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ORIGINAL PAPER

Cross-scale management strategies for optimal control of trees invading from source plantations

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Abstract Biological invasion by non-native tree species can transform landscapes, and as a consequence, has received growing attention from researchers and managers alike. This problem is driven primarily by the naturalisation and invasion of tree species escaping from cultivation or forestry plantations. Furthermore, these invasions can be strongly influenced by the land-use matrix of the surrounding region, specific management of the source populations, and environmental conditions that influence seed dispersal or habitat quality for the invader. A major unresolved challenge for managing tree invasions in landscapes is how management should be deployed to contain or slow the spread of invading populations from one or more sources (e.g. plantations). We develop a spatial simulation model to test: (1) how to best prioritise the control of invasive tree populations spatially to slow or contain the biological invader when habitat quality varies in the landscape, and (2) how to allocate control effort among different management units when trees spread from many source populations. We first show that to slow down spread effectively, management strategy is less important than management effort. We then identify the conditions affecting the relative performance of different management strategies. At the landscape scale, targeting peripheral stands consistently yielded the best results whereas at the regional scale, management strategies needed to account for both habitat quality and tree life-history. Overall, our findings demonstrate that knowledge of how habitat affects tree life-history stages can improve management to contain or slow tree invasions by improving the spatial match between management effort and efficacy.

Keywords Biological invasions · Cohort model · Spatial spread · Tree invasions · Weed management scenarios

Introduction

Many tree species have been widely introduced for agriculture, forestry, or ornamental purposes (e.g.

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gardening) and landscape transformation (e.g. habitat restoration, soil stabilization). However, many of these introduced tree species have exceeded their initial purpose and subsequently become naturalized and invasive (sensu Richardson et al. 2000). Because of their potential dominance in plant communities, invasive trees can transform ecosystems at the scale of entire landscapes (e.g. Hibbard et al. 2001; Haugo et al. 2011).

A common goal in weed management, including invasion by non-native tree species, is complete control or eradication from a site. However, these weed-centric goals are often unrealistic or are rarely achieved due to logistic or budgetary constraints (e.g., Moore et al. 2011; Hulme 2012). For example, despite long-term (>10 years) co-ordinated management of the invasive tree lodgepole pine (*Pinus contorta*) at a single location in New Zealand (mid-Dome), an additional >$5 million NZD is thought to be required to complete the initial phase of removing currently-established trees, and more resources will be required for eradication (The Mid Dome trust 2012). Consequently, managers must often modify the goal of eradication and shift their focus to efficiently slowing down or containing the invasion (e.g. Buckley et al. 2005). To this end, identifying the optimal strategies for minimising the spread of tree invasions or subsequent reinvasion is a rapidly emerging area of interest in non-native plant management (Buckley et al. 2005; Hastings et al. 2006; Graf et al. 2007; Maxwell et al. 2009; Epanchin-Niell and Hastings 2010).

Substantial progress has been made in understanding the long-term consequences of short-term management through modelling the potential response of biological invaders to different management strategies. For example, recent application of sophisticated population models has shed light on the importance of plant demographic processes to population persistence, spatial spread, and ultimately the speed and magnitude of biological invasions (Caplat et al. 2012a). These models are derived from reaction–diffusion models that use partial differential equations to incorporate population growth and random-walk-type dispersal with Gaussian dispersal kernels (Holmes et al. 1994). Such models have been further refined in several ways, for instance, through the inclusion of matrix population models to incorporate multiple or continuous life stages (Caswell 2001), by using integrodifference equations to incorporate highly skewed dispersal kernels (e.g. fat-tailed kernels with frequent long distance dispersal events) (Neubert and Caswell 2000; Hui et al. 2011b; Caplat et al. 2012b), and other approaches such as the linked process model of Maxwell et al. (2009).

To capture the complexity of regional and local management of invasions in real landscapes where both time and location are important considerations, spatially explicit models can be used to address issues of temporal dependence and environmental heterogeneity better than their spatially-implicit counterparts (e.g. Minor and Gardner 2011; Caplat et al. 2012a). Such models have provided evidence for invasion management success by targeting satellite (peripheral) rather than source (core) populations (e.g. Moody and Mack 1988). Peripheral populations play a more direct role in the spread of a population, particularly if the process of spatial sorting leads to the selection of individuals with strong dispersal ability at the periphery of a population (Phillips et al. 2006; Shine et al. 2011; Berthouly-Salazar et al. 2012; Hui et al. 2012). In contrast, core populations contribute less to spatial spread despite their major contribution to population growth. Thus a simple expectation is that the most effective means to slow down the spread of invasive trees is to target satellite or peripheral populations before core populations. However, in some situations, targeting core populations is a better management strategy if these populations are the only source contributing to population growth (Maxwell and Ghersa 1992). Therefore several competing strategies exist for managing plant invasions, reflecting different assumptions made about the processes driving tree invasions. A management strategy can target or prioritize peripheral sites (Moody and Mack 1988), sites with high density (thus decreasing propagule pressure,Von Holle and Simberloff 2005), or populations on highly suitable habitat (Higgins et al. 2000). However, most models have not integrated dispersal with spatial variation in habitat suitability and subsequent reproductive and recruitment response into a single assessment of strategies to slow or stop an invasion.

In addition, the spatial extent of management affects the prioritization of different control strategies. This is because the efficiency of a management strategy in slowing down or containing the spread of an invader likely depends on the spatial scale and context at which management is implemented. Managing trees escaping from deliberate cultivation such as forestry plantations is complex because the invading population is constantly growing from one or more initial source populations (i.e. seed sources from plantations) as well as subsequent naturalised populations, leading to multiple invasion fronts (Caplat et al. 2012a). Slowing down the spread from a single population might be unimportant if there are additional populations that are not controlled; this could be particularly important where multiple managers control different parts of the landscape. The question then becomes: how to best distribute effort amongst managed areas? Because species distribution are determined by ecological processes working at different spatial scales (McGill 2010), a strategy that is efficient at controlling spread from a single population (e.g., targeting the periphery) might be unimportant when considering multiple populations and metapopulations at larger spatial scales. As a consequence, the landscape-level control of non-native invasive trees necessitates consideration of management efficacy across multiple spatial scales.

Conservation managers are faced with complex decisions to negotiate this multi-scale conundrum and prioritize alternative feasible control efforts within budgetary or resource constraints (Roura-Pascual et al. 2010). Indeed, management decisions often occur at different geographical or administrative levels, and information accessibility and quality can vary significantly. Both introduction and management of tree invasions develops conflicts within and between different countries depending on what information is available, and the services or values associated with these species (van Wilgen et al. 2012). Managing a population without considering larger-scale outcomes often results in different choices than managing a population as part of a regional or national scheme (Epanchin-Niell et al. 2010).

Here we approach the multiple-strategies, multi-scale problem simply by contrasting control strategies at two levels of management. We determine the effectiveness of different management strategies to control the spread of tree invasions across heterogeneous landscapes using a nested spatial simulation model. At a first level (management units) we test how to best control the spread of an invasive tree from one or two sources, contrasting strategies including: prioritizing sites at the periphery, prioritizing sites with high density, or prioritizing sites of suitable habitat. At a second level (region), we test how to most efficiently distribute effort when multiple sources of invasions are managed independently. In tandem, these approaches provide new insights into how different management strategies can slow or stop tree invasions at the landscape scale.

Methods

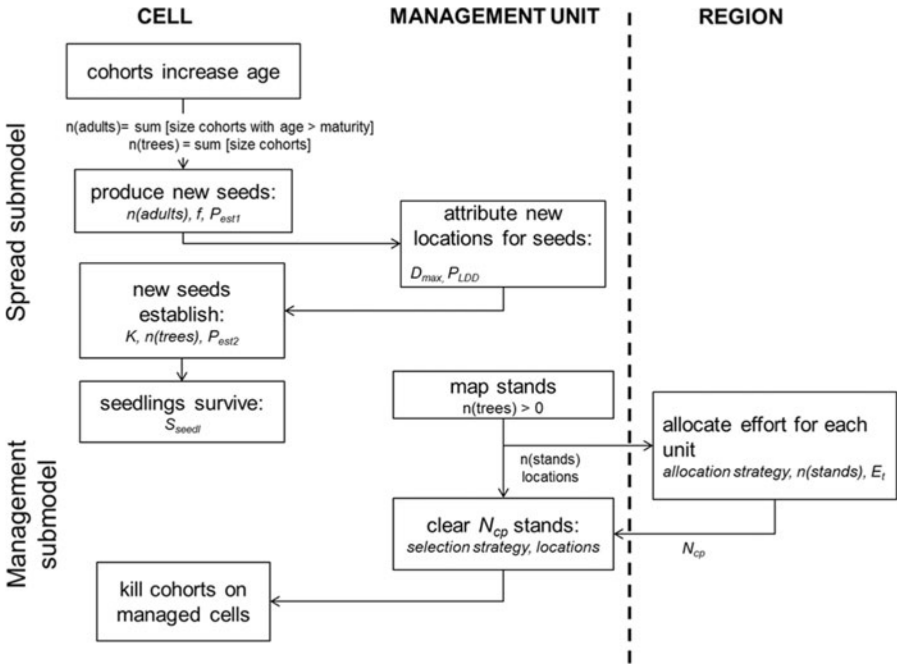
We determine how different management strategies can slow the spread of an invasive tree from single or multiple sources using a spatially explicit simulation model. For this we developed a nested model where: (1) tree cohorts grow and spread in a realistic fashion (see Fig. 1 and "Tree dynamics" section below); (2) invaded cells around plantations are cleared (e.g., the invasive trees are killed) following one of three potential spatial selection strategies (see Fig. 1 and "Spatial management" section below); (3) different spatial management units are allocated a given effort (number of patches that can be cleared) following one of three effort allocation strategies (see Fig. 1 and "Effort allocation" section below).

The model simulates an 8 km wide region composed of 20 m × 20 m cells. The region is comprised of 16 spatial management units (2 km wide = 10,000 cells each) (Fig. 2). The model was built and ran with NetLogo V5 (Wilensky 1999).

Tree dynamics

We simulated tree dynamics to capture the spatial components of spread, but avoided complex parameter settings. The model is composed of a grid where each cell is a cellular-automaton, driving the dynamics of cohorts (i.e. trees of the same age; Fig. 1). Most cells are initially devoid of trees, representing the original vegetation (e.g., grassland). Only a few cells are populated with adult cohorts (i.e. reproductively mature cohorts of age randomly drawn above A_{rep}, summing up to K individuals; see Table 1 for the description of all variables used in the model). Figure 1 shows the dynamics of a typical grid cell colonised by trees (thereafter, a "stand"). Within each time-step, invading tree cohorts increase in age. The cohort size in a cell is defined as the total number of trees (N_t), while the reproductive potential (N_a) is defined by the total

Fig. 1 Model flowchart, showing the spread and management submodels as they operate at level of a cell, management unit, and region



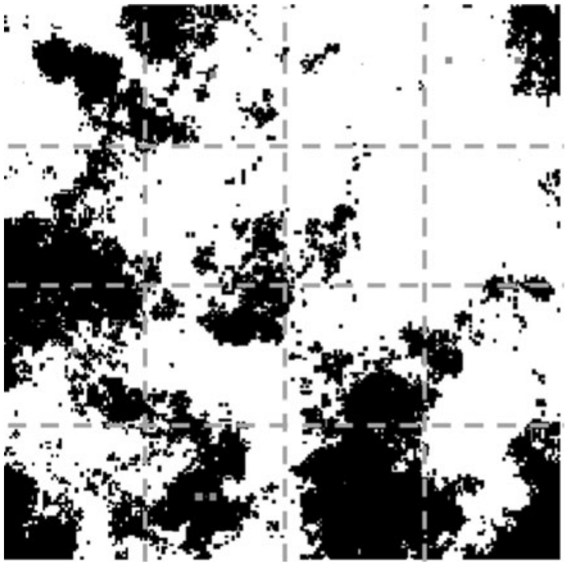


Fig. 2 Model grid showing the distribution of habitat ("good" habitat in *black* and "bad" habitat in *white*) and the 16 management units (delimited by *dashed grey lines*). Habitat cover and spatial autocorrelation values for this habitat grid were 0.25 and 0.5, respectively. The small *grey squares* show the location of the six initial populations

number of adult trees (age $\geq A_{rep}$). During each time step (1 year), the total number of seeds produced in a cell is $N_a \times f$. However, to save computing time the number of seeds dispersed from a given cell is $N_a \times f \times P_{est1}$, where P_{est1} is the maximum probability of establishment. This means that conceptually the model disperses established seedlings. These "established seeds" are dispersed following a two-parameter dispersal kernel that simulates both short- and long-distance dispersal. Long-distance dispersal occurs with a probability of P_{LDD}, with distances to the recipient cells uniformly drawn from 20 m to a user-defined maximum distance ($D_{\max}$). Short-distance dispersal occurs with probability ($1–P_{LDD}$), with distances uniformly drawn between 0 and 20 m. We favoured the simple kernel as it allows more transparency in the dispersal distances than more complex dispersal kernels. For simplicity, we did not include a seed-bank in our model. Seeds dispersed out of the grid extent are also discarded (i.e. the spatial model has absorbing boundaries). We did not consider natural tree mortality because the scenarios and model behaviour considered here operate within the typical lifespan of individual trees (i.e. 60 years). After reaching a cell with density N_t, a seedling has an additional probability P_{est2} of establishing if the local number of trees N_t is lower than the carrying capacity K, or is discarded from the model if N_t is equal to K.

To account for spatial heterogeneity in habitat quality, cells are characterized by a binary variable defining them as "good" or "bad" habitat. We

Table 1 Model parameters and their values

Name	Description	Values
Common parameters		
K	Carrying capacity of a cell	5, 20
f	Fecundity, seeds per adult*	500, 5,000 [50, 500]
A_{rep}	Age of first reproduction	10, 20
P_{LDD}	Probability of long distance dispersal	0.05
D_{max}	Maximum dispersal distance, m	100, 1,000
P_{est1}	Maximum establishment rate	0.01, 0.1
P_{est2}	Local establishment rate*	1 [0.1]
s_{seedl}	Seedling survival rate*	0.7, 0.9 [0.07, 0.09]
T_{init}	time before management starts, years	4
H_{target}	Process affected by habitat	Recruitment, fecundity, survival
Region		
E_t	Total effort	0, 80, 800
H_r	Proportion of good habitat in the grid	0.15, 0.25, 0.8
U_f	Interval between effort allocation updates	5, 20
Management unit		
N_s	Number of initial sources	0,1,2
N_{cp}	Number of stands cleared every year	0–800
H_l	Amount of good habitat in a unit, cells	0–10,100

Parameters are grouped according to the level at which they operate, with common parameters operating at both levels. Parameters marked with a star can be affected by habitat and take then the values shown in brackets in bad habitat

generated three maps of habitat using the midpoint displacement algorithm (Jackson and Fahrig 2012), with proportion of good habitat H_c taking three values (0.15, 0.25 and 0.8) and spatial autocorrelation fixed to 0.5 (e.g. Fig. 2). We use the habitat variable to modify local establishment (defining $P_{est2} = 1$ in good habitat, $P_{est2} = 0.1$ in bad habitat), fecundity (trees growing in bad habitat reproduce with fecundity $f/10$), or survival of seedlings (annual survival of trees younger than 5 years old is s_{seedl} in good habitat and $s_{seedl}/10$ in bad habitat). Whether habitat affects fecundity, establishment or survival of seedlings is indicated by the values of the variable H_{target}, "habitat target".

Spatial management around a source

When management applies around a given source, a number N_{cp} of stands are cleared every year, with all individuals in targeted cells killed. The way these stands are chosen defines the *selection strategy*, which can be (1) targeting stands with the highest tree density, (2) targeting stands that are at the largest distance from the source stand (periphery), or (3) targeting stands with good habitat only. Hereafter these are referred to as "density", "distance" and "habitat" selection strategies, respectively. The N_{cp} stands are then chosen randomly from the set of stands of equally high priority. The selection strategies reflect different assumptions about the processes driving tree invasions: the importance of peripheral sites ("distance" strategy) (Moody and Mack 1988), propagule pressure ("density" strategy) (Maxwell et al. 2009), and role of habitat ("habitat" strategy). The initial source of the invasion is never cleared, to better simulate spread from, for example, a plantation maintained for economic reasons (Caplat et al. 2012a, b).

Effort allocation

We determined how effort (e.g. budget or work force) should be allocated among multiple management units, by including 16 spatial management units within the spatial models (Fig. 2). The number of stands cleared of invaded trees per unit (N_{cp}) is a proportion of the total management effort (Et). We defined three *effort allocation strategies* for allocating effort between units: (1) evenly ("equal" strategy), where each unit gets an equal share; (2) by habitat ("habitat" strategy), where the share is scaled by the amount of suitable habitat in each management unit;

(3) by extent of the invasion (the number of invaded cells in each management unit; "extent" strategy). Effort allocation is updated every U_f (Table 1) years to account for newly invaded areas.

Simulations

To test the model behaviour we first ran a preliminary sensitivity analysis drawing the model's parameters randomly from a wide range of values across 2,000 simulations.

We then used the model to test both the effect of selection strategies (random, periphery or habitat) and the effect of allocation strategies on the area invaded after 60 years. Model parameters were drawn from a wide ranges of values (Table 1) all combined once, producing 2,880 unique settings. Each parameter setting was used to run simulations in turn, first without management and then with each of the nine strategies to be tested, combining an allocation strategy with a selection strategy. In each run the selection strategy was applied across all management units. Simulations ran for 60 iterations (years).

We assessed tree invasion spread rate by measuring the area invaded at the end of a simulation (I, expressed in percentage), at the regional level and within each management unit. For each setting, we measured the effectiveness of every strategy by comparing the final area invaded resulting from applying the strategy to the final area invaded obtained in the absence of management (I_0 thereafter).

Analysis of model outputs

We performed the same sequence of analyses for the two levels considered, using the model parameters to explain the effect of: (1) habitat, life-history traits and effort allocation strategy at the regional level ($n = 2{,}880$); (2) habitat, life-history traits and selection strategy within each management unit ($n = 13{,}119$) (Table 1). To simplify the results, we used when possible the percentage invaded in absence of management (I_0) as a predictor of management actions. I_0 can be seen as the ensemble of life-history traits and habitat conditions favouring invasion.

1. We tested the importance of the parameters on the final area invaded in the absence of management (I_0), using random forest models from the package "party" in R (R Development Core Team 2008). Random forests build a large number of classification trees (or regression trees for continuous response variables), and identify the global effect of predictors by assessing the effect of changing the values of the nodes (Breiman 2001). They have been shown to be extremely accurate across datasets (Caruana et al. 2008), and particularly adapted for comparison of continuous and categorical variables (Strobl et al. 2007). We defined variable importance using the "mean decrease in accuracy", which measures how much accuracy decreases when the values of a given variable are randomly permutated (Breiman 2001; Strobl et al. 2007).
2. We identified the combinations of parameter settings driving the overall effect of management on final area invaded (expressed in % of I_0), using random forest models. We excluded for the rest of the analysis the settings in which management effect was lower than 10 % of I_0.
3. To understand which strategies perform best under different settings, we ranked the strategies for each setting by the final invaded area they produced (from smallest to largest). We considered that two strategies performed equally if their final invaded area differed by less than 10 %. The relative performance of strategies allowed us to define conditions in which a strategy ranked first, alone or in a tie.

We identified the conditions leading to different performance of strategies using Conditional Inference Trees (CIT), with the "party" package in R. Like traditional classification trees, CIT recursively perform splits of a response variable (here, "strategy X is best") based on values of covariates (here, the model parameters) (Hothorn et al. 2006). CIT use permutation tests to evaluate the significance of covariates and the associated splits (tree branches). In a predictive framework, it is recommended to use ensemble modelling (e.g., random forests) rather than a single tree (e.g., CIT). However our analysis aimed to explain the system and we decided that communication of guidelines regarding management would benefit from clear decision rules provided by the individual trees of CIT (see Morelli et al. 2012 for a similar approach).

4. To formulate management recommendations, we rebuilt CITs excluding I_0 from the set of

predictors. We synthesized our results along a simple scenario based on: (a) whether or not the managers know about habitat suitability of the area (e.g., feasibility of the 'habitat' selection and allocation strategies), and (b) whether or not remote trees can be easily located and accessed (e.g., feasibility of the 'distance' selection strategy). When habitat suitability was not known, we excluded the three habitat parameters from the set of predictors.

Results

Response of spread to the model parameters

In the absence of management, the model showed a clear effect of the model parameters on spread. The sensitivity analysis revealed no inconsistency in the model's behaviour.

With the set of parameters used for the rest of our analyses (Table 1), final invaded area in all simulations ranged from 0.02 % of the grid to 100 % of the grid. The random forest models (Fig. 3) developed at the two management levels ranked maximum dispersal distance ($D_{\max}$) first, followed by seedling survival in good habitat (s_{seedl}), fecundity (f), maximum probability of establishment (P_{est1}), and the stage affected by habitat (H_{target}). The amount of good habitat (H_l or H_r) was found to play a role at the management unit level (Fig. 3, left), but not at the regional level (Fig. 3, right). The age of first reproduction (A_{rep}) and patch carrying capacity (K) ranked low at both levels, and the initial number of sources (N_s) ranked last at the management unit level. Final invaded area was lowest with short dispersal distances, low probability of establishment, survival, and fecundity, habitat affecting recruitment, low carrying capacity, and high age of reproduction.

Overall effectiveness of management

At both the regional and management unit levels, the effect of management (all strategies considered) varied greatly (from 0 to 100 % reduction of final area invaded). Management was defined as ineffective (i.e. lower than 10 % of I_0) in 63 and 50 % of the settings at the management unit and regional level.

The variables driving management effectiveness in the model are shown in Fig. 4. The ranking of variables shows that management effectiveness responded more to spread in the absence of invasion (I_0) and effort (number of patches cleared) than to any other variables. In addition to these variables,

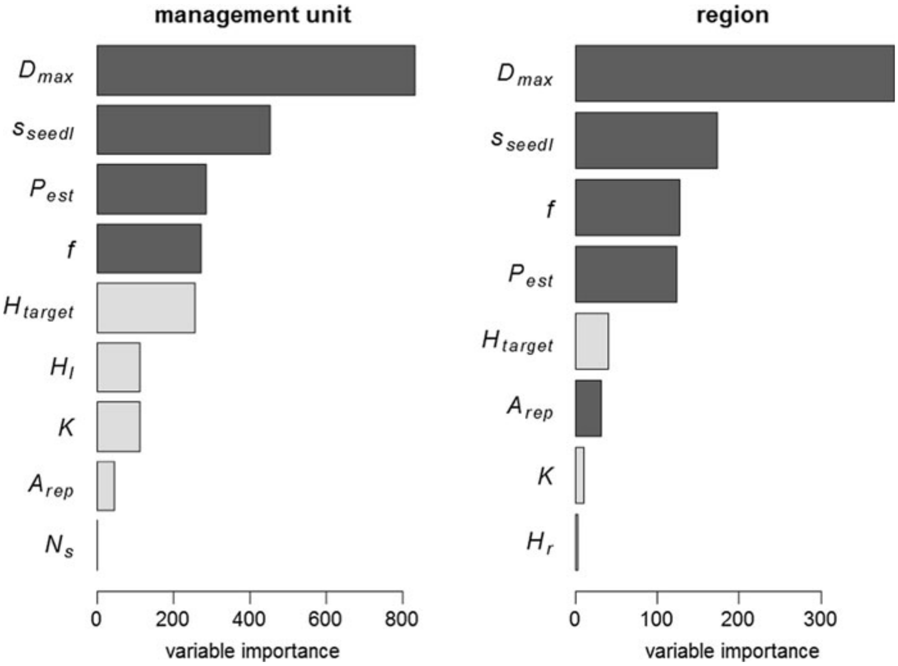


Fig. 3 Relative importance of model parameters for the final area invaded at two scales, from the random forest models (500 trees, 576 observations at the regional level, 9,216 observations at the management unit level). The importance was measured as an increase in node purity in every tree. *Light grey* columns correspond to habitat parameters and *dark grey* to life-history traits

maximum dispersal distance ($D_{\max}$) played an important role at the regional level (Fig. 4, right) but not at the management unit level (Fig. 4, left). Management strategies (*selection* and *allocation*) and effort allocation update frequency U_f were all ranked low in the model. The models developed at the regional and management unit level had a prediction accuracy of 0.8 and 0.9, respectively. The spread values at which management became ineffective varied with effort (83 % of the area invaded with $E_t = 800$; 24 % of the area with $E_t = 80$).

Selection strategy within management units

At the management unit level the three selection strategies performed equally in 92 % of the settings for which management was effective. A CIT run on all settings linked equal performance to conditions favouring low spread ($I_0 \leq 17$ and $N_{cp} \leq 3$, or $I_0 > 17$ and $N_{cp} \leq 80$). When conditions favoured higher spread (remaining 8 % of the settings), the "distance" selection strategy outperformed the other strategies in 98 % of settings, and the CIT could not find any subset of parameters where another selection strategy dominated.

Comparing only the 'habitat' and 'density' strategies revealed that selecting by habitat performed overall better than selecting by density of trees, although the two strategies performed equally in 92 % of the settings. The 'density' strategy outperformed the 'habitat' strategy in only 1 % of the settings, mostly when habitat affected establishment, dispersal distances were high and either the number of dispersed seedlings ($f \times P_{est1}$) was high or good habitat was rare (Fig. 5).

Allocation strategy at the regional level

The three allocation strategies performed equally in 75 % of the settings where an effect of management was observed. As at the management unit level, the three strategies performed equally when conditions were particularly unfavourable to spread ($I_0 < 3$ or $I_0 > 3$) and $H_r = 0.15$).

Amongst the settings where a difference between strategies was observed, distributing effort equally amongst management units ranked first more often than the two other strategies (70 % of settings, against 33 % for the 'habitat' strategy and 58 % for the 'extent' strategy). It is worth noting that the 'equal' strategy, however, rarely outperformed both strategies

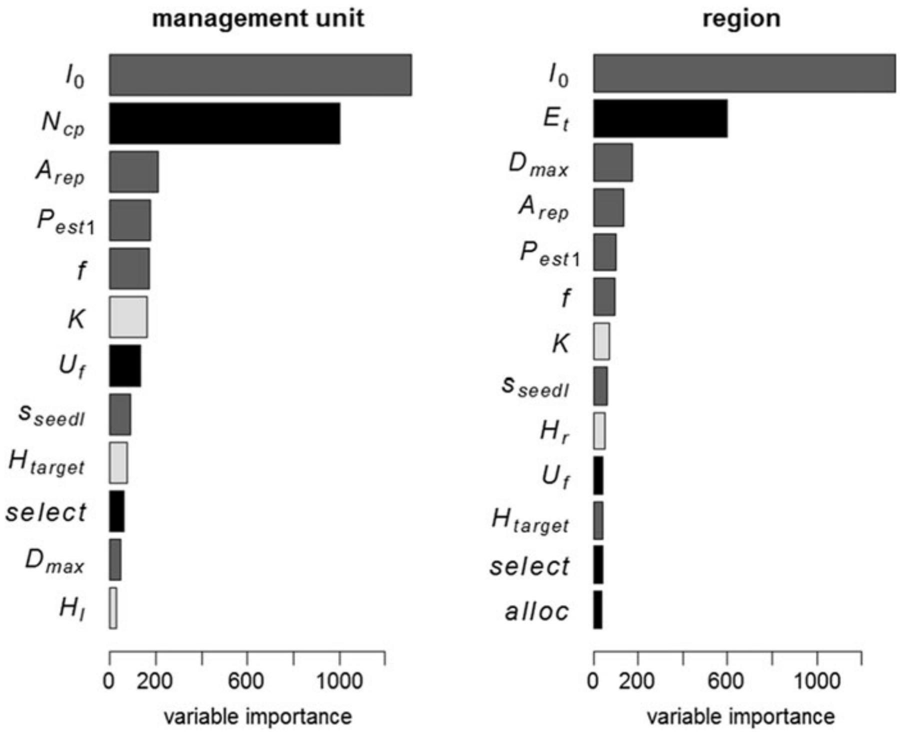


Fig. 4 Relative importance of model parameters for the reduction of final area invaded when management is applied at two scales, from the random forest models (500 trees, 13,284 observations at the regional level, 94,608 observations at the management unit level). The importance was measured as an increase in node purity in every tree. *Light grey* columns correspond to habitat parameters, *black* to management parameters, and *dark grey* to life-history traits. I_0 is the final area invaded in absence of management

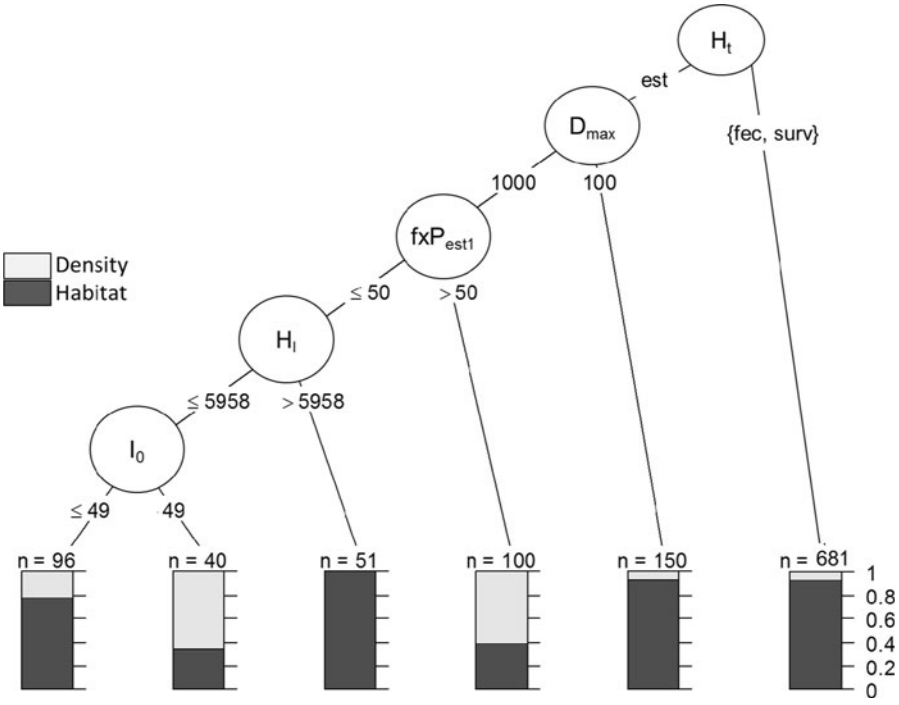


Fig. 5 Relative performance of the 'habitat' and 'density' selection strategies under different parameter combinations. This tree is part of conditional inference tree that was built on a subset of 1,120 parameter combinations in which the two management strategies did not perform equally. *Labels* in *circles* indicate the variables described in Table 1. The number 'n' indicates the size of each terminal node. I_0 is the final area invaded in absence of management. This tree had a predictive accuracy of 0.87

(e.g. it performed the same as either the 'habitat' or the 'extent' strategy in 83 % of settings.).

The 'habitat' and 'equal' strategy performed equally in 82 % of the settings. The 'habitat' strategy performed better than the 'equal' strategy in only 5 % of the settings. This occurred mostly when good habitat was abundant ($H_r = 0.8$), reproductive output was low (f * $P_{est1} \leq 50$) and spread was high ($I_0 > 15$) (Fig. 6).

The 'extent' and 'equal' strategies performed equally well in 88 % of the settings. Allocating effort by extent of invasion performed better than an equal allocation in only 5 % of the settings. This occurred mostly when: 1) reproductive output was low (f * $P_{est1} \leq 50$), spread was high ($I_0 > 50$); 2) effort was high ($E_t = 800$) and either carrying capacity was high ($K = 20$) or extent was updated every 5 years ($U_f = 5$); 3) good habitat was rare and habitat affected establishment (Fig. 7).

Management scenarios

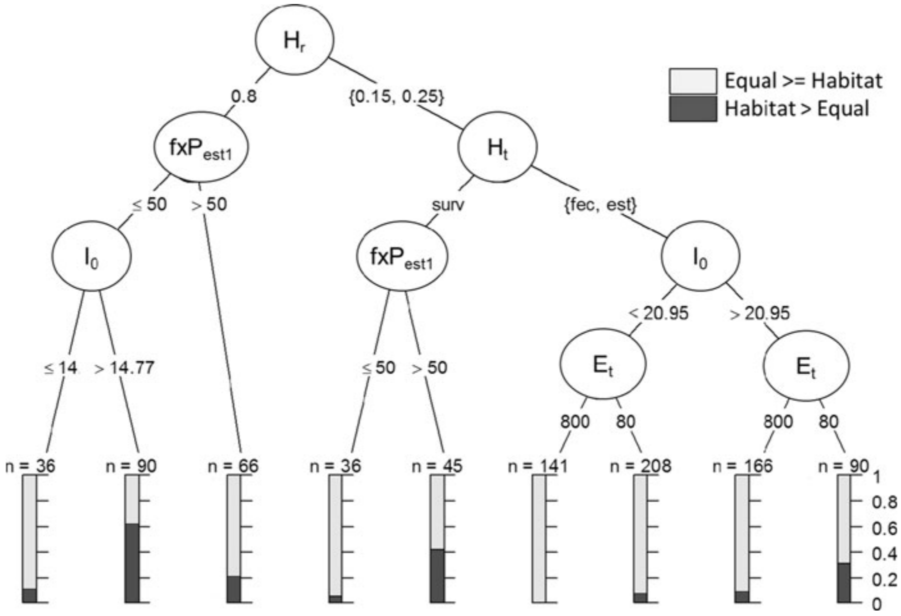
In all subsets considered, regardless of information regarding habitat, allocating effort equally to the different management units largely outperformed the other strategies (Table 2). No clear combination of parameters could be identified that led the 'habitat' or 'extent' strategies to perform better than the 'equal' strategy.

To identify the best selection strategy when remote trees cannot easily be accessed, we considered only the relative performance of the 'habitat' and 'density' strategies. The two strategies performed equally in 93 % of settings; the 'habitat' strategy outperformed the 'density' strategy in an additional 6 % of settings, leading the 'density' strategy to be selected only when no other strategy was available.

Discussion

Our results demonstrate that the effectiveness of different management practices for slowing the spread of tree invasions depends strongly on both habitat heterogeneity and tree demography. These results were robust across a wide range of parameter values in the spatial simulation model (Table 1). Similarly, the parameters driving spread in our model including seed dispersal ($D_{\max}$), recruitment rates (S_{seedl}), and fecundity (*f*) were identified as important at both scales, and agree with previous modelling studies (e.g. Coutts et al. 2011). Thus, our spatial simulation model

Fig. 6 Conditions leading to the ‘habitat’ allocation strategy outperforming the ‘equal’ allocation strategy. This conditional inference tree was built on a subset of 878 parameter combinations in which the three allocation strategies did not perform equally. *Labels* in *circles* indicate the variables described in Table 1. The number ‘n’ indicates the size of each terminal node. I_0 is the final area invaded in absence of management. This tree had a predictive accuracy of 0.85



produced a consistent, robust description of the dynamic behaviour of tree invasions. It is worth noting that, due to our choice of modelling the dispersal of “established seedlings”, fecundity and establishment had similar ranking in the spread analysis. An interesting result was the low ranking of the variable that quantified the amount of habitat at the regional level, while habitat was ranked higher at the landscape level. This suggests that habitat suitability plays a key role in the early stages of invasion, even when habitat differences are not extreme, but does not affect large scale dynamics as much as life-history traits.

Management strategies to slow the spread of tree invasions included effort allocation and the spatial selection of stands; these multi-scale strategies are both practical and in line with the dominant theory for reducing the spread of biological invaders (e.g. Moody and Mack 1988; Higgins et al. 2000). However, in most of the simulations no differences were observed among management strategies, particularly when management effort was high enough to strongly reduce the final area invaded. Indeed, the analysis of the importance of different variables with random forests revealed that management effort (i.e. the number of stands cleared of invaders per year) was more important than management strategy (i.e. spatial selection of stands) in reducing the spread (Fig. 4). This result is driven by the complexity of managing multiple source populations; because the conditions of spread vary across space, it is unlikely that a single management strategy would fit all conditions. When strategies did differ in efficiency, their ranking depended on tree life-history and the response of tree to habitat (Figs. 5, 6).

Single-source management

During tree invasions of landscapes, populations may begin as single or discrete sources, but as the invasion progresses to second and higher generations, multiple seed sources are the norm (e.g. Moody and Mack 1988). Multiple seed sources favour a management strategy that targets peripheral sites (i.e. the “distance” strategy). Indeed, the management strategy of targeting peripheral tree populations first largely outperformed the habitat quality or tree density strategies. This is because targeting peripheral sites has the effect of minimising spread from the source population. In practical terms, this implies that the location of source populations is known, and that peripheral sites can be identified and are accessible for treatment. We expect that making accessibility of sites explicit in the model might change the ranking of the strategies. However, some test simulations including increasing cost with increased distance travelled did not change the relative efficiency of the periphery selection strategy (data not shown). Our results are

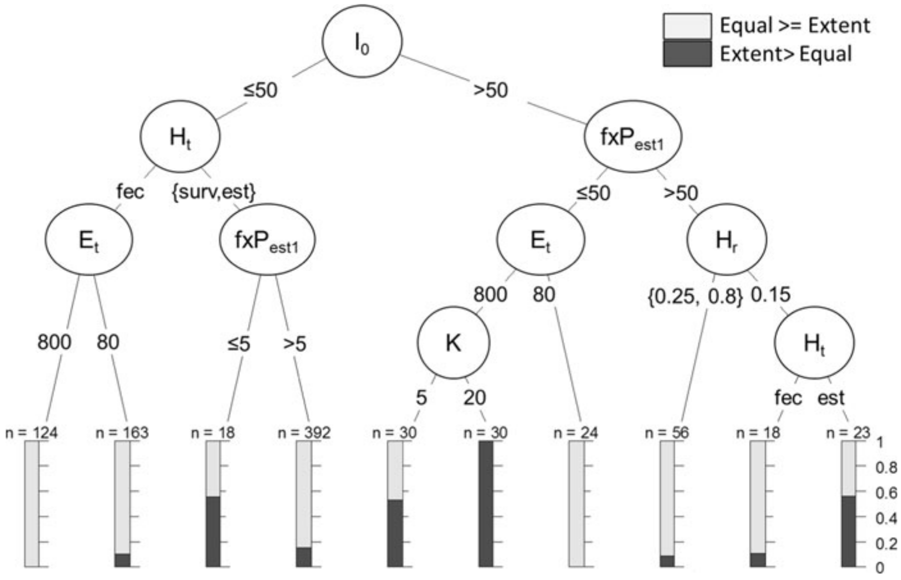


Fig. 7 Conditions leading to the 'extent' allocation strategy outperforming the 'equal' allocation strategy. This conditional inference tree was built on a subset of 878 parameter combinations in which the three allocation strategies did not perform equally. *Labels* in *circles* indicate the variables described in Table 1. The number 'n' indicates the size of each terminal node. I_0 is the final area invaded in absence of management. This tree had a predictive accuracy of 0.87

Table 2 Synthesis of which allocation and stand selection strategies should be chosen depending on available options (information on habitat suitability top; feasibility of the distance strategy, bottom)

Habitat suitability is known	Yes		No	
Allocation of effort	Equal (91 %)	Equal (94 %)	Equal (96 %)	Equal (95 %)
Selection of stands by	Habitat (99 %)	Distance (99.7 %)		Density (na)
Remote individuals can be accessed	No	Yes		No

Percentages in brackets represent the frequency at which a given strategy ranked first in our analysis

consistent with previous studies suggesting that a strategy of containment can be most appropriate for slowing the spread of biological invaders having known source population (e.g. Epanchin-Niell and Wilen 2012).

The relative performance of the 'habitat' and 'density' management strategies emphasized some stages of the spread dynamics. Selecting by habitat performed better when habitat affected survival or fecundity. This highlights the fact that, when habitat affects establishment, any tree detected has passed the establishment hurdle, and is likely to perform the same, regardless of the habitat type. On the other hand, when habitat affects survival or fecundity, trees located in good habitat will contribute relatively more to the spread, and are thus a good target for management. However, selecting by habitat still outperformed selecting by density in most cases, probably because habitat was spatially autocorrelated by design. A tree established in good habitat was likely to disperse offspring into good habitat. This was less true when spread was high, or habitat was rare (less than 50 % of a management unit), leading to the 'density' strategy to perform relatively better.

Multi-source management

When dealing with multiple source populations of invasion, the allocation strategy was not important in 90 % of the settings. Although the equal allocation performed well in most of the remaining settings, it can be seen as a "default" strategy (i.e. no choice is made to allocate the budget based on any particular criteria), which translates into a very consistent frequency of good performance across subsets of settings (Fig. 6). The fact that the 'equal' strategy rarely outperformed both other strategies confirms the idea that it is a generalist strategy, which can be outperformed in specific conditions but overall outcompetes more sophisticated schemes (see also Hui et al. 2011a for a similar result).

Allocating management effort equally among units was less effective than the other strategies in settings having low reproductive output and high spread. With low reproductive output, spread was sufficiently slow to be affected by management, leading to all strategies performing similarly. However, in the settings favouring faster spread (e.g., no dispersal limitation) other management units were invaded. Spatial heterogeneity in either habitat (high habitat cover combined with high autocorrelation) or extent of invasion (combined with frequent updates on invasion extent) would select for the 'habitat' or 'extent' allocation strategy, respectively. With an equal distribution of effort on the other hand, some of the effort would be wasted on management units with little population growth. And because large, fast growing populations are also often located in suitable habitat, the 'habitat' and 'extent' strategies often performed equally.

Management implications

An unresolved problem in managing invasive trees is the relative effort that should be allocated to the detection of new populations versus controlling known populations given resource constraints or limitations on these activities (e.g. Maxwell et al. 2009; Epanchin-Niell and Hastings 2010; Giljohann et al. 2011). Here we focussed on disentangling the biological effects of different management strategies across spatial scales, and did not explicitly model detection effort, cost, or effectiveness. Rather, we assumed that surveillance and control were closely coupled, for example, the effectiveness of the "distance" selection strategy in our model relies on the immediate cost efficient detection of satellite trees. This assumption will likely hold for systems in which detection of new invasive populations is relatively easy, i.e. for tree invasions into grasslands (e.g. Ledgard 2001). In contrast, for systems in which the detection of new invading populations is non-trivial, decoupling the costs and efforts required for surveillance and control would be a logical next step. Management of biological invaders is often accomplished by multiple agencies, or more generally, 'actors'. Here we made the simplifying assumption in our simulation models that management activities were universal and unitary. However, managers may not collaborate fully, may utilise different approaches or techniques for management, or may have conflicting goals for management of invasions that introduce complexity or conflicts in management by multiple actors (e.g. Epanchin-Niell et al. 2010, Dickie et al. this issue, also reviewed in Caplat et al. 2012a). The beneficial or detrimental effect of having different management units implementing different strategies was beyond the scope of this paper, but could be incorporated into our spatial simulation model (Coutts et al. 2012).

Although inclusion of detection or multiple management approaches could be useful refinements or extensions to this modelling approach, this does not undermine our major finding that no single management approach is optimal across spatial scales. This result is consistent with Maxwell et al. (2009), indicating that there may be long-term improvement of managing an invader by replacing some management with specific observations to identify source trees or populations. Rew et al. (2007) also suggested the surveys to discern the habitat constraints of the invader is a valuable first step toward prioritizing populations to manage. Clearly, early detection followed by an intense management response will be most effective, provided that detection is good for trees in the seedling and pre-reproductive stages. However, effort is often limited, and prioritization strategies are generally an appropriate and practical means to improve the efficiency of management.

Our results demonstrate that successful landscape-scale management of tree invasions depends on the spatial arrangement of populations relative to good habitat. Several clear management principles or recommendations emerged from our analyses. First, the best strategy to control tree invasions is to manage sites most distant from the source (Table 2). If distant trees cannot be accessed, then one should select stands by habitat suitability. Second, to control tree spread over a region having multiple source populations, effort can be allocated equally to all management units where trees are detected, with two exceptions: (1) where habitat is highly heterogeneous between units, matching management resources to habitat quality can prevent future spread, and (2) for relatively rapid invasions, resources should be allocated to areas with the largest populations—if estimates of population size can be updated regularly. Overall, these findings demonstrate that knowledge of *how* habitat affects tree life-history stages help improve control when effort is limited. This confirms the interest in developing cost-and time-efficient methods to measure life-history traits, and to create maps of habitat suitability for invasive trees.

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