PREPRINT

*Author-formatted, not peer-reviewed document posted on 21/08/2024*

DOI: https://doi.org/10.3897/arphapreprints.e135147

# Similar drivers but distinct patterns of woody and herbaceous alien plant invasion

**David Gregory, Matt White, Jane Catford**

# Similar drivers but distinct patterns of woody and herbaceous alien plant invasion

David Gregory[1], Matt White[2] and Jane A. Catford[1,3,4]*

[1]Department of Geography, King's College London, 40 Aldwych, London, WC2B 4BG, UK

[2]Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water & Planning, Victoria, Australia

[3]School of Agriculture, Food & Ecosystem Sciences, The University of Melbourne, Vic 3010, Australia

[4]Fenner School of Environment & Society, Australian National University, Canberra, ACT 2601, Australia

***Corresponding author:** Jane Catford, jane.catford@kcl.ac.uk, ORCID 0000-0003-0582-5960

**Running header:** Similarities and differences in woody and herbaceous invasion

**Keywords:** Alien vegetation management, invasive plant species risk, plant growth form, ecosystem invasibility, Habitat suitability models, Boosted Regression Trees, species distribution models

## Abstract

The extent of alien plant invasion and numbers of invasive species are increasing, exacerbating invasion impacts. Effective and efficient management requires understanding the drivers and distribution of plant invasions at the landscape scale. In this study, we used a species distribution modelling approach to determine whether the patterns and correlates of alien invasion vary by plant growth form. Focusing on the occupancy and abundance of forbs, graminoids and woody vegetation, we used boosted regression trees (BRTs) to characterise alien plant invasion risk in two major catchment regions in Victoria, Australia. Of 7,630 quadrats surveyed between 1970 and 2019, 69% contained alien plants, with forbs being the most prevalent. Alien plants constituted 22% of the total number of plant species recorded. Alien species cover varied widely, with forbs and graminoids showing higher mean cover compared to woody plants. Abiotic conditions, particularly temperature and precipitation, had the greatest influence on alien plant invasion overall, explaining 41-76% of observed variation. Summer mean maximum temperature was a strong predictor across all growth forms. Forbs and graminoids showed increased occupancy with higher vegetation cover but lower proportional cover, while woody plants had a negative relationship with their own cover type. High levels of invasion were predicted in areas with intensive land use, such as urban and agricultural zones. Forbs had a high probability of occupancy throughout the region, even in higher elevations, while graminoids and woody vegetation were more restricted to lower elevations and areas with human activity. The study highlights that alien plant invasion is influenced by a complex interplay of abiotic factors, propagule pressure, human activity and biotic conditions. The findings underscore that while there are common drivers across growth forms, specific patterns and influences vary. For instance, forbs are more widespread but less dominant in high vegetation areas, while woody plants were less common and more constrained by existing vegetation. Management strategies should prioritize maintaining and restoring native vegetation to limit the dominance of alien species and controlling invasive plants after disturbance. Although single-species models remain valuable, our study shows that species distribution models based on growth form offer a practical approach for assessing plant invasions across diverse landscapes.

## INTRODUCTION

Increases in trade and travel have increased incidence of human-mediated alien species introduction, and human-induced environmental change has facilitated higher rates of alien plant establishment (Seebens et al. 2018, Pyšek et al. 2020b). Invasive alien species, including plants, are considered one of the major threats to global biodiversity and have the potential to cause substantial environmental and economic damage (Diagne et al. 2021, Novoa et al. 2021, IPBES 2023). In Australia alone, estimates of the cost of alien plant invasions exceed AU$13.6 billion per year (Hoffmann and Broadhurst 2016), with totals of at least AU$299 billion since the 1960s (Bradshaw et al. 2021). The efficient and effective management of alien species is of high economic, social and ecological importance. However, to be able to manage alien plant species effectively, it is vital to understand what drives invasion, how these drivers might differ across different groups of plants, and how this information can be used to spatially predict the location of alien species on a landscape scale.

Many ecosystems are invaded by multiple alien plant species (Kuebbing et al. 2013) and vegetation management organisations are often mandated to control multiple invasive species across a landscape (Brandt et al. 2023). Invasive species management is more cost effective when multiple species are managed in concert, rather than individually (Januchowski-Hartley et al. 2011, Lohr et al. 2017). Effective spatial prioritisation of invasive species control requires information about where alien plants occur in the landscape, enabling hotspots of invasion to be targeted. Because vegetation surveys are limited and data on invasive species distributions are imperfect, there is a need to predict areas that are likely to experience high levels of invasion. Such predictive approaches must be applicable to a wide range of plant species and habitats. However, understanding about the factors that drive alien plant invasions across various landscapes is still limited and even less is known about how these drivers may differ across types of plants.

Species distribution models (SDMs) are commonly used to predict the spatial distribution of individual invasive species. However, SDMs can be data- and resource-demanding with many individual SDMs required to provide a general picture of alien plant invasion. For example, at least 175 individual SDMs would be required to estimate the spatial distribution of alien graminoids that occur in a 42,000 $km^2$ region of Victoria, Australia. Such an exercise would require considerable time, and the lack of temporally and spatially unbiased data for individual species could result in unreliable predictions (Cordier et al. 2020). Trait-based studies that examine characteristics associated with species invasiveness provide insight into general drivers of plant invasion, combining data from tens to hundreds of species (Catford et al. 2016, Fristoe et al. 2021, Palma et al. 2022). However, these studies also demand considerable amounts of data and most trait-based studies do not provide spatially explicit predictions (Catford et al. 2019, Junaedi et al. 2021, Palma et al. 2021). A major axis of variation among plants is growth form, with different growth forms responding to environmental gradients and anthropogenic pressures in distinct ways (Giorgis et al. 2016, Šímová et al. 2018, Bartlett et al. 2023). Growth form information is readily available for all known taxa. When combined with species occupancy and abundance records, this enables group-based distribution models of invasion risk on a landscape scale (Catford et al. 2011). Growth form-based distribution models could enable spatial prioritisation of multi-species alien vegetation management without the need to build hundreds of individual SDMs.

In this study, we use a species distribution modelling approach to determine whether the patterns and correlates of alien invasion vary by plant growth form. Focusing on the occupancy and abundance of forbs, graminoids and woody vegetation, we use boosted regression trees (BRTs) to characterise alien plant invasion risk at a landscape scale in two major catchment regions in Victoria, Australia to address two questions:

1) How does the relative influence of variables linked to propagule pressure, human disturbance, biotic and abiotic characteristics differ between alien forbs, graminoids and woody vegetation?

2) how do spatial patterns in alien plant invasion differ between the three growth forms?

To provide context, we also examine the extent of invasion in the study region. Identifying how landscape vulnerability to invasion varies between different plant growth forms will enable more efficient mapping and monitoring techniques, facilitating management prioritisation (Foxcroft et al. 2017).

## METHODS

### Study region

This study focuses on a region encompassing two Catchment Management Authorities within Victoria, south-eastern Australia: West Gippsland and Goulburn Broken (Fig. 1). The Catchment Management Authorities are responsible for planning and coordination of environmental management within their catchments. West Gippsland (~17,700 $km^2$) stretches from the Bass Strait coast in the south to the Great Dividing Range where it borders with Goulburn Broken (~24,300 $km^2$), which extends to the agricultural floodplains of the River Murray in the north.

The southern catchment management area in the study region (West Gippsland) experiences dry hot summers with the majority of the ~850 mm annual rain occurring in winter months, with the central uplands often receiving triple that of the southern lowlands (Bureau of Meteorology and CSIRO 2019b). The climate of the northern catchment area (Goulburn Broken) varies with topography resulting in annual rainfall ranging from 1600 mm at Lake Mountain to 460 mm in Kyabram in the north (Bureau of Meteorology and CSIRO 2019a). The study region has a total population of approximately 415,000 people who mainly reside in regional cities and rural towns (WGCMA 2019). More than 50% of land is under private ownership and is mainly used for agriculture resulting in habitat fragmentation. Public lands associated with the Great Dividing Range experience significantly lower levels of human activity (GBCMA 2013, WGCMA 2019).

The study region contains a variety of habitats ranging from coastal salt marshes, mangroves and heathlands in the south to alpine and heavily forested regions in the centre to floodplain forests and semi-arid woodlands in the north. The study region was selected based on its wide variety of environmental and anthropogenic conditions, high levels of invasion, and invasive plant management interest from management agencies.

ARPHA Preprints Author-formatted, not peer-reviewed document posted on 21/08/2024. DOI: https://doi.org/10.3897/arphapreprints.e135147

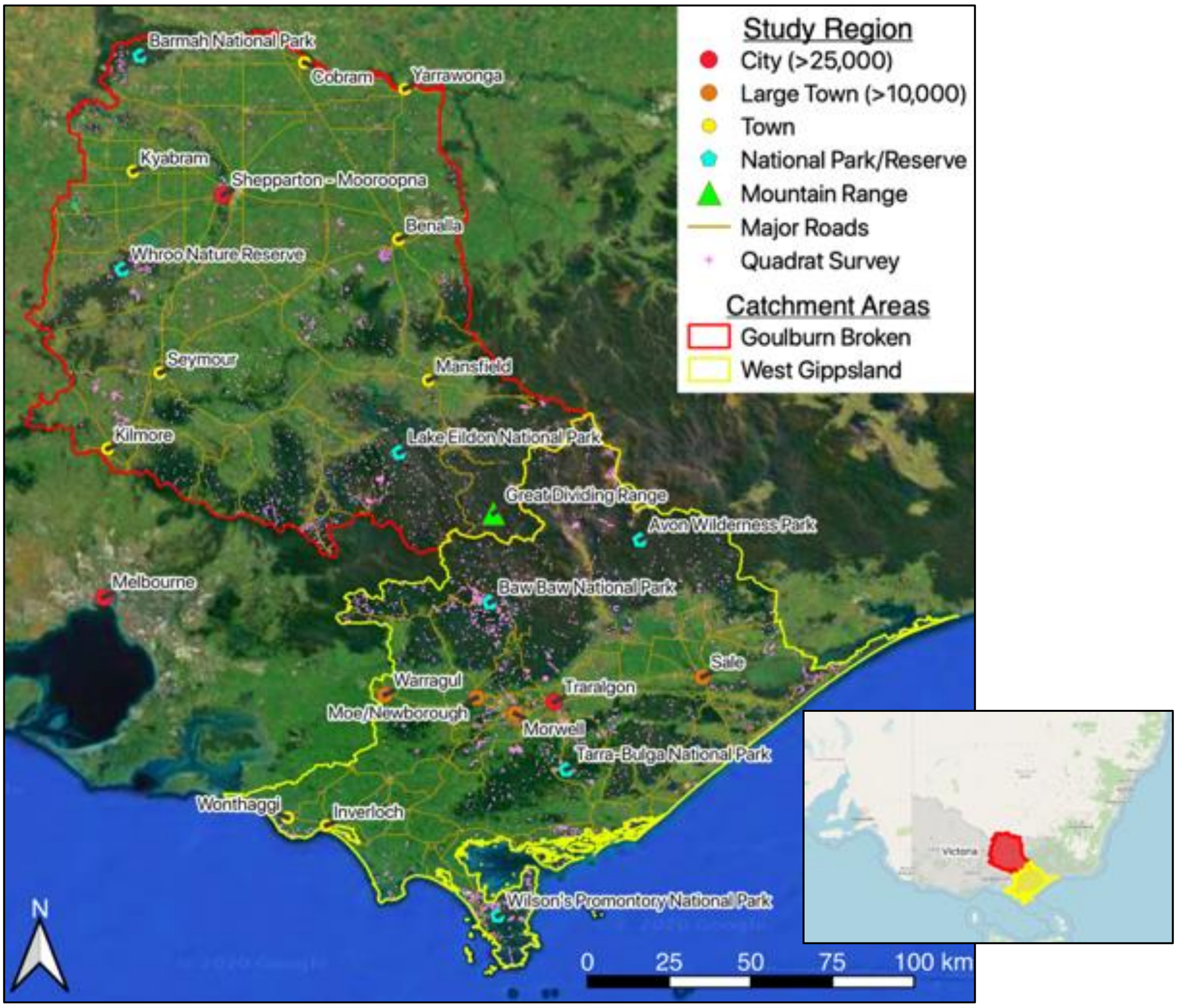



**Figure 1:** A map of the study region in Victoria, Australia. The map illustrates areas of the two Catchment Management Authorities: Goulburn Broken (outlined in red) and West Gippsland (outlined in yellow), which were combined to create the study region. The map highlights the main characteristics of the study region including major towns and cities, roads, national parks, landforms, and locations of the 7,630 vegetation quadrat survey sites.

## Vegetation composition

We used vegetation survey data collected from 7,630 quadrats between 1970 and 2019 by the Victorian Department of Environment, Land, Water and Planning (DELWP). These data provide information on plant occupancy (presence/absence) and cover abundance for all native and alien (non-native to Australia) plant species in the study region.

The coordinates of the centre of each 30 m x 30 m quadrat were recorded with either a map (pre-1993: ±100m accuracy) or Geographical Positioning System (post 1993 ±7m accuracy). Foliage cover of all plant taxa found within the quadrats was estimated using the Braun-Blanquet scale (Kent and Coker 1992). For the purposes of statistical analyses, Braun-Blanquet scale values were converted to percentages on a proximal ordinal scale (+: 1%, 1: 2%, 2: 10%, 3: 30%, 4: 60%, 5: 80%) to estimate growth form and total vegetation cover abundance for each quadrat. Total cover abundance values per quadrat could exceed 100% where multiple layers of vegetation (e.g. ground and aerial cover) were present.

The cover abundance of combined alien taxa was then calculated as a percentage of total (i.e. native and alien) plant cover. Cover of alien forbs, graminoids and woody plants was taken as a percentage of their total growth form cover. By producing alien cover abundance as a proportion of total cover, exotic species contribution to the surrounding flora community can be better understood (Catford et al. 2011).

**Environmental variables**

We assembled a range of environmental variables as proxies for propagule pressure, human activity, abiotic and biotic conditions that are likely to influence alien plant invasion (Catford et al. 2009, Catford et al. 2011, Szymura et al. 2018, Pyšek et al. 2020a). Raw data for over 30 variables was sourced from DELWP and VicData before being compiled in QGIS 3.14 where variable data was sampled for each quadrat survey location. Although boosted regression trees (BRTs) are robust to effects of moderate multicollinearity amongst independent variables (Elith et al. 2008), we used correlation analysis and the literature to reduce the number of variables to avoid model overfitting (De Marco and Nóbrega 2018). Correlation analysis highlighted variables with high levels of correlation (Pearson correlation coefficient >|0.7|). When multicollinearity was found, the variable(s) most distal in its influence on plant invasion was removed in favour of the more proximal. For this reason, temperature and rainfall variables were chosen ahead of latitude and longitude due to their more proximal influence on plant growth. The model for combined alien taxa included 19 variables and the models for woody, forb and graminoids included 20 environmental variables following the addition of a variable for each specific growth form (Table 1).

**Table 1:** Independent variables used in the study and their corresponding number ID and descriptive statistics. [B] indicates biotic conditions; [A] indicates abiotic conditions; [P] indicates propagule pressure; [H] indicates human activity. Descriptions of the independent variables can be found in Table S1 and their correlations in Fig. S1.

| ID | Independent Variable | Mean (SE) | Range |
|---|---|---|---|
| 1 | Forb cover[B] | 25.7 (0.3) | 1 – 290 |
| 2 | Graminoid cover[B] | 32.2 (0.4) | 1 – 317 |
| 3 | Woody vegetation cover[B] | 57.7 (0.5) | 1 – 425 |
| 4 | January mean maximum temperature[A] | 24.2 (0.04) | 15.7 – 30.9 |
| 5 | Land use intensity[PH] | 2332.0 (47) | 0.643 – 26526.5 |
| 6 | Survey year[P] | 1996 (0.1) | 1972 – 2019 |
| 7 | Geology[A] | Sandstone (Mode) | See Table S1 |
| 8 | Land cover[PAH] | Native Trees (Mode) | See Table S1 |
| 9 | Vegetation cover[B] | 120 (0.6) | 1 – 665 |
| 10 | Wind exposition[PA] | 1.1 (0.002) | 0.8 – 1.4 |
| 11 | January mean rainfall[A] | 58.3 (0.2) | 28 – 103 |
| 12 | Radio-element Thorium[A] | 8.6 (0.06) | -0.26 – 38.7 |
| 13 | Vertical Height Above River (HAR)[A] | 0.79 (0.002) | 0 – 1.0 |
| 14 | Normalise Difference Vegetation Index (NDVI)[B] | 0.67 (0.002) | -0.33 – 0.91 |
| 15 | Road-demographic cost distance analysis[PH] | 11.2 (0.02) | 0 – 15.1 |
| 16 | July mean rainfall[A] | 101 (0.6) | 38 – 223 |
| 17 | Distance to river[PA] | 0.43 (0.01) | 0 – 11.2 |
| 18 | Time since fire[A] | 35 (0.4) | 0 – 98 |
| 19 | Diurnal anisotropic heating x ruggedness index[A] | 0.01 (0.0001) | $0.3 \times 10^{-5}$ – 0.09 |
| 20 | July mean minimum temperature[A] | 2.9 (0.02) | -2.7 – 6.7 |
| 21 | Historical land use 1888[PAH] | Dryland Agriculture (Mode) | See Table S1 |
| 22 | Topographic wetness index[A] | 0.62 (0.002) | 0.18 – 1.0 |

A landcover variable (Tables 1 & S1) was included to maximise the ability of BRT models to predict areas susceptible to alien invasion to a fine resolution. The landcover classifications used in this study were split into five-year periods between

1985-2019 and contained 19 landcover categories (Table S1). By selecting the landcover period closest to that of the survey date, landcover classification accuracy at each quadrat site was maximised. To ensure the invasion models can be applied to large regions, not just small specific areas, the landcover categories used were broad enough to be used internationally across various climatic environments (e.g. “urban”, “irrigated horticulture”, “native trees”; Table S1).

## Gap analysis

We undertook gap analysis to ensure the training data on which the model was built (i.e. quadrat survey locations) encompassed the full extent of environmental conditions found across the study region. The maximum, minimum and mean values of the environmental variables used as model training data were compared to values across the study region to confirm the quadrat environmental conditions were representative of the study region. The values of independent variables from quadrat survey locations were found to represent up to 100% of those experienced across the study region. The lack of scores over 100% suggest that models did not extrapolate beyond conditions found within the training data and study region.

## Modelling

We ran eight models, using boosted regression trees (BRTs), to model relationships between the environmental variables and the occupancy and cover abundance of combined alien taxa, and alien forbs, graminoids and woody vegetation growth forms. BRTs use a two-stage modelling method, which fits a series of simple regression tree analyses and then combines their results in a forward stagewise manner using iterative machine learning algorithms to maximise predictive power with high accuracy (De'ath 2007). BRTs are robust when modelling ecological data due to their ability to handle various data types (continuous and discrete), missing data and non-linear relationships whilst providing strong performing predictive and explanatory models (Elith et al. 2008). BRTs are also useful for predicting alien invasion due to their ability to provide simple graphical and numerical interpretations of complex relationships between independent variables (De'ath 2007, Elith et al. 2008).

This study followed the BRTs methods set out by Elith *et al.* (2008) and Elith & Leathwick (2017) to model the relationships between independent variables and alien plant invasion. BRTs for alien occupancy and cover abundance were run separately, with the cover abundance models only using quadrat sites where alien species were present. This was done to ensure currently unoccupied sites that are otherwise suitable for high levels of alien invasion were not inadvertently excluded. The separation of occupancy and cover abundance models overcomes issues associated with data containing a high zero count, allows easy interpretation, and also provides insight into how invasion drivers differ among invasion metrics (Catford et al. 2012). Occupancy models provide insight into alien species ability to occupy sites and thus tolerate their biotic and abiotic conditions, while cover abundance models indicate when an alien species becomes dominant at a site, resulting in increased impacts on the native ecosystem structure and function.

BRTs were run in R (version 1.3.1056) using packages “gbm” (version 2.1.8; Ridgeway 2019) and “dismo” (version 1.1-4; Hijmans et al. 2017) and code provided in Elith et al. (2008) and Elith and Leathwick (2017). Bernoulli (binomial) and Gaussian error distribution models were fitted for occupancy and cover abundance models respectively. Upon inspection of the models’ residual plots, cover abundance models for combined alien taxa and alien growth forms (forbs, graminoids and woody vegetation) were normalised using log-transformations. BRT models were adjusted to maximise performance with alien plant occupancy models run using a learning rate of 0.01, a tree complexity of four and a bag fraction of 0.7 to maximize predictive performance, following Catford et al. (2011). The parameters remained the same for the alien proportional cover models except for tree complexity, which was increased to five.

We used three performance metrics to select the best performing models for each dependent variable: 1) Percentage deviance explained, expressed as a percentage of the null deviance for each response variable (Leathwick et al. 2008), provided a ‘goodness-of-fit’ metric between predicted and raw values by predicting to data excluded from the original model training data; 2) a CV correlation analysis indicated correlation between predicted values and raw data unused in model training; and 3) Area Under the receiver operating Characteristic curve (AUC) was used to determine occupancy models' ability to discriminate between quadrats with or without alien species (Leathwick et al. 2008). An AUC score of 1.0 indicates perfect discrimination and a score of 0.5 suggests no discrimination accuracy.

We then used the selected models to predict occupancy and cover abundance of three plant growth forms (forbs, graminoids and woody vegetation) across the study region in Victoria, Australia. These predictions were mapped in R, using the "raster" package (version 3.3-13; Hijmans 2019), to provide study region wide spatial predictions of combined alien taxa and individual alien growth form predicted probability of occupancy and expected proportional cover (with resolution limited to 50 m x 50 m due to the resolution of independent variables). To produce a more realistic representation of alien invasion, expected cover was produced by multiplying the predicted percentage cover with the probability of an alien species being present, as carried out by Catford et al. (2011).

## RESULTS

### Level of invasion

Of the 7,630 quadrats surveyed, 69% contained alien plant species, and alien species made up 22% of the 3,087 plant species recorded (688 alien species, of which 14.2% were Woody plants, 25.4% Graminoids and 71.7% Forbs). The mean species richness across all quadrats was 28.4 (0.16 SE), ranging from 1-115 species. Total vegetation cover was weakly correlated with species richness ($r = 0.248$; $P < 0.001$), but no relationship was found with total vegetation cover and alien species richness ($r = 0.067$; $P < 0.001$). When examining only the 5,239 quadrats that contained alien species, the mean alien proportional cover was 16.67% (0.31% SE) but this ranged from 0.19-100%, while the mean alien species richness per quadrat was 6.6 (0.09 SE) and ranged from 1-45 species. Total vegetation cover was strongly correlated with total native cover ($r = 0.877$; $P < 0.001$) but not with total alien cover ($r = 0.263$; $P < 0.001$) or total alien proportional cover ($r = - 0.078$; $P < 0.001$). Both alien proportional cover and alien proportional species richness were negatively correlated with total native cover and native species richness.

**Relative influence of environmental variables on level of invasion**

As expected, all eight BRT models demonstrated that alien plant occupancy and cover were linked to numerous biotic and abiotic factors, propagule pressure and human activity (Fig. 2). Although the relative influence of specific variables varied somewhat across response variables (most notably in relation to vegetation cover, as discussed below), drivers of forb, graminoid and woody invasion were similar overall (Fig. 2). Variables representing abiotic conditions had the strongest links with invasion in general, with their summed relative influences varying from ~41% to ~76% (Fig. 2). The alien forb occupancy model differed, however, having the strongest association with biotic conditions (B) with summed relative influences of 47.7% (Table S2). January (summer) mean maximum temperature was among the top two most influential variables in six of the eight models and was among the top six variables for the other two models. Relationships between January mean maximum temperature and invasion were very similar across all response variables; occupancy and cover of combined alien taxa and individual growth forms increases sharply at ~23°C January mean maximum until levels plateaued around 25-26°C (Fig. 3).

For each alien growth form occupancy and cover model, total cover of the respective growth form (e.g. forbs for forbs) was among the top two most influential independent variables, and the most influential biotic variable (Fig. 2), except for the woody vegetation occupancy model. The occupancy of combined alien taxa was positively associated with total vegetation cover, while proportional cover was negatively associated with total vegetation cover (Fig. 4). This trend extended to the relationships between alien forb and graminoid occupancy and proportional cover with their respected total growth form cover. As their respective growth form cover increased, the alien forb and graminoid occupancy increased while their proportional cover decreased (Fig. 4). Unlike forbs and graminoids, both the occupancy and proportional cover of alien woody plants were negatively associated with total woody plant cover.

Survey year had a strong relationship with all alien cover variables, with cover increasing over time. The probability of alien occupancy rose gradually between 1972 and c. 2015, after which it dropped sharply (Fig. 5).

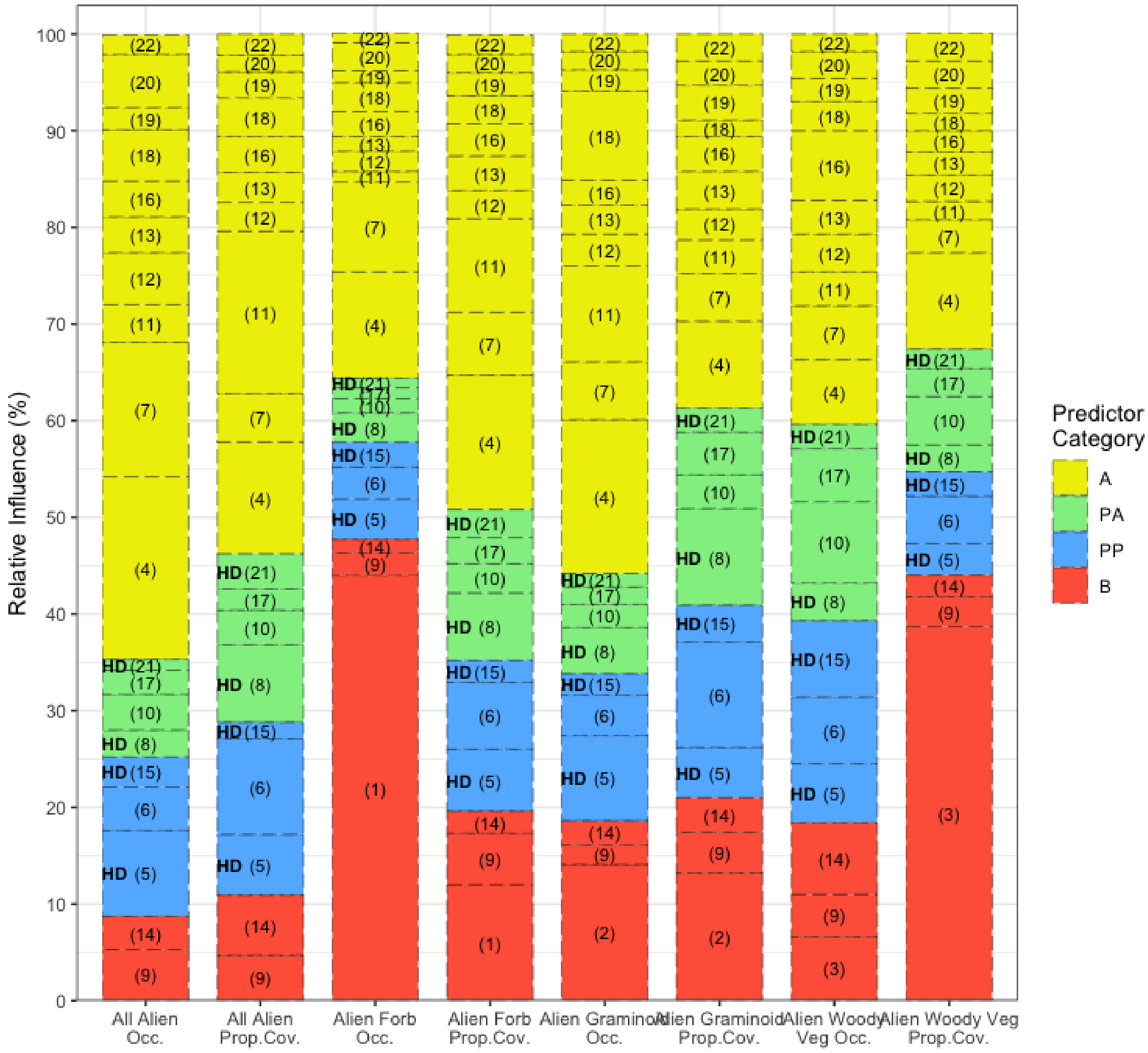



**Figure 1:** Stacked bar charts showing the relative explanatory power of the independent variables used to model the occupancy and cover of combined alien taxa, alien forbs, zalien graminoids and alien woody vegetation across the study region. Variables were grouped by whether they represent: abiotic characteristics (A), propagule pressure and abiotic characteristics (PA), propagule pressure (PP), biotic characteristics (B). 'HD' indicates variables capturing human activity. Bracketed numbers relate to the independent variable numbers in Table 1. Models fit in the CV analyses explained 38.0-59.4% of the reduction in the null deviance, had CV correlations of between 0.62 and 0.78 and AUC scores of between 0.90 and 0.94. The difference between training AUC and CV AUC was always less than 0.01 suggesting overfitting of the models was not an issue.

ARPHA Preprints Author-formatted, not peer-reviewed document posted on 21/08/2024. DOI: https://doi.org/10.3897/arphapreprints.e135147

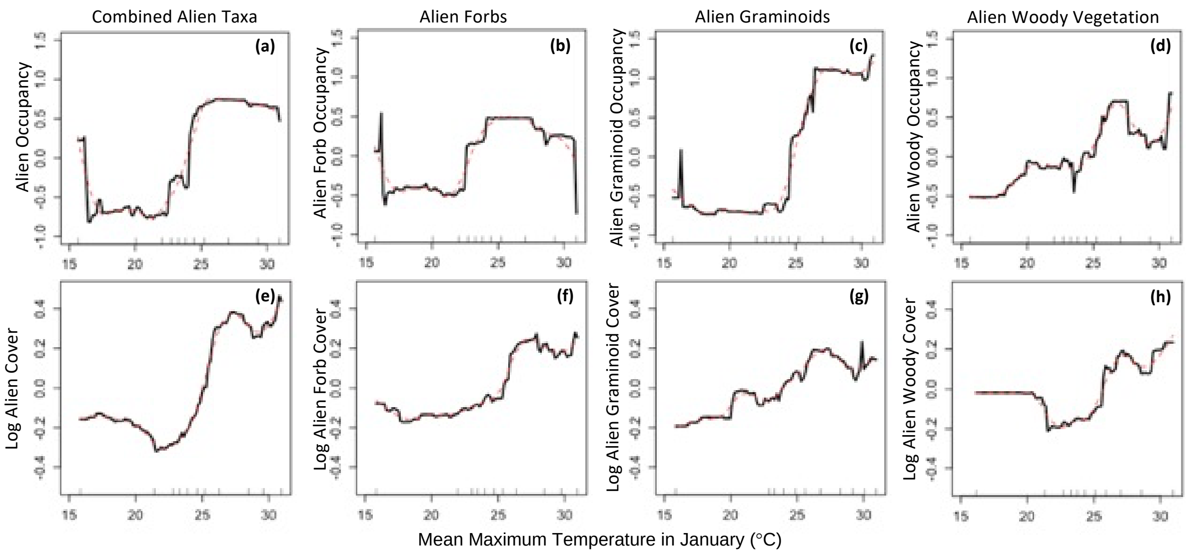



**Figure 2:** Partial dependence plots illustrating the marginal effect of mean maximum temperature in January on the probability of (a) alien occupancy, (b) alien forb occupancy, (c) alien graminoid occupancy, (d) alien woody occupancy, and the expected (e) alien cover, (f) alien forb cover, (g) alien graminoid cover, and (h) alien woody cover across the study region. Markings on the inner x-axis denote the training data deciles. Expected cover was log-transformed in all cases.

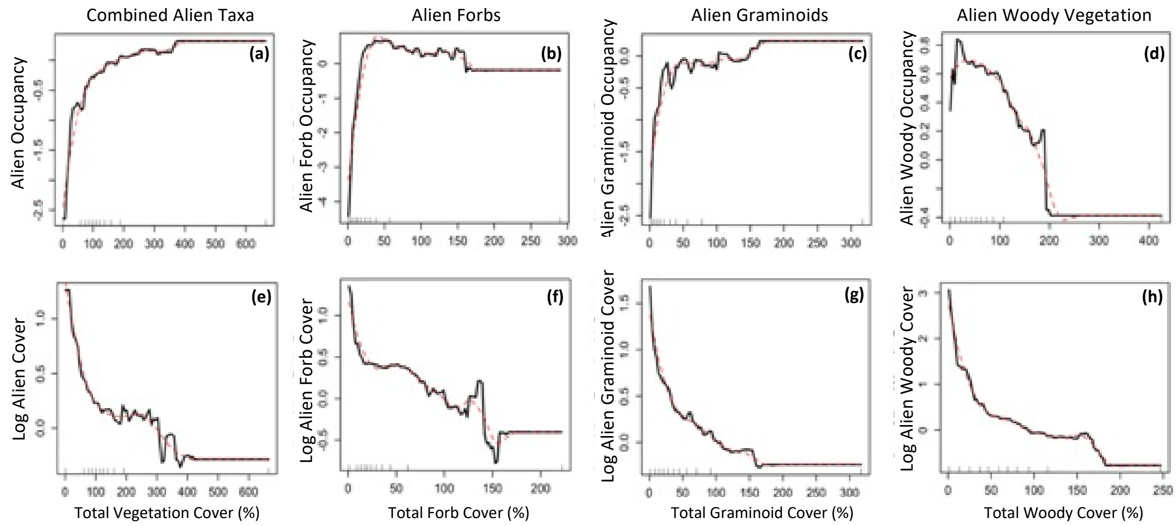



**Figure 3:** Partial dependence plots illustrating the marginal effect of total vegetation cover on (a) the probability of alien occupancy, (e) log-transformed alien cover, and the marginal effect of total growth form cover on the probability of (b) alien forb occupancy, (c) alien graminoid occupancy, (d) alien woody occupancy, and the expected (f) log-transformed alien forb cover, (g) log-transformed alien graminoid cover, and (h) log-transformed alien woody cover across the study region. Markings on the inner x-axis denote the training data deciles.

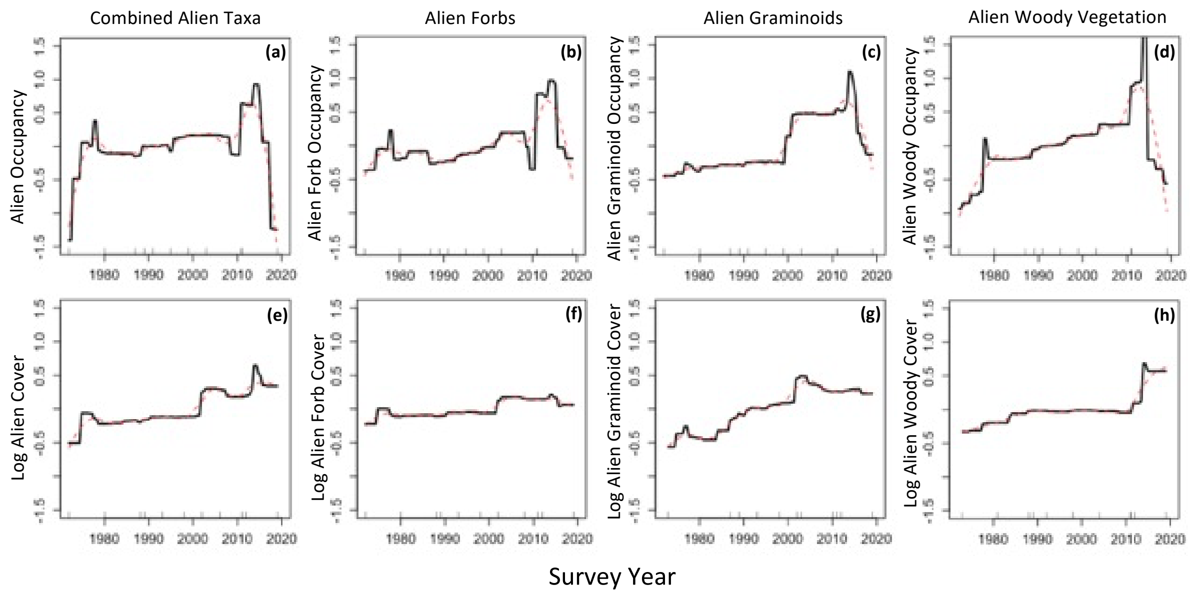



**Figure 5:** Partial dependence plots illustrating the marginal effect of survey year on the probability of (a) alien occupancy, (b) alien forb occupancy, (c) alien graminoid occupancy, (d) alien woody occupancy, and the log-transformed expected (e) alien cover, (f) alien forb cover, (g) alien graminoid cover, and (h) alien woody cover across the study region. Markings on the inner x-axis denote the training data deciles.

## Spatial predictions of invasion

Predictions of invasion indicate that, for almost any given location across the study region, there was a high probability of occupancy of alien taxa from at least one growth form, especially forbs (Fig. 6). Higher elevation areas, sandplains and regions of low human settlement were predicted to have lower levels of alien plant occupancy and cover, although this pattern varied among growth forms. Alien graminoids and woody vegetation predictions indicated very low levels of invasion across the Great Dividing Range, but alien forbs still exhibited high occupancy in these higher elevation areas (Fig. 6b), though levels of alien forb cover remained low (Fig. 8b). Despite the lower probability of alien taxa occupancy in the Great Dividing Range (>500 m above sea level), probabilities still reached ~0.80 in areas of high vegetation cover (Fig. 6). This contrasts with combined alien cover, which remained very low (<3.0% expected alien cover) across this elevated region and across national parks and reserves located in southern West Gippsland, which are characterised by high tree and vegetation cover (Figs 1 & 6).

Consistent with the similarity in their drivers (Figs 2-5), the predicted levels of invasion were highly correlated across the eight response variables we examined: maps with combined alien taxa, alien forb and alien graminoid models displayed similar patterns of both occupancy and expected relative cover. Predicted invasion of alien woody vegetation was notably lower across the study region compared to forbs and graminoids (Fig. 6). Areas characterised by high levels of human activity and land use intensity were predicted to have high levels of alien occupancy and cover. Areas of high land use intensity, such as agriculture and urban areas, had the highest levels of predicted occupancy and cover (>0.90 occupancy probability, >50% cover). This was most obvious for alien forb and graminoids where towns and cities (e.g. Mansfield, Seymour and Benalla in Goulburn Broken; Sale and Traralgon in West Gippsland) had predicted occupancy of >0.90 and proportional cover levels were frequently >70%. Despite woody vegetation invasion levels not being as high at these locations, urban regions were still more vulnerable to alien woody plant invasion (~0.70 occupancy probability; ~8% proportional cover) compared to more rural areas (<0.45; <5%).

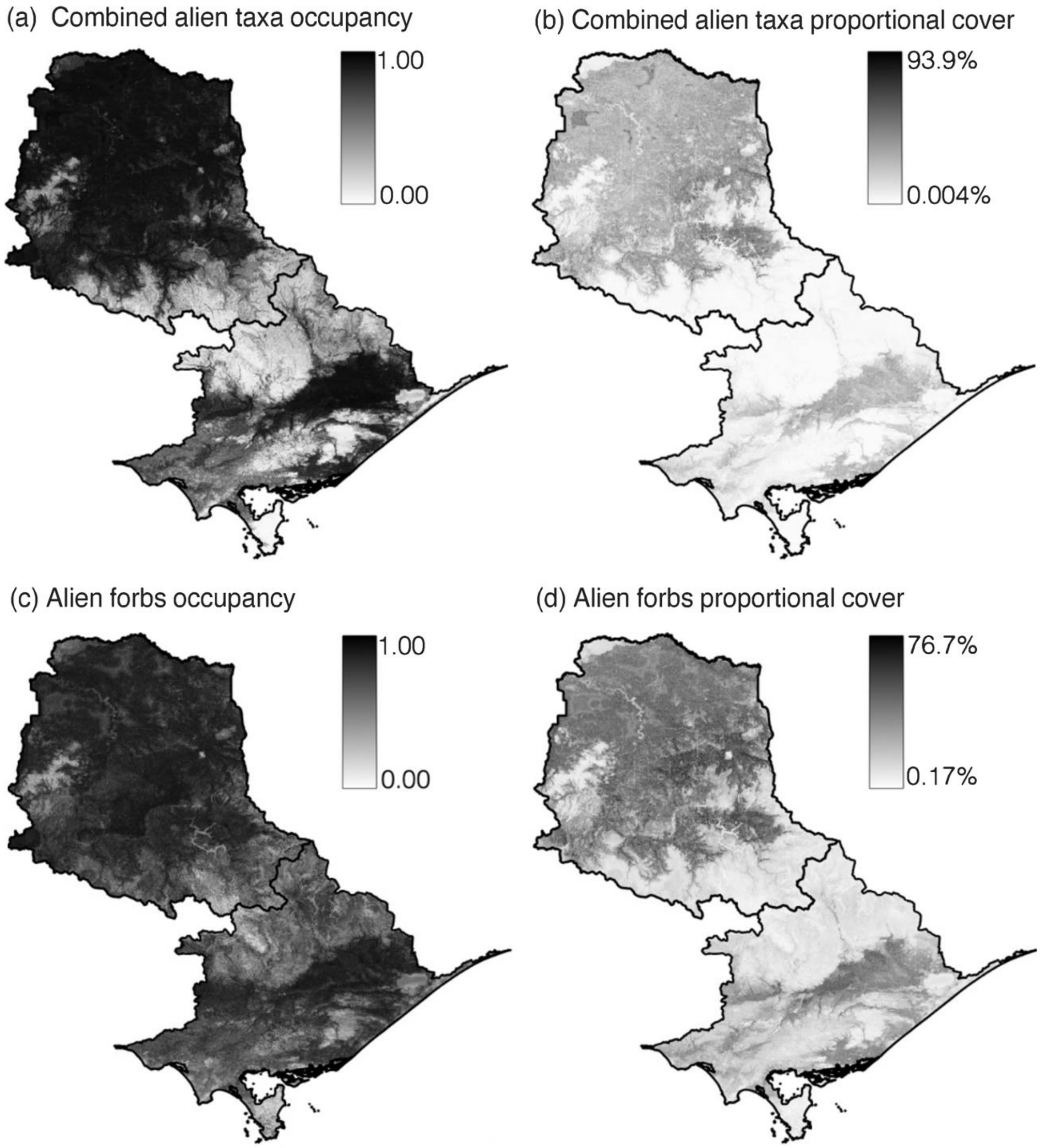
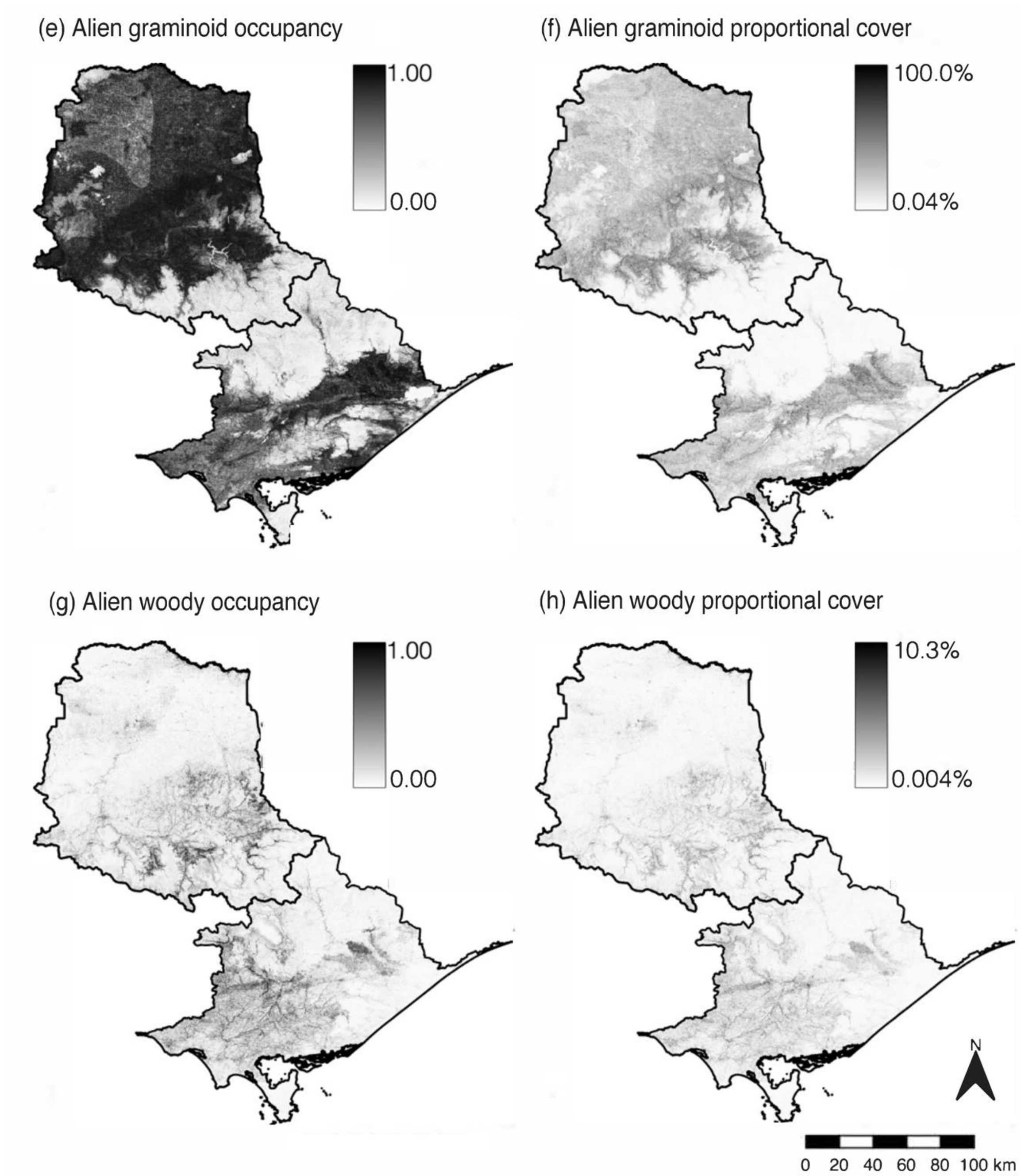



**Figure 6:** Maps showing predicted probability of occupancy (left panels) and proportional cover, dependent on the probability of occupancy (right panels), for: (a & b) combined alien taxa; (c & d) alien forbs; (e & f) alien graminoids; and (g & h) alien woody vegetation.

**[continued on next page]**




**[Figure 6 continued:** Maps showing predicted probability of occupancy (left panels) and proportional cover, dependent on the probability of occupancy (right panels), for: (a & b) combined alien taxa; (c & d) alien forbs; (e & f) alien graminoids; and (g & h) alien woody vegetation].

## DISCUSSION

By examining drivers and patterns of plant invasion in south-eastern Australia, in this study we identified common themes in alien forb, graminoid and woody vegetation occupancy and abundance at the landscape-scale. While there was some variation in the influence of specific drivers across the eight response variables, the boosted regression tree (BRT) model results confirm that plant invasion is multifaceted and the result of interactions between propagule pressure, biotic and abiotic conditions, and influenced by human activity (Fig. 2; Catford et al. 2009, Pyšek et al. 2020a, Hulme et al. 2023). The most vulnerable areas to invasion in the 42,000 $km^2$ study region were in lower elevation regions close to human activity, especially for forbs and graminoids, which reached higher predicted levels of occupancy and cover abundance than woody alien vegetation. Identifying similarities and differences across plant growth forms can inform invasion science and management.

### Factors associated with invasion of alien graminoids, forbs and woody plants

Variables indicating abiotic conditions (e.g., January mean maximum temperature and mean precipitation, geology, landcover) had the strongest link with alien plant occupancy and cover abundance. This is consistent with hypotheses proposing that resource availability and climatic conditions are the major limiting factors of invasion (Davis et al. 2000, D'Antonio et al. 2017). However, it may have also reflected the spatial grain of our study, which was based on 30 m x 30 m quadrats. We thus less likely to detect effects of biotic interactions, which typically manifest at finer resolutions, at least for herbaceous plants (Brian and Catford 2023, Pérez-Navarro et al. 2023). Occupancy and abundance of all growth forms were positively associated with summer maximum temperature, presumably because warmer conditions were more hospitable for plant growth regardless of invader growth form.

While temperature had a consistent relationship across response variables, relationships with quadrat vegetation cover varied, with alien occupancy generally increasing with vegetation cover and invader abundance declining. The positive relationship between alien herb occupancy and vegetation cover is consistent with ideas related to habitat filtering (Catford et al. 2009, Enders et al. 2020). Alien colonisation was likely elevated in areas of high vegetation cover because growing conditions were suitable for most plant species, thereby increasing the probability of an alien plant being present (Catford et al. 2011). Conversely, proportional cover likely remained low in high-cover areas because of high competition from resident plants (Nunez-Mir et al. 2017). Unlike forbs and graminoids, alien woody occupancy and abundance both declined with increasing woody vegetation cover (Fig. 4). This may reflect biotic resistance from resident biota, but also likely reflects that denser woody vegetation is more intact, with likely lower levels of human-mediated disturbance and introduction of alien plant propagules. The relationships with vegetation cover highlight how factors facilitating invasion can vary between growth forms and stages of invasion (Catford et al. 2022).

**Spatial patterns of invasion**

Alien plant invasion was predicted to be highest in areas with intensive land use, where urban and agriculture are the dominant landcover, and areas immediately adjacent to roads where habitat is fragmented and propagule pressure and resource availability are high (Fig. 6). These patterns are consistent with those elsewhere and point to the role of human activities and human-mediated dispersal in facilitating invasion (González-Moreno et al. 2014, Rauschert et al. 2017, Szymura et al. 2018).

Despite similar responses of alien woody and herbaceous vegetation to human activities, there was some variation in the level and spatial distributions of the three growth forms examined (Fig. 6). Forbs could be found almost everywhere in the study region, though their cover was lower in the high elevation areas. Compared with alien forbs and woody vegetation, graminoid invasion was largely confined to lower elevation areas dominated by human activities and was much more limited in areas dominated by native vegetation, like in national parks and reserves and in the Great Dividing Range (Figs 1 & 6). Giorgis *et al.* (2016) also found that graminoid invasion was lower in native woodlands. Woody invasion was much more limited than herbaceous invasion, which may reflect a range of factors including lower colonisation and propagule pressure, lower habitat suitability and shorter effective residence times (i.e. especially when considering species generation times).

**Management implications**

Our study has illustrated that invasion is driven by a suite of factors, many of them shared across different growth forms, highlighting multiple vulnerabilities and levers for management. Focusing on proportional abundance of alien taxa, our results suggest that further native vegetation loss will facilitate alien plant dominance in the study region. Deforestation, wildfire and other land use changes that disturb native vegetation thus all pose a risk for further invasion. The study region – and south-eastern Australia more broadly – is prone to wildfire, as the devastating bushfires of 2019-2020 demonstrated, a risk that is set to rise as climate change strengthens (Turbelin and Catford 2021). Our results highlight the importance of maintaining or restoring native vegetation to limit dominance of alien plants, especially for woody alien species that may otherwise struggle to colonise. By extension, our findings also confirm the value of actively managing alien plant populations while native vegetation recovers from disturbances like fire (Lindenmayer et al. 2015)

As well as reducing native vegetation and associated biotic resistance, urban and agricultural expansion will increase habitat fragmentation and propagule pressure, likely increasing invasion in areas that currently have low levels of invasion. Based on our study, alien graminoids should benefit the most from this sort of landcover change (Fig. 6e-f). In addition to increasing wildfire risk, climate change may facilitate invasion in the study region by increasing temperatures (Fig. 3, Catford and Jones 2019). Counteracting these changes (among others; Nolan et al. 2021) with local and regional management measures, like strategic land use planning or vegetation restoration, will be important for limiting further invasion (O'Reilly-Nugent et al. in press).

Identifying common drivers of invasion, and regions highly susceptible to invasion, can help identify areas and actions that should be prioritised for management. While useful to examine trends of all alien plants combined, grouping species by growth form enables more targeted science and management. Single-species models will remain a key tool in understanding and managing invasive plants, but more general models based on plant growth form offer an efficient and informative approach for assessing plant invasion across variable landscapes.

## Author contributions

JC, DG & MW conceptualised the study; MW provided the data; DG undertook the modelling; DG wrote the first draft of the manuscript; all authors contributed to later versions of the manuscript; JC acquired funding.

## Acknowledgements

We acknowledge the Traditional Owners of the land on which this work is based. Funding was provided to JC by King's College London Geography Research Impact Fund and the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No. [101002987]).

## REFERENCES


Bartlett, A. C., T. M. Blackburn, R. Randall, and J. A. Catford. 2023. Characteristics of Australia's alien flora vary with invasion stage. Global Ecology and Biogeography **32**:1163-1177.

Bradshaw, C. J. A., A. J. Hoskins, P. J. Haubrock, R. N. Cuthbert, C. Diagne, B. Leroy, L. Andrews, B. Page, P. Cassey, A. W. Sheppard, and F. Courchamp. 2021. Detailed assessment of the reported economic costs of invasive species in Australia. NeoBiota **67**:511-550.

Brandt, A. J., G. K. Png, I. Jo, C. McGrannachan, K. Allen, D. A. Peltzer, C. D'Antonio, I. A. Dickie, K. French, M. R. Leishman, R. Ostertag, I. M. Parker, M. C. Stanley, K. N. Suding, and P. J. Bellingham. 2023. Managing multi-species plant invasions when interactions influence their impact. Frontiers in Ecology and the Environment **21**:370-379.

Brian, J., and J. Catford. 2023. Ecological scale and context dependence. Page 17 *in* R. D. Cousens, editor. Effective Ecology: Seeking Success in a Hard Science. CRC Press, Boca Raton.

Bureau of Meteorology, and CSIRO. 2019a. Regional Weather and Climate Guide – Goulburn Broken.

Bureau of Meteorology, and CSIRO. 2019b. Regional Weather and Climate Guide – West Gippsland.

Catford, J. A., J. B. Baumgartner, P. A. Vesk, M. White, Y. M. Buckley, and M. A. McCarthy. 2016. Disentangling the four demographic dimensions of species invasiveness. Journal of Ecology **104**:1745-1758.

Catford, J. A., R. Jansson, and C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity & Distributions **15**:22-40.

Catford, J. A., and L. P. Jones. 2019. Grassland invasion in a changing climate. Pages 149-171 *in* D. J. Gibson and J. A. Newman, editors. Grasslands and Climate Change. Cambridge University Press, Cambridge.

Catford, J. A., A. L. Smith, P. D. Wragg, A. T. Clark, M. Kosmala, J. Cavender-Bares, P. B. Reich, and D. Tilman. 2019. Traits linked with species invasiveness and community invasibility vary with time, stage and indicator of invasion in a long-term grassland experiment. Ecology Letters **22**:593-604.

Catford, J. A., P. A. Vesk, D. M. Richardson, and P. Pyšek. 2012. Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. Global Change Biology **18**:44-62.

Catford, J. A., P. A. Vesk, M. D. White, and B. A. Wintle. 2011. Hotspots of plant invasion predicted by propagule pressure and ecosystem characteristics. Diversity and Distributions **17**:1099-1110.

Catford, J. A., J. R. U. Wilson, P. Pyšek, P. E. Hulme, and R. P. Duncan. 2022. Addressing context dependence in ecology. Trends in Ecology & Evolution **37**:158-170.

Cordier, J. M., R. Loyola, O. Rojas-Soto, and J. Nori. 2020. Modeling invasive species risk from established populations: Insights for management and conservation. Perspectives in Ecology and Conservation **18**:132-138.

D'Antonio, C. M., R. Ostertag, S. Cordell, and S. Yelenik. 2017. Interactions Among Invasive Plants: Lessons from Hawaiʻi. Annual Review of Ecology, Evolution, and Systematics **48**:521-541.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88**:528-534.

De Marco, P. J., and C. C. Nóbrega. 2018. Evaluating collinearity effects on species distribution models: An approach based on virtual species simulation. PLoS ONE **13**:e0202403.

De'ath, G. 2007. Boosted trees for ecological modeling and prediction. Ecology **88**:243-251.

Diagne, C., B. Leroy, A.-C. Vaissière, R. E. Gozlan, D. Roiz, I. Jarić, J.-M. Salles, C. J. A. Bradshaw, and F. Courchamp. 2021. High and rising economic costs of biological invasions worldwide. Nature.

Elith, J., and J. R. Leathwick. 2017. Boosted Regression Trees for ecological modeling. Page R Documentation.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology **77**:802-813.

Enders, M., F. Havemann, F. Ruland, M. Bernard-Verdier, J. A. Catford, L. Gómez-Aparicio, S. Haider, T. Heger, C. Kueffer, I. Kühn, L. A. Meyerson, C. Musseau, A. Novoa, A. Ricciardi, A. Sagouis, C. Schittko, D. L. Strayer, M. Vilà, F. Essl, P. E. Hulme, M. van Kleunen, S. Kumschick, J. L. Lockwood, A. L. Mabey, M. A. McGeoch, E. Palma, P. Pyšek, W.-C. Saul, F. A. Yannelli, and J. M. Jeschke. 2020. A conceptual map of invasion biology: Integrating hypotheses into a consensus network. Global Ecology and Biogeography **29**:978-991.

Foxcroft, L. C., P. Pyšek, D. M. Richardson, P. Genovesi, and S. MacFadyen. 2017. Plant invasion science in protected areas: progress and priorities. Biological Invasions **19**:1353-1378.

Fristoe, T. S., M. Chytrý, W. Dawson, F. Essl, R. Heleno, H. Kreft, N. Maurel, J. Pergl, P. Pyšek, H. Seebens, P. Weigelt, P. Vargas, Q. Yang, F. Attorre, E. Bergmeier, M. Bernhardt-Römermann, I. Biurrun, S. Boch, G. Bonari, Z. Botta-Dukát, H. H. Bruun, C. Byun, A. Čarni, M. L. Carranza, J. A. Catford, B. E. L. Cerabolini, E. Chacón-Madrigal, D. Ciccarelli, R. Ćušterevska, I. de Ronde, J. Dengler, V. Golub, R. Haveman, N. Hough-Snee, U. Jandt, F. Jansen, A. Kuzemko, F. Küzmič, J. Lenoir, A. Macanović, C. Marcenò, A. R. Martin, S. T. Michaletz, A. S. Mori, Ü. Niinemets, T. Peterka, R. Pielech, V. Rašomavičius, S. Rūsiņa, A. S. Dias, M. Šibíková, U. Šilc, A. Stanisci, S. Jansen, J.-C. Svenning, G. Swacha, F. van der Plas, K. Vassilev, and M. van Kleunen. 2021. Dimensions of invasiveness: Links between local abundance, geographic range size, and habitat breadth in Europe's alien and native floras. Proceedings of the National Academy of Sciences **118**:e2021173118.

GBCMA. 2013. Goulburn Broken Regional Catchment Strategy 2013-2019.

Giorgis, M. A., A. M. Cingolani, P. A. Tecco, M. Cabido, M. Poca, and H. von Wehrden. 2016. Testing alien plant distribution and habitat invasibility in mountain ecosystems: growth form matters. Biological Invasions **18**:2017-2028.

González-Moreno, P., J. M. Diez, I. Ibáñez, X. Font, and M. Vilà. 2014. Plant invasions are context-dependent: multiscale effects of climate, human activity and habitat. Diversity and Distributions **20**:720-731.

Hijmans, R. 2019. raster: Geographic Data Analysis and Modeling. .

Hijmans, R. J., S. Phillips, J. Leathwick, and J. Elith. 2017. Package 'dismo': Species Distribution Modeling.

Hoffmann, B. D., and L. M. Broadhurst. 2016. The economic cost of managing invasive species in Australia. NeoBiota **31**:1-18.

Hulme, P. E., T. Ikeda, V. Vandvik, R. Blanchard, M. Camacho-Cervantes, I. Herrera, A. Koyama, C. L. Morales, L. K. Munishi, P. K. T. N. S. Pallewatta, E. Per, J. Pergl, A. Ricciardi, and R. O. Xavier. 2023. IPBES Invasive Alien Species Assessment: Chapter 3. Drivers affecting biological invasions. IPBES, Zenodo. .

IPBES. 2023. Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES secretariat, Bonn, Germany.

Januchowski-Hartley, S. R., P. Visconti, and R. L. Pressey. 2011. A systematic approach for prioritizing multiple management actions for invasive species. Biological Invasions **13**:1241-1253.

Junaedi, D. I., G. Guillera-Arroita, P. A. Vesk, M. A. McCarthy, M. A. Burgman, and J. A. Catford. 2021. Traits explain invasion of alien plants into tropical rainforests. Ecology and Evolution **11**:3808-3819.

Kent, M., and P. Coker. 1992. Vegetation Description and Analysis: A Practical Approach. John Wiley & Sons, Chichester.

Kuebbing, S. E., M. A. Nuñez, and D. Simberloff. 2013. Current mismatch between research and conservation efforts: The need to study co-occurring invasive plant species. Biological Conservation **160**:121-129.

Leathwick, J. R., J. Elith, W. L. Chadderton, D. Rowe, and T. Hastie. 2008. Dispersal, disturbance and the contrasting biogeographies of New Zealand's diadromous and non-diadromous fish species. Journal of Biogeography **35**:1481-1497.

Lindenmayer, D. B., J. Wood, C. MacGregor, Y. M. Buckley, N. Dexter, M. Fortescue, R. J. Hobbs, and J. A. Catford. 2015. A long-term experimental case study of the ecological and cost effectiveness of invasive plant management in achieving conservation goals: Bitou Bush control in Booderee National Park in eastern Australia. PLoS ONE **10**:e0128482.

Lohr, C. A., J. Hone, M. Bode, C. R. Dickman, A. Wenger, and R. L. Pressey. 2017. Modeling dynamics of native and invasive species to guide prioritization of management actions. Ecosphere **8**:e01822.

Nolan, R. H., L. Collins, A. Leigh, M. K. J. Ooi, T. J. Curran, T. A. Fairman, V. Resco de Dios, and R. Bradstock. 2021. Limits to post-fire vegetation recovery under climate change. Plant, Cell & Environment **44**:3471-3489.

Novoa, A., D. Moodley, J. A. Catford, M. Golivets, J. Bufford, F. Essl, B. Lenzner, Z. Pattison, and P. Pyšek. 2021. Global costs of plant invasions must not be underestimated. NeoBiota **69**:75-78.

Nunez-Mir, G. C., A. M. Liebhold, Q. Guo, E. G. Brockerhoff, I. Jo, K. Ordonez, and S. Fei. 2017. Biotic resistance to exotic invasions: its role in forest ecosystems, confounding artifacts, and future directions. Biological Invasions **19**:3287-3299.

O’Reilly-Nugent, A., D. M. Blumenthal, E. M. Wandrag, R. P. Duncan, and J. A. Catford. in press. Active restoration after three decades: seed addition increases native dominance compared to landscape-scale secondary succession. Journal of Applied Ecology.

Palma, E., P. A. Vesk, and J. A. Catford. 2022. Building trait datasets: effect of methodological choice on a study of invasion. Oecologia **199**:919-935.

Palma, E., P. A. Vesk, M. White, J. B. Baumgartner, and J. A. Catford. 2021. Plant functional traits reflect different dimensions of species invasiveness. Ecology **102**:e03317.

Pérez-Navarro, M. A., A. T. Clark, J. Brian, H. E. R. Shepherd, and J. A. Catford. 2023. Influence of functional and phylogenetic dissimilarity on exotic plant invasion depends on spatial scale. bioRxiv:2023.2008.2018.553820.

Pyšek, P., S. Bacher, I. Kühn, A. Novoa, J. A. Catford, P. E. Hulme, J. Pergl, D. M. Richardson, J. R. U. Wilson, and T. M. Blackburn. 2020a. MAcroecological Framework for Invasive Aliens (MAFIA): disentangling large-scale context dependence in biological invasions. NeoBiota **62**:407-461.

Pyšek, P., P. E. Hulme, D. Simberloff, S. Bacher, T. M. Blackburn, J. T. Carlton, W. Dawson, F. Essl, L. C. Foxcroft, P. Genovesi, J. M. Jeschke, I. Kühn, A. M. Liebhold, N. E. Mandrak, L. A. Meyerson, A. Pauchard, J. Pergl, H. E. Roy, H. Seebens, M. van Kleunen, M. Vilà, M. J. Wingfield, and D. M. Richardson. 2020b. Scientists' warning on invasive alien species. Biological Reviews **95**:1511–1534.

Rauschert, E. S. J., D. A. Mortensen, and S. M. Bloser. 2017. Human-mediated dispersal via rural road maintenance can move invasive propagules. Biological Invasions **19**:2047-2058.

Ridgeway, G. 2019. Package ‘gbm’: Generalized Boosted Regression Models.

Seebens, H., T. M. Blackburn, E. E. Dyer, P. Genovesi, P. E. Hulme, J. M. Jeschke, S. Pagad, P. Pyšek, M. van Kleunen, M. Winter, M. Ansong, M. Arianoutsou, S. Bacher, B. Blasius, E. G. Brockerhoff, G. Brundu, C. Capinha, C. E. Causton, L. Celesti-Grapow, W. Dawson, S. Dullinger, E. P. Economo, N. Fuentes, B. Guénard, H. Jäger, J. Kartesz, M. Kenis, I. Kühn, B. Lenzner, A. M. Liebhold, A. Mosena, D. Moser, W. Nentwig, M. Nishino, D. Pearman, J. Pergl, W. Rabitsch, J. Rojas-Sandoval, A. Roques, S. Rorke, S. Rossinelli, H. E. Roy, R. Scalera, S. Schindler, K. Štajerová, B. Tokarska-Guzik, K. Walker, D. F. Ward, T. Yamanaka, and F. Essl. 2018. Global rise in emerging alien species results from increased accessibility of new source pools. Proceedings of the National Academy of Sciences **115**:E2264-E2273.

Šímová, I., C. Violle, J.-C. Svenning, J. Kattge, K. Engemann, B. Sandel, R. K. Peet, S. K. Wiser, B. Blonder, B. J. McGill, B. Boyle, N. Morueta-Holme, N. J. B. Kraft, P. M. van Bodegom, A. G. Gutiérrez, M. Bahn, W. A. Ozinga, A. Tószögyová, and B. J. Enquist. 2018. Spatial patterns and climate relationships of major plant traits in the New World differ between woody and herbaceous species. Journal of Biogeography **45**:895-916.

ARPHA Preprints Author-formatted, not peer-reviewed document posted on 21/08/2024. DOI: https://doi.org/10.3897/arphapreprints.e135147

Szymura, T. H., M. Szymura, M. Zając, and A. Zając. 2018. Effect of anthropogenic factors, landscape structure, land relief, soil and climate on risk of alien plant invasion at regional scale. Science of the Total Environment **626**:1373-1381.

Turbelin, A. J., and J. A. Catford. 2021. Invasive plants and climate change *in* T. M. Letcher, editor. Climaet Change: Observed Impacts on Planet Earth. Elsevier.

WGCMA. 2019. West Gippsland Regional Catchment Strategic Plan 2019-2024.