



# Hotspots of plant invasion predicted by propagule pressure and ecosystem characteristics

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## ABSTRACT

**Aim** Biological invasions pose a major conservation threat and are occurring at an unprecedented rate. Disproportionate levels of invasion across the landscape indicate that propagule pressure and ecosystem characteristics can mediate invasion success. However, most invasion predictions relate to species' characteristics (invasiveness) and habitat requirements. Given myriad invaders and the inability to generalize from single-species studies, more general predictions about invasion are required. We present a simple new method for characterizing and predicting landscape susceptibility to invasion that is not species-specific.

**Location** Corangamite catchment (13,340 km<sup>2</sup>), south-east Australia.

**Methods** Using spatially referenced data on the locations of non-native plant species, we modelled their expected proportional cover as a function of a site's environmental conditions and geographic location. Models were built as boosted regression trees (BRTs).

**Results** On average, the BRTs explained 38% of variation in occupancy and abundance of all exotic species and exotic forbs. Variables indicating propagule pressure, human impacts, abiotic and community characteristics were rated as the top four most influential variables in each model. Presumably reflecting higher propagule pressure and resource availability, invasion was highest near edges of vegetation fragments and areas of human activity. Sites with high vegetation cover had higher probability of occupancy but lower proportional cover of invaders, the latter trend suggesting a form of biotic resistance. Invasion patterns varied little in time despite the data spanning 34 years.

**Main conclusions** To our knowledge, this is the first multispecies model based on occupancy and abundance data used to predict invasion risk at the landscape scale. Our approach is flexible and can be applied in different biomes, at multiple scales and for different taxonomic groups. Quantifying general patterns and processes of plant invasion will increase understanding of invasion and community ecology. Predicting invasion risk enables spatial prioritization of weed surveillance and control.

## Keywords

Alien weed management, boosted regression tree, community assembly, generality, habitat suitability models, invasive species risk.

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## INTRODUCTION

Invading species can alter the structure and function of ecosystems and are a major threat to biodiversity (Pyšek & Richardson, 2010). Over 28,000 plant species are currently

considered to be weeds world-wide (Randall & Thomas, 2007). In North America, 1481 plant species are listed as being invasive [Center for Invasive Species and Ecosystem Health (CISEH, 2009)], and this number will increase in time (Lockwood *et al.*, 2005; Hellmann *et al.*, 2008). In a global

assessment of invasive woody plants, Richardson & Rejmánek (2011) consider 622 species to be 'invasive' sensu Pyšek *et al.* (2004). Weed risk assessment, biosecurity and quarantine procedures traditionally focus on individual species that pose an invasion threat (Pheloung *et al.*, 1999). A species-based approach has also been dominant in predictions of weed spread and areas vulnerable to future invasion (e.g. Crossman & Bass, 2008; Keller *et al.*, 2008; Ibáñez *et al.*, 2009; Jacobs & MacIsaac, 2009), which may reflect the single-species approach of habitat suitability modelling more generally (Hirzel & Lay, 2008). Notwithstanding recent evidence suggesting a link between plant invasiveness and performance-related traits (van Kleunen *et al.*, 2010), species that are invasive in one ecosystem will not necessarily be invasive elsewhere (Moles *et al.*, 2008). Given the vast number of invaders and problems inherent in generalizing from single-species studies, more general predictions that focus on landscape susceptibility to invasion are required.

Theory indicates that plant invasion is a function of propagule pressure, the abiotic characteristics of a site and the biological characteristics of invaders and recipient community (Richardson & Pyšek, 2006; Catford *et al.*, 2009). Although the influence of propagule pressure and environmental conditions are well recognized in invasion ecology (Catford *et al.*, 2009), using the two to jointly predict areas vulnerable to invasion is rare (Eschtruth & Battles, 2009): most invasion predictions focus on species' characteristics (invasiveness) and habitat requirements (though, there are exceptions, e.g. Thuiller *et al.*, 2006; Chytrý *et al.*, 2009). However, plant invasion across the landscape is far from homogenous: some habitats are more invaded than others (Chytrý *et al.*, 2008a,b). If the level of invasion across a landscape correlates with geographic and ecological attributes, this would suggest that propagule pressure and ecosystem characteristics mediate invasion success. Rather than predicting areas at risk of invasion by individual species, we envisage a more general approach where patterns of invasion (by multiple species) may be used to infer key drivers of, and map landscape susceptibility to, invasion. Because they are not species-specific, such predictions also indicate areas at risk of future invasion by new species that are functionally similar to previous invaders. Given the threat posed by increasing numbers of invaders, such a general approach to predicting invasion risk may be an extremely valuable tool for ecologists, land managers and regulators.

The primary aim of this study is to develop a method for characterizing invasion risk at the landscape scale that is not species-specific. In a case study region, we use surrogates of propagule pressure and environmental conditions to predict areas vulnerable to invasion by exotic species. Unlike previous studies (Chytrý *et al.*, 2008a, 2009), we do not use habitat types as predictor variables in our models but rather select (mostly continuous) variables that could have a more direct effect on the process of invasion. We test our approach by modelling relationships between four response variables (occupancy and cover abundance of all exotic plant species and exotic forbs) and 18 predictor variables using boosted regression trees

(BRT) (Elith *et al.*, 2008). Our study provides (i) a quantitative analysis of environmental predictors that explain patterns of exotic plant invasion, thus offering insights into and evidence about ecological processes that mediate invasion, and (ii) a template method for mapping landscape susceptibility to invasion as a basis for weed risk assessment and surveillance.

## METHODS

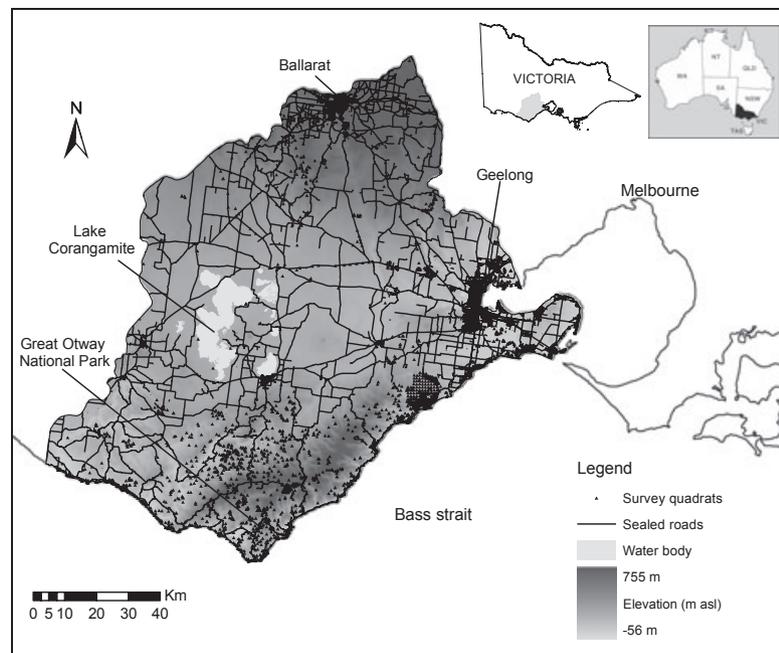
### Study region

Our study centred on the Corangamite catchment in Victoria, Australia, which extends from 37°26' S to 38°51' S and 142°47' E to 144°43' E. The Corangamite catchment covers 13,340 km<sup>2</sup> and encompasses a wide range of environmental conditions and anthropogenic influences, including the Great Otway National Park (NP) and the cities of Geelong and Ballarat (Fig. 1). Geelong was established in 1836 and Ballarat in 1838 (Billot, 1969), and the majority of the 350,000 people in the region reside in these two cities. The region has a temperate climate with the majority of annual rainfall (mean varied between 550 and 900 mm across the region) occurring in the cooler winter months [Bureau of Meteorology (BOM, 2007)]. There are 17 types of vegetation communities in the region, but most of the remnant vegetation persists in dry, wet and lowland forests [Department of Sustainability and Environment (DSE, 2009)]. Descriptive statistics of the environmental characteristics of the region are in Table S1.

### Plant occupancy and cover abundance data

Plant occupancy (i.e. presence/absence) and cover abundance data were obtained from 3118 quadrats surveyed in the Corangamite catchment by the Victorian DSE between 1972 and 2006. Foliar projective cover of plant taxa found in 30-m<sup>2</sup> quadrats was estimated with the Braun-Blanquet scale (Kent & Coker, 1992). Prior to statistical analysis, the Braun-Blanquet scale values were converted to mid-point averages (+: 0.5%, 1: 2.5%, 2: 15.5%, 3: 38%, 4: 63%, 5: 87.5%). Taxa were identified in accordance with *A Census of the Vascular Plants of Victoria* (Ross & Walsh, 2007). The geographic coordinates of the central point of the quadrats were recorded in the field using a map (before 1993; ±100 m accuracy) and Geographic Positioning System (1993 onwards; ±7 m accuracy).

We extracted data about occupancy and cover abundance of all exotic species (i.e. all species non-native to Australia) and exotic forbs. Forbs were the most abundant and frequently occurring exotic growth form in the region, and exotic forb species constitute the majority of the noxious weeds listed for the Corangamite catchment and the state of Victoria (DSE, 2008). Cover of all exotic species was analyzed as a proportion of total vegetation cover in each quadrat, and exotic forb cover as a proportion of forb cover. Proportional abundance of exotic taxa indicates the relative contribution that they make to the local plant community (one structural component in the case of forbs), disentangling the measure of exotic plant cover



**Figure 1** Map of the Corangamite catchment study region in Victoria, Australia, showing the two large regional cities (Ballarat and Geelong), the Great Otway National Park and the location of the 3118 survey quadrats.

from measures of total vegetation cover. Of the 3118 quadrats surveyed, exotic species were present in 1521 quadrats and exotic forbs in 1266 quadrats. Throughout the paper, we use ‘all exotic species’ occupancy/abundance’ and ‘exotic forbs’ occupancy/abundance’ when referring to the four response variables; when discussing occupancy/abundance of all exotic species and exotic forbs together, we use the terms ‘exotic taxa’ or ‘exotic plants’. Reference to ‘exotic plant invasion’ is a general, catch-all term that includes the occupancy and abundance of exotic plant taxa.

### Environmental predictors

We compiled a broad range of variables as potential surrogates for propagule pressure, and abiotic and biotic conditions (Catford *et al.*, 2009) that are likely to influence landscape susceptibility to invasion (Table S1). Data were sourced from Geoscience Australia and the Victorian Departments of Sustainability and Environment and Primary Industries. From these raw data, 90 variables were generated using ARCGIS 9.3 (Esri Inc.) (e.g. building density, distance to nearest water course). To avoid problems associated with data dredging and over-fitting (Chatfield, 1995; Wintle *et al.*, 2005), we used correlation analysis and expert opinion to reduce the number of predictor variables from 90 to 17 for the all exotic models and 18 for the exotic forb models (forb models included total forb cover as a predictor; Tables 1 and S1). Correlation analysis removed cases of extreme multicollinearity by excluding variables that had a Pearson correlation coefficient  $\geq 0.8$  [variables deemed most proximal (*sensu* Austin, 2002) to processes of invasion were retained, e.g. minimum temperature

in coldest period instead of altitude]. Expert opinion reduced the total number of candidate predictor variables further. Our choice was informed by invasion theory and previous studies, and the extent to which the variables encompassed variation in other factors.

By quantifying interactions among predictor variables, our modelling approach (see below) enabled more complex (i.e. interacting) relationships to be detected between predictor and response variables. For instance, resource availability – a key driver of invasion (Davis *et al.*, 2000) – was represented by interactions among disturbance, resource levels and vegetation cover (Huston, 2004).

We did not use vegetation classification (habitat) type in the models because we aimed to increase understanding of the process of invasion, as well as indicate areas susceptible to invasion. Habitat type is a useful predictor in that it integrates factors like climate, geography and propagule pressure (Chytrý *et al.*, 2009). However, to increase understanding of the factors that drive invasion, it is important to use variables that can directly affect plant invasion; we therefore used the most proximal predictor variables available (i.e. variables based on environmental characteristics and propagule pressure). Further, habitat types can lack generality because they are specific to an area (as are many classification schemes), and high-resolution habitat data were only available for 33% of the region.

### Survey gap analysis

Using the multivariate environmental similarity surface (MESS) algorithm in MAXENT (Version 3.3.3a: Phillips *et al.*,

**Table 1** Model performance and relative influence of variables on the occupancy and cover abundance of all exotic species and exotic forbs.

Variable	All exotic occupancy <sup>tc4</sup>	All exotic proportional cover <sup>tc5</sup>	Exotic forb occupancy <sup>tc4</sup>	Exotic forb proportional cover <sup>tc4</sup>
<b>Model performance</b>				
Deviance explained (%)	34.3	39.3	43.5	33.1
CV correlation (SE)	0.64 (0.006)	0.63 (0.015)	0.70 (0.01)	0.59 (0.031)
AUC (SE)	0.87 (0.003)	NA	0.91 (0.005)	NA
<b>Predictor variables*</b>				
1 Forb cover <sup>B</sup>	NA	NA	22.5 (1)	20.8 (1)
2 Distance to edge <sup>PHA</sup>	28.3 (1)	19.1 (1)	19.2 (2)	9.2 (3)
3 Vegetation cover <sup>B</sup>	8.4 (2)	10.0 (2)	3.7 (8)	6.1 (6)
4 Distance to river <sup>PA</sup>	8.2 (3)	5.4 (8)	5.3 (5)	6.1 (5)
5 Thorium inverse-Potassium <sup>A</sup>	7.2 (4)	6.8 (6)	6.2 (4)	5.0 (8)
6 Distance to road <sup>PH</sup>	6.8 (5)	4.7 (11)	4.3 (7)	3.1 (15)
7 Normalised Difference Vegetation Index (NDVI) <sup>B</sup>	6.6 (6)	7.5 (5)	9.3 (3)	5.2 (7)
8 Time since fire <sup>A</sup>	5.2 (7)	6.7 (7)	5.1 (6)	9.2 (2)
9 Radiation (direct) <sup>A</sup>	4.8 (8)	3.7 (13)	3.4 (9)	3.1 (14)
10 Maximum temperature warmest period <sup>A</sup>	3.9 (9)	8.5 (3)	3.4 (10)	4.9 (9)
11 Wetness index <sup>A</sup>	3.7 (10)	7.6 (4)	2.4 (12)	4.4 (10)
12 Summer rainfall <sup>A</sup>	3.7 (11)	2.4 (14)	2.3 (15)	4.1 (11)
13 Building density <sup>PH</sup>	3.5 (12)	5.2 (9)	2.7 (11)	6.3 (4)
14 Relevant land use <sup>PHA</sup>	2.9 (13)	1.4 (16)	2.4 (13)	1.8 (17)
15 Minimum temperature coldest period <sup>A</sup>	2.3 (14)	4.1 (12)	2.3 (16)	2.7 (16)
16 1888 land use <sup>PHA</sup>	2.1 (15)	1.4 (15)	1.9 (17)	3.8 (12)
17 Survey year <sup>P</sup>	1.7 (16)	5.2 (10)	2.4 (14)	3.6 (13)
18 Geology <sup>A</sup>	0.8 (17)	0.1 (17)	1.1 (18)	0.4 (18)

Performance indices: percentage of null deviance explained; cross-validation (CV) correlation between observed and expected values; AUC, area under the receiver operator curve (only applicable to binary dependent variables); SE, standard error; NA, not applicable.

\*Predictor variables' relative influence is given as a percentage and rank (in brackets); variables primarily indicate: <sup>P</sup>propagule pressure, <sup>H</sup>human influence, <sup>A</sup>abiotic conditions, <sup>B</sup>biotic conditions (forb cover only included in Exotic forb models). Abundance models used exotic cover as a proportion of total vegetation cover and exotic forb cover as a proportion of forb cover. Models were developed with 10-fold CV on data from 1521 presence and 1597 absence records of all exotic species, and 1266 presence and 1852 absence records of exotic forbs using learning rates of 0.01, bag fractions of 0.7, and tree complexities (tc) of 4 or 5 as indicated by superscripts. Refer to Table S1 for details about predictor variables.

2006; Elith *et al.*, 2010), we undertook gap analysis to determine how representative the survey data were of the environmental conditions in the study region. We selected 11 variables that would likely encompass environmental heterogeneity and relate to exotic plant occupancy and abundance [aspect, elevation above sea level, topographic wetness index, annual temperature range, maximum temperature in the warmest period, precipitation in the warmest quarter, soil radiometric characteristics (Thorium-inverse Potassium; Table S1), building density, road density, latitude, longitude], and used them to characterize the range of environmental conditions in the region.

### Statistical modelling

We used BRT to model relationships between the occupancy and relative cover abundance of all exotic species and exotic forbs and surrogates of propagule pressure and ecosystem characteristics. BRT is an ensemble method that combines regression analysis and machine learning techniques (Elith *et al.*, 2008). Instead of fitting a single parsimonious model,

BRTs fit a series of models that are then combined through 'boosting'. The use of boosting and sophisticated numerical and graphical presentation of model outputs in BRTs has alleviated the limited accuracy and difficult interpretation associated with traditional regression tree methods (De'ath, 2007; Elith *et al.*, 2008). Further, the ability of BRTs to handle different forms of data, naturally model interactions and nonlinear relationships, and be robust to missing data is useful for predicting exotic invasion (Elith *et al.*, 2008), which is characterized by such complexity (Eschtruth & Battles, 2009). BRTs have been shown to perform well for both explanatory and predictive models (Elith *et al.*, 2006) and are now being applied to a variety of ecological problems (Leathwick *et al.*, 2008; Vesik *et al.*, 2010).

Because many sites that are currently unoccupied by exotic taxa may offer suitable habitat, we used separate models to analyse occupancy and abundance data. This ensured that sites susceptible to high exotic taxa abundance could be identified regardless of whether sites are presently occupied by exotic taxa (and for how long they have been occupied). Using separate occupancy and abundance models overcame the problem

associated with the high number of zeros in the data (i.e. abundance models only used abundance data from occupied sites). Rather than integrative mixture models (Martin *et al.*, 2005), a two-stage modelling process (Potts & Elith, 2006) was selected because (i) results are easier to interpret, (ii) results from both types of models will be of interest as they reflect different stages of invasion and (iii) the models are compatible with available BRT software. The most influential factors are likely to vary depending on stage of invasion (Catford *et al.*, 2009; Dawson *et al.*, 2009), so examining two stages of invasion (i.e. introduction/colonization versus naturalization: Richardson *et al.*, 2000; Catford *et al.*, 2009) can offer greater insight than aggregating them into one.

Boosted regression tree models were run in R (version 2.9.0, R Development Core Team, 2009) using the GBM package (version 1.6-3, Ridgeway, 2007) and additional code provided by Elith and Leathwick (see Elith *et al.*, 2008). Binomial and Gaussian models were fit for occupancy and abundance data respectively. Following inspection of residual plots, cover of all exotic species was normalized using a logit-transformation and exotic forb cover was normalized using a log-transformation. Tailored to maximize model performance (Elith *et al.*, 2008), BRT models were fitted using learning rates of 0.01 and contained up to five-way interactions among the predictor variables. To maximize 'out-of-sample' predictive performance, we used bag fractions of 0.7. The 'bag-fraction' determines the size of the random sample of raw data used to build the model at each iteration of the cross-validation (CV) modelling procedure (Elith *et al.*, 2008). Performance of the models was determined through CV where the model was trained on nine of tenfolds (or subsets) of data and tested on the remaining (independent) fold. This testing occurred ten times, and the average deviance from the ten tests indicated model performance (Vesk *et al.*, 2010).

Observation data were spatially aggregated indicating that spatial autocorrelation in the observation data may exist. Un-modelled spatial autocorrelation in observation data, leading to spatial structure in model residuals, may result in inflated Type 1 error rates, underestimation of model prediction uncertainty and diminished predictive performance (Legendre, 1993; Wintle & Bardos, 2006; Dormann *et al.*, 2007). We interrogated the residuals of each model for spatial autocorrelation using a Moran's *I* correlogram analysis (*sensu* Wintle & Bardos, 2006; Dormann *et al.*, 2007).

We used three metrics to indicate the performance of the BRT models: CV correlation, percentage deviance explained and – for the occupancy models – area under the receiver operating characteristic curve (AUC). The CV correlation measures the correlation between the predicted and raw data that were withheld from the model. Explained deviance indicates the goodness-of-fit and is calculated by predicting to data not used for training the model and comparing between the predicted and raw (observed) values. It is expressed as a percentage of the null deviance for each response variable (Leathwick *et al.*, 2008). AUC scores indicate how well models discriminate between occupied and

unoccupied sites (Elith *et al.*, 2006). This is performed by comparing predicted values to observed ones (Leathwick *et al.*, 2008). Ranging from 0 to 1, an AUC score of 0.5 indicates that predictions are no better than random and 1 indicates perfect discrimination (Swets, 1988). Using a formula described by Friedman (2001), the relative percentage influence of each predictor variable is calculated based on the number of times it is selected for tree splitting, weighted by the variation that each split explains, averaged over all trees.

We used the best BRT models to predict occupancy and cover abundance of all exotic species and exotic forbs throughout the case study region. Predictions were mapped in GIS to provide region-wide maps of invasion risk at 30-m resolution. Predictions of both probability of occupancy and expected proportional cover of all exotic species and exotic forbs were generated. We multiplied predicted percentage cover by the probability of exotic taxa being present to produce single maps of expected cover.

## RESULTS

### General patterns

A total of 1746 species were recorded in the study region, 441 of which were exotic. On average, 25 species (0.25 SE) were in each quadrat, but species numbers ranged between 2 and 105. Vegetation cover was weakly correlated with total species richness ( $r = 0.318$ ,  $P < 0.001$ ), but not with exotic species richness ( $r = -0.079$ ,  $P = 0.002$ ). In the 1521 quadrats in which exotic species were present, the mean exotic species richness was 5 (0.13 SE) and ranged between 1 and 28 species. As a proportion, all exotic species constituted 10% (0.32% SE) of the vegetation cover per quadrat on average, with a range of 0.04–50.0%. Correspondingly, total vegetation cover had a very strong correlation with native cover ( $r = 0.974$ ,  $P < 0.001$ ), but not with exotic cover ( $r = 0.379$ ,  $P < 0.001$ ) or proportional exotic cover ( $r = -0.059$ ,  $P = 0.021$ ). Proportional exotic cover had weak negative relationships with native species cover ( $r = -0.294$ ,  $P < 0.001$ ) and native species richness ( $r = -0.281$ ,  $P < 0.001$ ). However, proportional exotic species richness was not correlated with native cover ( $r = -0.058$ ,  $P < 0.001$ ) or native richness ( $r = -0.019$ ,  $P = 0.455$ ). Exotic forbs made up 52.5% (0.98% SE) of exotic cover and 30% (0.75% SE) of total forb cover per quadrat (range = 0.2–100%). Exotic forb occupancy was highly correlated with the occupancy of all exotic species ( $r = 0.847$ ,  $P = 0.001$ ), and the cover of exotic forbs and all exotic species was also positively correlated ( $r = 0.597$ ,  $P = 0.001$ ).

### Survey gap analysis

Results showed that the entire range of environmental conditions in the study region was represented by the surveyed quadrats. Positive values indicate that the full range of conditions are included in the training data, and higher

numbers indicate areas that are well represented by training data (maximum value = 100; Elith *et al.*, 2010). Our values ranged from 2 to 100, indicating that the model did not extrapolate beyond the training data (though, the model was approaching its limit in a very small geographic area for one variable).

### Model performance

The BRT models performed well, indicating that predicted relationships between the response and predictor variables were reliable. In independent CV tests, the model fitting accounted for a 33–44% reduction in the null deviance, had CV correlation values between 0.59 and 0.70, and AUC scores between 0.87 and 0.91 (full details in Table 1).

The Moran's *I* correlograms revealed that the moderate spatial autocorrelation in the raw data at inter-site separation distances of < 10 km ( $I = 0.2 \pm 0.05$ ) was absent in model residuals ( $I < 0.02$ ). This indicated that the spatial structure in the raw data was adequately modelled by the spatially structured independent model variables used in the BRT analysis.

### Responses to environmental predictors

Responses of all exotic species and exotic forbs to the predictor variables were similar in rank order (Table 1), and when separated into occupancy and abundance models, the shape of the curves was also similar (Fig. S1). All the response variables were linked to propagule pressure and human impacts, abiotic characteristics and the state of the recipient community (i.e. vegetation and forb cover; Table 1, Fig. 2). Overall, the occupancy and abundance of all exotic species and exotic forbs were most strongly related to the physical characteristics of a site (A and PA, Fig. 2). Both the occupancy and the proportional cover of the exotic taxa were highest near the edge of vegetation fragments (Fig. 3). Over 93% of quadrats were within 3 km of the edge of vegetation fragments and 6% were between 4.8 and 6 km. This distribution of quadrats meant that distant sites had large leverage resulting in the U-shaped pattern in Fig. 3, which is thus a statistical artefact rather than a meaningful ecological trend. Plant invasion was linked with human activities as revealed by the positive association of all exotic species (occupancy and cover) with roads and building density (Fig. S1). Occupancy and cover of all exotic species and exotic forbs showed a generally positive response to distance from stream.

Interestingly, occupancy of all exotic species and exotic forbs was positively associated with total vegetation cover, whereas their proportional cover was negatively associated with total vegetation cover (Fig. 4). Total forb cover had the greatest influence on exotic forb occupancy and cover (Table 1). Responses mimicked responses to vegetation cover (Fig. 4c,d): occupancy increased with forb cover, but exotic forb abundance decreased. Cover of exotic forbs was unimodally related to time since last wildfire and peaked around 30 years since the

last fire. Survey year only had a minor (positive) influence on the response variables (Table 1, Fig. S1b). The interactions among predictor variables effectively magnified the effects of single variables on invasion outcomes and did not alter interpretation of relationships (Table S2, Fig. S2). None of the abundance models had interactions greater than 5% indicating minor importance.

### Predictions of invasion risk

The predicted maps for the occupancy and expected cover abundance (i.e. conditional on occupancy) of all exotic species (Fig. 5a,b) reflect the contrasting responses of occupancy and abundance to vegetation cover. The predicted probability of all exotic species occupancy was the highest in the flat, central region ( $\sim > 0.95$  probability of predicted occupancy) where elevation is low and the land use is predominantly dryland agriculture. The likelihood of an exotic species occupying a site is lowest around the Great Otway NP and in the other higher elevation, forested area east of Ballarat (Fig. 5a).

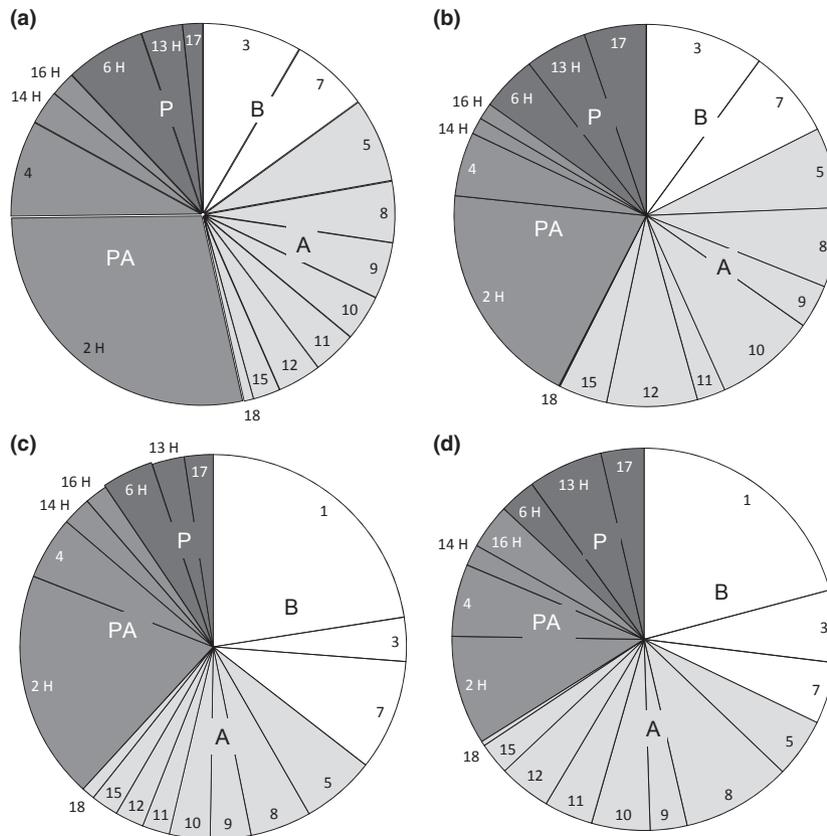
Driven by building density, the expected abundance of all exotic species is highest around towns ( $\sim 40\%$  of total vegetation cover; Fig. 5b). All exotic species were predicted to constitute about 20–25% of vegetation cover in the central region, but only  $\sim 7\%$  in higher elevation areas like the Great Otway NP. Expected abundance was elevated along watercourses and roads (i.e. to 200 m either side of watercourses/roads). Consistent with the partial dependence plot (Fig. S1), after an initial steep fall in predicted abundance within 250 m of a road, abundance increased reaching a plateau at about 5 km from the roads before a sharp decline. As a result, a banded pattern associated with roads is visible in the central, low-relief region where other predictor variables are less variable (and influential; Fig. 5b). This idiosyncratic banding reflects the concentration of quadrats along roads and streams because of access restrictions on privately owned land. The circular shape in the east of the region that marks an area of lower predicted abundance was burnt in 1985 (Fig. 5b).

Predicted probabilities of exotic forb occupancy were very similar to those of all exotic species (Fig. 5c). The expected abundance of exotic forbs (as a percentage of total forb cover) peaked around towns ( $\sim 40\%$  near Geelong), but was also elevated in the central region and around the Great Otway NP. It was at its lowest in the region just north of the Great Otway NP that was burnt in 1939. In the central region, building density had a negative effect on expected abundance.

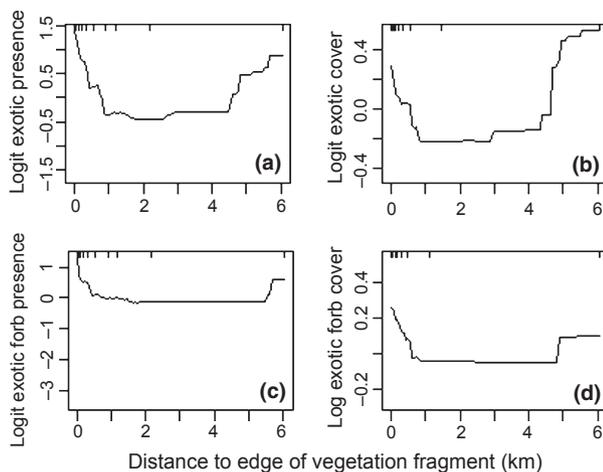
## DISCUSSION

### Value of general models of invasion risk

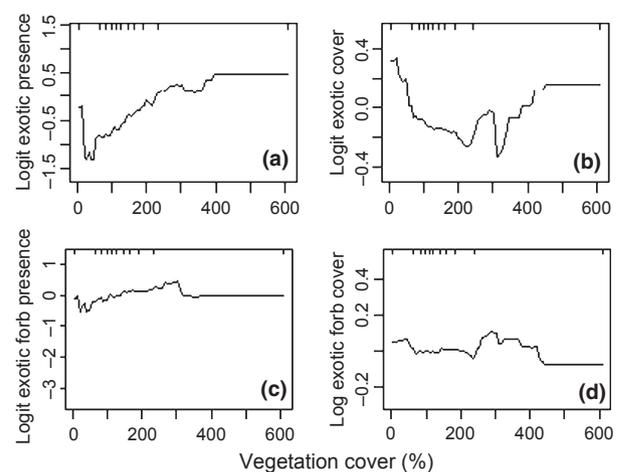
This study has demonstrated that it is possible to take a general approach to modelling landscape susceptibility to plant invasion. In a case study region, we modelled invasion of all exotic species and exotic forbs with BRTs to test the potential



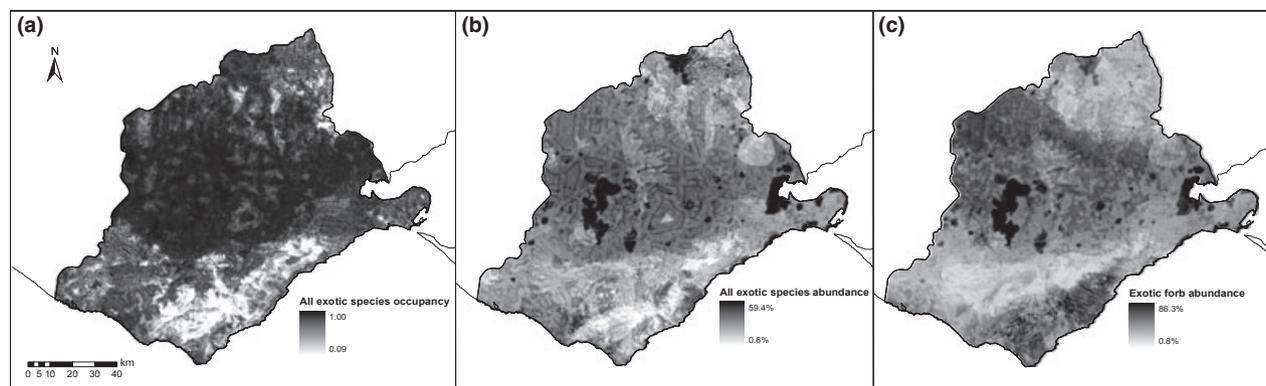
**Figure 2** Pie charts showing relative explanatory power of predictor variables in the models of (a) all exotic species occupancy, (b) all exotic species abundance, (c) exotic forb occupancy and (d) exotic forb abundance. Numbers refer to predictor variables in Table 1; variables relate to: P, propagule pressure; A, abiotic characteristics; PA, propagule pressure and abiotic characteristics; B, community characteristics; H indicates that variable is affected by human activities.



**Figure 3** Partial dependence plots showing marginal effect of distance to edge of vegetation fragment on (a) the probability of all exotic species occupancy (logit-transformed), (b) all exotic species cover (logit-transformed), (c) the probability of exotic forb occupancy (logit-transformed) and (d) exotic forb cover ( $\log_{10}$ -transformed). Tick marks on top axis of graphs indicate deciles of training data.



**Figure 4** Partial dependence plots showing marginal effect of vegetation cover on (a) the probability of all exotic species occupancy (logit-transformed), (b) all exotic species cover (logit-transformed), (c) the probability of exotic forb occupancy (logit-transformed) and (d) exotic forb cover ( $\log_{10}$ -transformed). Multiple layers of vegetation meant that values of vegetation cover exceeded 100%.



**Figure 5** Maps of the study region showing predicted (a) probability of all exotic species occupancy, (b) expected abundance of all exotic species and (c) expected abundance of exotic forbs in 2006. Abundance is conditional on occupancy and is a percentage of total vegetation cover for (b) and percentage of total forb cover for (c).

of predicting areas at risk of invasion. By highlighting influential factors, our multispecies models point to dominant pathways of invasion and identify areas vulnerable to plant invasion. On average, the BRT models explained 38% of the variation in invasion of all exotic species and exotic forbs, and the high AUC scores indicated that the models correctly ranked a randomly chosen occupied site higher than a randomly chosen unoccupied site approximately 90% of the time.

The approach we have used is flexible in that it can be applied across biomes, at multiple scales and for different groups of taxa. Unlike many models used to predict plant invasion (e.g. Crossman & Bass, 2008; Ibáñez *et al.*, 2009; Jacobs & MacIsaac, 2009), this approach uses variables that are not taxon- or region-specific and can predict to a range of spatial and temporal scales. By enabling comparison across taxa, regions and scales, this method can identify general predictors of invasion. In this 'proof-of-concept' study, we applied the approach to the most general of understandings of invasion: relative abundance of all exotic species. Such a general model has merit (Thuiller *et al.*, 2006), but more targeted predictions can be made by grouping species according to their functional characteristics, life history and weed status (Randall & Thomas, 2007; van Kleunen *et al.*, 2010). Likewise, rather than selecting proportional exotic cover as the dependent variable as we have performed here, measures of invasion that address other research questions or management goals can be used instead (e.g. absolute exotic abundance, proportion of total diversity that is exotic) (Chytrý *et al.*, 2008a).

While the approach can be applied to individual species, there are currently 441 exotic species in this study region alone and, although many will not pose an ecological or economic threat, predicting the potential occupancy of even a quarter of the species would be labour intensive. Further, interpretation of a collection of single-species models and the subsequent allocation of management resources would be difficult. We do not suggest that multispecies models replace models that target individual invasive species, but rather are used to complement

them. Predictions based on multiple exotic species will enable more efficient management and surveillance, will ensure that the majority of species causing an exotic plant incursion are addressed and can indicate areas vulnerable to future invasion by functionally similar species. Even though the composition of the exotic species pool may change if propagule biases shift (Colautti *et al.*, 2006), it is unlikely that new invaders will be qualitatively different from the 441 species already present in the region, so predictions of invasion risk should possess some generality.

### Ecology of invasion

Variables indicating propagule pressure (P) and human impacts (H), abiotic characteristics (A) and the state of the recipient community (i.e. vegetation and forb cover – biotic characteristics, B) were rated in the top four most influential variables in each model. The collective influence of these three factors (PAB), as well as the indirect influence of human activities (H), on invasion patterns is consistent with previous studies (Richardson *et al.*, 1994; Thuiller *et al.*, 2006) and invasion and community assembly theory (Belyea & Lancaster, 1999; Catford *et al.*, 2009). While some invasion trends were unexpected [e.g. the positive relationship with time since fire (Hobbs & Huenneke, 1992), negative relationship with summer rainfall (Davis *et al.*, 2000), weak relationship with survey year (Sullivan *et al.*, 2004) and lack of response to radiation], the strongest trends complied with theory- and evidence-based expectations [e.g. relationships with habitat fragmentation (Cadenasso & Pickett, 2001), road proximity (von der Lippe & Kowarik, 2007) and land use (Mosher *et al.*, 2009; Parker *et al.*, 2010)].

Areas most vulnerable to exotic plant invasion were predicted to be at edges of vegetation fragments, along roads, in areas where dryland agriculture is the dominant land use and where native vegetation cover is relatively low. Habitat fragmentation presumably facilitated invasion because of higher propagule pressure and availability of light, water and

nutrients near the edge of vegetation fragments (Saunders *et al.*, 1991; Cadenasso & Pickett, 2001; Ibáñez *et al.*, 2009). The concentration of exotic plants around areas of human activities may reflect human-mediated dispersal (von der Lippe & Kowarik, 2007; Botham *et al.*, 2009) and anthropogenic disturbance (Jodoin *et al.*, 2008). Using naturally disturbed areas as a quasi-control (Downes *et al.*, 2002), the lower level of invasion along water courses and in recently burnt areas, compared to around towns and roads, suggests that human spread of exotic plants facilitates rapid invasion more than disturbance *per se*. However, lower watercourse density and more frequent fire in the forested uplands (which were not accounted for interactions between land use variables and watercourse density/fire history) may have contributed to the unusual trends observed.

Responses to environmental factors can vary depending on the stage of invasion (White & Shurin, 2007; Dawson *et al.*, 2009). In our study, the occupancy of exotic taxa was most likely driven by processes that mediate colonization, while exotic abundance can be considered a measure of the suitability of locations for population growth following colonization (i.e. naturalization: Richardson *et al.*, 2000; Catford *et al.*, 2009). In the study region, the two invasion stages of colonization and naturalization were influenced differently by vegetation cover and forb cover. All exotic species and exotic forbs were more likely to occupy sites with high vegetation cover, but their relative abundance was predicted to be lower. Consistent with the habitat filtering hypothesis (Catford *et al.*, 2009), it is likely that sites with high vegetation cover (or forb cover) would have conditions suitable for many plant species, increasing the chance that at least one exotic taxon would establish successfully. However, at the same time and corresponding with the negative correlation between native cover and proportional exotic cover, competition from incumbents would typically confer higher biotic resistance to invasion, which would limit the overall abundance of invading taxa (Eschtruth & Battles, 2009).

Like all species distribution models that deal with invading species, our models are necessarily constrained by the non-equilibrium nature of the species' distributions (Dullinger *et al.*, 2009; Jones *et al.*, 2010). However, there is a greater chance that species with long residence times will be included in multispecies models so, because they may be close to reaching their equilibrium distributions, our general approach to modelling invasion risk is arguably less susceptible to this limitation than single-species models. The vast majority of study sites were surveyed as exemplars of pre-European vegetation for the purposes of a regional biodiversity inventory. As such, areas less impacted by humans may have been overrepresented in the dataset, which would lead to conservative estimates of exotic plant occupancy and abundance. This slight bias in the dataset may have partially obscured the effect of time on invasion level. Corresponding with other studies (Castro *et al.*, 2005; Wilson *et al.*, 2007), invasion levels increased with time, but the effect was only slight. Reflecting the limited sampling on private land, predictions in the central

agricultural area of the study region should be interpreted with care (Fig. 5b).

## CONCLUSION

We have presented a method for building models that predicts invasion risk at the landscape scale using patterns of exotic plant invasion. This work holds out the promise that by quantifying processes that influence the occupancy and abundance of exotic plants, areas that are vulnerable to invasion can be predicted irrespective of biome or geographic region. The capacity to generalize and compare findings gathered from a range of systems and range of taxa will help progress invasion ecology, as well as community ecology (Shea & Chesson, 2002). For instance, how general is our finding that communities with higher vegetation cover are more susceptible to colonization by exotic plants, but competition for resources apparently limits exotic plant abundance once they are present? With further validation and testing, the robustness of the method and its predictive capability can be ascertained. Predictions of landscape susceptibility to invasion can be used to spatially prioritize weed surveillance and control. Such prioritization will increase the efficiency of management by targeting factors that cause and facilitate invasion.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Partial dependence plots showing relationship between the 12 most influential predictor variables and fitted values of (a) the probability of all exotic species occupancy (logit-transformed), (b) all exotic species proportional cover (logit-transformed), (c) the probability of exotic forb occupancy (logit-transformed), and (d) exotic forb proportional cover ( $\log_{10}$ -transformed).

**Figure S2** Interaction plot showing combined effect of Thorium-inverse Potassium and time since last fire on the fitted value of all exotic species occupancy.

**Table S1** Key predictor variables used to explain and predict the occupancy and abundance of all exotic species and exotic forbs in the Corangamite catchment.

**Table S2** Correlation matrix showing relationship among the environmental predictors. Values reported are the Pearson correlation coefficient. Strong correlations ( $> 0.6$ ) are in bold.

**Table S3** Summary table showing the most important interactions in the BRT models. Only the occupancy models had interactions  $> 10\%$ . Model details as in Table 1.

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## BIOSKETCH

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Author contributions: all authors conceived the ideas; M.W. provided the data; J.C. led the data analysis and writing.

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