihood estimates of the parameters, as we do not estimate all of them simultaneously. However, the high dimensionality of the search space when attempting to estimate all parameters simultaneously made convergence of the model difficult, and thus more reliable estimates are derived using our approach. The confidence we can have in these estimated parameter values is indicated by parametric bootstraping (electronic supplementary material, S2). Finally, the predictions from each of the parameterized models was compared with the observed data, with two cases considered: first, we condition on the initial configuration only (i.e. data from 1985); second, we recondition on the observed configuration from the data at each census. The latter case is considered because the actual realization of the process that was observed is likely to have a significant impact on the subsequent dynamics of the process; therefore, it provides a more accurate prediction from our model for comparison with the data.

**3. RESULTS**

(a) **Observed forest stand structure and invasion dynamics**

Forest stand structure was dynamic over the 35 years of monitoring: 30, 20 and 28 per cent of stands changed from one developmental stage to another between the measurement years 1985–1993, 1993–1999 and 1999–2004, respectively. In addition, the proportions of stands in each developmental stage changed over time (figure 1c); for example, the proportion of ‘regenerating’ stands increased from 2.4 per cent in 1985 to 29 per cent in 2004. *Hieracium* occurrence in stands differed significantly between the five developmental stages ($\chi^2 = 15.8$, $p = 0.0033$; repeated-measures analysis of variance), with mean stand occupancy across all measurement years being 86 per cent for major-disturbed, 82 per cent for minor-disturbed, 73 per cent for regenerating, 41 per cent for competitive-thinning and 54 per cent for mature-thinning stands (electronic supplementary material, S3a). Within-stand *Hieracium* abundance also differed significantly between stand developmental stages ($\chi^2 = 16.4$, $p = 0.0026$; electronic supplementary material, S3b), with mean abundance being 0.32 for major-disturbed, 0.22 for minor-disturbed, 0.13 for regenerating, 0.02 for competitive-thinning and 0.07 for mature-thinning stands.

(b) **Fitted and predicted forest stand dynamics**

The fitted forest stand dynamics model shows close agreement to the observed data (figure 1b, c; see electronic supplementary material, S2, for bootstrap simulations and a discussion of our confidence in the parameters). The model parameters indicate that a major-disturbed stand remains disturbed for an average of 2 years, then progresses to a regenerating stand (table 1). Regenerating stands remain as such for 43 years, on average, and move with probability 0.4 back to major-disturbed (disturbance rate of approx. 1% regenerating plots per year), otherwise moving to the competitive-thinning stage. Competitive-thinning stands remain as such for 21 years, on average, and experience a major-disturbance with probability 0.54 (disturbance rate of approx. 2.5% mature-thinning plots per year) otherwise experiencing minor disturbance. Those stands that experience a minor disturbance remain in a minor-disturbed stage for 2.5 years, on average, and return to a mature stage with probability 0.68, otherwise they experience a major disturbance (disturbance rate of approx. 13% minor-disturbed plots per year).

(c) **Alternative invasion model trajectories**

We used the models to predict long-term *Hieracium* dynamics under different scenarios. The best-supported model was extrapolated to 2050 (i.e. 45 years beyond the observed data collection) with all the estimated parameters held constant except for those defining either the rate of major or minor disturbance; the rate of stochastic *Hieracium* extinction; propagule supply rates; and the rate of invasion from within-stand sources. These rates were altered in magnitude, but still assumed constant over time: we compared predictions for rates of stochastic extinction, within-stand invasion and propagule supply that were either doubled, quadrupled or halved; and rates of major and minor disturbance that were doubled, halved or set at zero.

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Figure 2. Observed (solid lines) and fitted (dashed lines) *Hieracium* invasion dynamics over time for (a,b) stand-level; and (c,d) within-stand level. (a,c) Model fit conditioned on initial values only. (b,d) Model fit re-conditioned at each observation in time. Upper and lower red-dashed lines indicate two standard deviations of the mean.

indicate that disturbed stands are 9.2 times more susceptible to invasion than non-disturbed stands (table 1). Only one parameter is retained in the best-supported model for stochastic ($E_{\text{stoch}}$) and disturbance-induced ($E_{\text{dist}}$) extinction, showing that the likelihood of *Hieracium* extinction from invaded stands is independent of stand-developmental stage; both these parameter values indicate a low likelihood of *Hieracium* extinction from a stand. Stand proximity to both the forest edge and nearest stream are retained in the best-supported model as parameters affecting the likelihood of propagule dispersal into stands ($a$, $P$, and $P_2$) but there is no support for another unidentified source of propagules in the system. The quantitative effect of propagule dispersal is such that, regardless of development stage, a stand positioned next to a stream and forest edge is 1.7 times more likely to be invaded than a stand of maximum distance (600 m) from the forest edge, and 2.4 times more likely to be invaded than a stand of maximum distance (580 m) away from a stream. Extrapolation of the best-fitting stand-level model into the future under scenarios of altered parameter values showed that alteration of (major and minor) disturbance rates and the probability of *Hieracium* removal from a stand following disturbance caused only small differences in the long-term predictions of *Hieracium* occupancy across the landscape (figure 3a,b). There was only a 4 per cent decrease or 1 per cent increase in occupancy by 2050 caused by the removal or doubling of disturbance rates, respectively; while halving or doubling the probability of *Hieracium* removal following disturbance caused a 1 per cent increase or 3 per cent decrease in occupancy. A much greater effect was caused by changes to the stochastic *Hieracium* extinction rate (figure 3c) and propagule supply rates (figure 3d). Doubling or halving the predicted stochastic extinction rate caused a 13 per cent decrease or 8 per cent increase in occupancy, respectively, by 2050. Alteration of propagule supply rates affected stand-level *Hieracium* dynamics in two ways: halving the rates resulted in a 17 per cent decrease in the predicted *Hieracium* occupancy by 2050 and a trajectory that rises continually, while doubling the rates resulted in a 13 per cent increase in occupancy and a trajectory that plateaued at around 2020 (figure 3d).

**Figure 3**. Fitted and predicted dynamics of within-stand invasion

The unconditioned within-stand invasion model does not show as close a fit to the observed dynamics as seen at the stand-level (figure 2c), however, the model fit is much closer upon re-conditioning for the observed data at each measurement (figure 2d). The best-supported within-stand invasion model has score 4, arising from ranks 2, 1 and 1 (AIC, HQ and BIC), with the next best model score being 9. It has three parameters for the likelihood of *Hieracium* spread within stands: one each for major-disturbed ($\theta_2$), minor-disturbed ($\delta_3$) and non-disturbed stands ($\theta_{\text{RCM}}$, electronic supplementary material, S4c,d). These parameter values indicate that the rate of within-stand *Hieracium* spread is 3.4 times higher on minor-disturbed stands, but only 1.4 times higher on major-disturbed stands, relative to non-disturbed stands (conditional on the same initial subplot occupancy; table 1). As at the stand-level, there is only one parameter for the likelihood of extinction following a disturbance ($\delta_{\text{dist}}$), in contrast, there are two parameters for the likelihood of stochastic *Hieracium* extinction from a subplot in the best-supported within-stand model; these values indicate a higher extinction rate on non-disturbed stands ($\theta_{\text{stoch,RCM}}$) than disturbed stands ($\theta_{\text{stoch,DN}}$), although all extinction rates are relatively low.
There was only a small effect of different disturbance scenarios on the long-term predictions of *Hieracium* within-stand invasion: doubling or removing the major-disturbance rates caused mean *Hieracium* abundance on stands to be 2 per cent lower, or 13 per cent higher, respectively, by 2050 (figure 3e), while doubling or removing the minor-disturbance rate caused abundance to be 5.5 per cent higher, or 8 per cent lower, respectively.
A similarly small effect is seen when we alter the probability of Hieracium removal from each subplot following disturbance (figure 3g). In contrast, large effects on Hieracium abundance are predicted through alteration of stochastic subplot extinction, propagule supply or within-stand spread rates. Doubling the stochastic extinction rates reduced mean abundance by 79 per cent of that predicted in 2050, while halving increased abundance by 76 per cent (figure 3h). Alteration of propagule supply rates had a similar effect at the within-stand level as at the stand-level: doubling and halving rates causing a 29 per cent increase and 21 per cent decrease in abundance, respectively (figure 3i). Finally, doubling or halving the rates of within-stand Hieracium spread, caused a 104 per cent increase and 75 per cent decrease, respectively, in mean abundance in stands (figure 3j).

4. DISCUSSION

(a) Short-term invasion patterns dependent on magnitude of disturbance

Hieracium invasion patterns observed in the empirical data, and the parameters in our fitted model, provide strong support for the facilitation of invasion into mountain beech forest stands by disturbance to tree structure and dynamics. This corroborates the widely recognized role of disturbance as an important driving force of exotic plant invasion [2–4], and our results suggest that natural disturbance events such as wind-throw, landslides and insect damage, promote the colonization of invasive species in a similar way to human-caused disturbance such as clear-felling and fire [4,38].

Our use of a process-driven, categorical, assessment of disturbance rather than a continuous measure, such as change in basal area (cf. [19]), has provided a more detailed perspective on the effect of canopy disturbance on invasion at a small spatial scale. The local abundance of Hieracium following establishment within-stands is increased by higher minor-disturbance rates, while higher major-disturbance rates decrease local Hieracium abundance. This appears to be owing to the concomitant loss of Hieracium from subplots following disturbance (around a 7% chance of removal from each occupied subplot)—for example, in some cases, a major disturbance may be a landslide that exposes mineral soil and removes all plants. On major-disturbed stands, this initial loss on disturbance is not compensated for by the small increase in within-stand spread (factor 1.4 higher), while on minor-disturbed stands, the increase in within-stand spread is greater and can compensate for this initial loss (factor 3.4 higher). In addition, minor-disturbed stands remain in that state for a longer period of time and an increase in the rate of major-disturbance decreases the proportion of minor-disturbed stands across the landscape. The standard interpretation of structural disturbance is that the resultant tree death increases light and precipitation supply to the forest floor, locally reduces below-ground competition from trees, and hence increases nutrient and water supply [6,8,39,40], which creates an 'invasion window' of favourable conditions for exotic establishment [7]. However, while a major disturbance such as an earthquake would cause a much higher basal area loss and hence a greater pulse of resources such as light availability in a short period of time than lower intensity disturbance such as insect damage [17,25], it may negatively affect the availability of other resources such as nutrients and moisture owing to the exposure of mineral soil and bare rock, and expose seedlings to more extreme levels of temperature and drought. Our results indicate that the intermediate disturbance hypothesis [41,42] may apply to invasions, such that the small-scale disturbance may provide a more effective invasion window for local reproduction and spread. As mountain beech stands develop after disturbance from regenerating, to competitive-thinning, to mature-thinning stages, the accumulating biomass parallels a decline in soil nitrogen and cation availability as well as pH [26,43]. This decline in resources could well explain the relatively low stand-level invasion of non-disturbed stands and the relatively high within-stand extinction rate in non-disturbed stands (table 1).

(b) Propagule supply a significant determinant of Hieracium spread over decades

Our fitted model supports propagule supply as a factor limiting Hieracium invasion at both the stand and within-stand level, irrespective of stand-development stage, and shows that disturbance in itself is not a sufficient pre-requisite for invasion but must be accompanied with an adequate propagule supply [44,45]. A confounding factor when inferring the role of propagule limitation is that other variables, such as a gradient of decreasing resource supply with increasing distance from stream, could create a similar pattern in the population density of an exotic species as would the decay of a dispersal curve [34]. However, the increased nutrient concentrations associated with forest streams, or increased light availability at the forest edge, decline more rapidly from the forest margin than does the observed decay of propagule supply into the forest fitted by our model. The sustained importance of propagule supply as a determinant of Hieracium occupancy across the landscape over decades is contrary to the standard view of the sequence of invasion, which cites a diminishing role of propagule supply from external sources once local invader populations achieve reproductive capacity (cf. [19]). Our result contributes towards a growing body of evidence suggesting a more prolonged influence of propagule pressure on invasion patterns [46].

(c) Long-term invasion patterns determined by invader persistence, not disturbance rates

A strength of our modelling approach is that it has allowed the extrapolation of dynamics fitted to observed data, to predict the level of invasion in the future under different scenarios of disturbance and Hieracium dynamics. This has generated the interesting conclusion that, despite having a significant facilitative effect in the short-term, forest disturbance rates do not have a long-term effect on the stand- or within-stand level occupation of Hieracium across the landscape. This appears to be because the persistence of Hieracium following invasion is very high at both spatial scales [19], irrespective of stand-development stage, and the invasion rate of non-disturbed stands though lower than that of disturbed stands is sufficient to allow Hieracium to invade the
majority of stands across the landscape under any scenario of prevalent disturbance rates. The high persistence rate of *Hieracium* in the sub-optimal conditions of closed forest and the higher rates of invasion associated with canopy disturbance are typical of many woodland herbs (e.g. [9,10,47]), and implies that *Hieracium* may be a significant invader of these mountain beech forests in the future owing to its demographic attributes, rather than an opportunist in the past decades of high disturbance.

A factor that may affect the reliability of our predictions of *Hieracium* invasion is that the disturbance rate prevalent during the study period was higher than the long-term background rate [18], and this may have resulted in a higher incidence of invasion into closed forest stands owing to the proximity of disturbed sites and effective forest edge habitat. Other studies have shown that the effect of forest disturbances can have ramifications beyond the immediate locality of the disturbance [20,48]. However, although widespread disturbance could affect rates of stand-level invasion, the within-stand spread is less likely to be influenced by disturbance, making these predictions more robust. The high rate of disturbance prevalent during the study period is also likely to have led to an underestimate of the average length of time a stand spends in a mature-thinning stage. Before the current spate of disturbances, the forest structure in the study area largely consisted of mature-thinning stands [24], and these stands suffered a disproportionate amount of disturbance compared with competitive-thinning stands [18].

**5. CONCLUSIONS**

The patterns of exotic distribution observed at a single point in time can be misleading if one is trying to understand either the factors affecting invasion, or to predict invader distributions in the future [15]. Here, we present a technique for using field data to model invasion scenarios and overcome some of the limitations imposed by partial sampling of the processes driving invasion, even when relatively long-term data are available. We also develop a process-based metric of forest disturbance that is more discriminating than the more usual continuous measures. Our results indicate that exotic invaders can respond to disturbance events in the short-term, but long-term success of an invader within a landscape may be more dependent on an ongoing supply of propagules and its ability to persist once established. This conclusion could influence prioritization decisions of invasive species management that must consider disturbance, abundance and impact, since management may be more effective if targeted on those exotic species most likely to persist within a habitat, rather than those which show an initial invasive ability in disturbed habitats.

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