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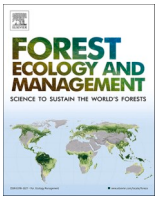

Biotic predictors improve species distribution models for invasive plants in Western U.S. Forests at high but not low spatial resolutions

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ABSTRACT

Invasions by non-native plants threaten forest health and sustainability. The ability to predict areas at greatest risk to invasion is essential for informing both monitoring and management of invasive species. Species distribution models (SDMs) are often used to identify environmental correlates of a species' occurrence and predict geographic areas that may be suitable for its presence and are commonly constructed using solely abiotic predictors. However, mounting evidence implies that not including biotic predictors in SDMs may yield less accurate models at some resolutions typical of landscape-scale models, although this possibility has rarely been evaluated in invasive plants. In this study, we determined whether including descriptors of the biotic environment improved the accuracy of SDMs built at five decreasing spatial resolutions for infestations of five common invasive plants in forests of California, Oregon, and Washington, USA and described environmental correlates of each species' presence.

Predictors of occurrence often echoed those identified in previous studies of the focal species, indicating that our models accurately identified important environmental drivers of occurrence. Including biotic predictors in the SDMs consistently improved model accuracy only at the highest resolution we examined, which may be due to the spatial scale at which biotic interactions primarily act to constrain species' distributions, the particular biotic predictors we used in our models, or correlations between attributes of the abiotic and biotic environment. This finding suggests that, while the practice of building SDMs using abiotic predictors alone may generally yield models whose accuracy does not differ substantially from those that also include biotic predictors, the effects of biotic interactions on the distribution of invasive plants in forests may be detectable at larger scales than previously thought.

1. Introduction

Improved ability to predict the extent and trajectory of invasions within forested systems is a key goal of forest ecology and management (Moser et al., 2016). Invasions can threaten sustainable forestry (Chornesky et al., 2005), alter disturbance regimes (Pyšek et al., 2012), reshape ecosystem processes (Vitousek et al., 1987; D'Antonio and Vitousek, 1992; Mack et al., 2000; Ehrenfeld, 2003; Levine et al., 2003; Vilà and Weiner, 2004; D'Antonio and Hobbie, 2005), transform community composition in recipient ecosystems (Mack and D'Antonio, 1998), and yield substantial economic costs (Pimentel et al., 2000; Pimentel et al., 2005; Holmes et al., 2009). Determining which environmental attributes may serve as useful predictors of invasions and the spatial scale at which these attributes primarily act may allow managers to better understand invasive species' current distributions, forecast the potential extent and direction of their spread, and develop targeted strategies for monitoring and control across spatial scales.

The distributions of both native and exotic species are thought to arise from a complex interplay of processes acting across spatial and temporal scales, including evolutionary constraints, abiotic conditions (including past and present climate, resource availability, and topography), biotic interactions, and the species' capacity for dispersal (Carter and Prince, 1988; Gaston, 2009; Sexton et al., 2009; Wiens, 2011). A species' distribution is hypothesized to represent the geographic space

Abbreviations: SDM, Species Distribution Model; FIA, Forest Inventory and Analysis; AUC, Area Under the Curve of the receiver operating characteristic; TSS, True Skill Statistic; ΔTSS, Difference in TSS between full and abiotic models for a species at a particular resolution.

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where suitable abiotic and biotic environmental conditions and sufficient dispersal among areas of environmentally suitable habitat overlap (the BAM- biotic, abiotic, and migration- model; Soberón, 2007). However, the relative influence exerted by the abiotic environment and biotic interactions on species' distributions is thought to vary according to spatial scale that is examined, with constraints operating in a spatially hierarchical manner. Abiotic conditions such as climate and topography are anticipated to act as the primary environmental filter at global to landscape scales, while the relative influence of biotic interactions on species' distributions is expected to increase at finer local to micro scales due to the more locally-variable nature of these interactions (Willis and Whittaker, 2002; Pearson and Dawson, 2003; Soberón and Nakamura, 2009). Rather than referring to abiotic or biotic attributes of the environment, Hutchinson (1978) and Soberón (2007) referred to the distinction between a 'scenopoetic' class of environmental variables comprising broad, non-interactive attributes of the environment which dictate species distributions at large scales and a 'bionomic' class of interactive environmental variables comprising biotic conditions and resource-consumer interactions whose influence on species distributions is likely to play out primarily at local scales.

The concept that abiotic mechanisms are the primary determinant of species' distributions at large spatial scales is commonly cited in support of constructing low-resolution ($\geq$1 km^2) landscape- to global-scale species distribution models (SDMs; Guisan and Thuiller 2005; Elith et al., 2006) using solely abiotic predictors (Guisan and Zimmermann, 2000; Pearson and Dawson 2003; Guisan and Thuiller 2005; Elith et al., 2006). This practice is bolstered by the broad availability of large-scale abiotic data (particularly those describing climatic conditions) and a general lack of data describing the biotic environment across the landscape. While several studies have supported the practice of predicting native species' distributions using solely abiotic predictors by demonstrating predominantly abiotic control over large-scale patterns of distribution (Wiens, 2011; Schweiger and Beierkuhnlein, 2016), a growing body of literature suggests that incorporating data describing disturbance and biotic interactions in regional- to landscape-scale SDMs can significantly improve model accuracy and potentially illuminate the drivers of species' distributions. For example, models including variables describing the distribution of a competitor, facilitator, or forage species may often yield improved predictions compared to those containing solely abiotic predictors (Leathwick and Austin, 2001; Araújo and Luoto, 2007; Heikkinen et al., 2007; Giannini et al., 2013; Gherghel et al., 2018). The same has been observed for models that incorporate data describing land cover, canopy cover, or attributes of plant communities which may serve as proxies for disturbance or competition (Bradley and Fleishman, 2008; Ibáñez et al., 2009; Meier et al., 2010; Ervin and Holly, 2011; Nieto-Lugilde et al., 2015; Peeler and Smithwick, 2018; *but see* Thuiller et al., 2004).

Studies that evaluate scale-dependence in the influence of abiotic and biotic conditions on the distribution of invasive plants are rare and come to contrasting conclusions regarding the extent to which the impacts of biotic interactions are detectable beyond local and micro scales (Collingham et al., 2000; Fraterrigo et al., 2014; Cabra-Rivas et al., 2016). Furthermore, we are aware of none which have examined this question in forested systems. An improved understanding of the conditions that make a forested area more or less susceptible to invasion by non-native species and the spatial scale at which these attributes of the environment act may allow for the development of more targeted monitoring strategies tailored to the spatial scale and resolution of interest to forest managers.

In this study, we used ensemble SDMs to model the distributions of infestations of five common invasive plants in Western U.S. forests across five spatial resolutions. This approach allowed us to determine abiotic, biotic, and disturbance-related predictors of invasion by these species and to evaluate how the relative importance of biotic predictors changed across resolutions. We tested the hypothesis that the contribution of biotic predictors to models would decline with decreasing model resolution such that improvements would be greatest at the highest resolution and either minimal or absent at intermediate to low resolutions.

2. Materials and methods

All data manipulations, model construction and evaluation were performed in ArcGIS version 10.6.1 (ESRI, 2018) and R Statistical Software version 4.1.0 (R Core Team, 2021).

2.1. Invasive species occurrence data

Spatially-referenced data on the presence and absence of invasive species were extracted from the USDA Forest Service's Forest Inventory and Analysis (FIA) Phase 2 Vegetation (P2VEG) dataset collected from 2004 to 2011 on plots located on forested lands throughout California,

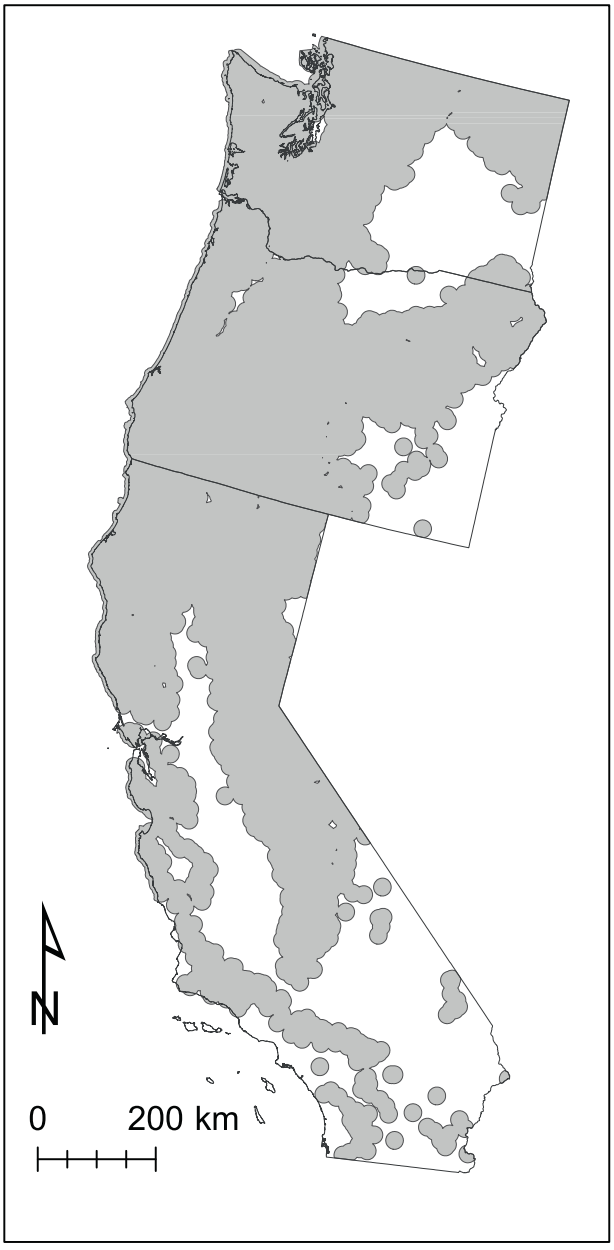

Fig. 1. Map of study area denoted by a grey polygon across Washington, Oregon, and California, USA. The study area comprised a 15 km buffer zone surrounding the locations of forested inventory plots.

Oregon, and Washington, USA (Fig. 1). Inventory sample locations were placed at a distribution of 1 per 24.3 km^2 except on National Forest lands outside of designated Wilderness Areas in Oregon and Washington (1 per 7.5 km^2). Plots were installed where locations intersected forested areas and consisted of an 87.8 m diameter circle containing four 14.6 m diameter circular subplots (Bechtold and Patterson 2005). The study area comprised a 15 km buffer surrounding 10,786 FIA plots included in the analysis (Fig. 1); this buffer size was chosen to ensure that forested areas surrounding inventory plots were represented in model outputs while simultaneously excluding large areas of continuous non-forested conditions. In accordance with the P2VEG protocol, field crews recorded up to four of the most dominant vascular plant species per growth habit (forb, graminoid, shrub, and tree) with ≥3% foliar cover within each subplot (USDA Forest Service, 2017). This cover threshold means that species which typically occur at low densities may be missed, but species present at ≥3% cover were not among the four dominant plants in a growth habit on a subplot only 6% of the time (Gray et al., 2021). It is highly unlikely for the invasive plants investigated here to be present at ≥3% cover and not be recorded on one or more subplots within a plot. Therefore, we expect that our dataset offers a comprehensive sample of the presence of populations of invasive species with ≥3% cover across the study area.

The five invasive species included in this study were among the most commonly recorded non-native plants across the study area (>70 records each; Gray et al., 2021). These invasive species included three graminoids, (1) *Bromus diandrus* (ripgut brome; 107 records), (2) *Bromus hordeaceus* (soft brome; 71 records), and (3) *Bromus tectorum* (cheatgrass; 1275 records), one forb (4) *Hypericum perforatum* (St. John's wort; 207 records), and one shrub (5) *Rubus armeniacus* (Himalayan blackberry; 312 records). We assigned each plot in the dataset a binary value for the presence or absence of each of the invasive species. Each species was recorded as present in a plot if it had been recorded in any of the four subplots, and absent if it had not been recorded on the plot. As the P2VEG protocol requires ≥3% foliar cover for a species to be recorded on a subplot, presence in this study represents the presence of an infestation (≥3% cover) rather than the simple presence or absence of the species within the plot. While absolute presence or absence regardless of cover is arguably a more accurate metric, understanding the environmental predictors of invasive species infestations is potentially of greater interest to managers attempting to track and control their extent.

After determining the presence or absence of an infestation (*hereafter,* occurrence) by each focal species within each plot, we created aggregated datasets describing occurrence within spatial grids at each of five increasing grid sizes across the study area: 1 km (1 × 1 km), 2 km (2 × 2 km), 3 km (3 × 3 km), 5 km (5 × 5 km) and 10 km (10 × 10 km). It was not uncommon for multiple plots to occur within a single grid cell when the sampling area was divided into lower resolution grids (2 km to 10 km). In cases where multiple plots occurred within a single grid cell, the species was recorded as present within the cell if it had been recorded in any plots within the cell and as absent if it did not occur in any plots within the cell.

2.2. Environmental conditions

We paired spatially-referenced presence data for each focal species at each grid size with data describing the attributes of the abiotic environment, disturbance history, and biotic environment in the grid cell where the presence or absence record occurred. We chose a maximum resolution of 1 km^2 for raster data describing environmental conditions that were paired with occurrence data in order to avoid errors associated with increasing the resolution of the original raster datasets. Sources of environmental data and original raster resolutions are presented in Appendix 1. Rasters were aggregated as necessary to 1 km, 2 km, 3 km, 5 km, and 10 km resolutions to be paired with occurrence data at the corresponding resolution (aggregate, raster package, Hijmans, 2017). Unless otherwise noted, raster aggregation was accomplished by calculating the mean value of aggregated raster pixels.

The abiotic environment was characterized using 19 standard bioclimatic variables (WORLDCLIM v 2.0; Fick and Hijmans, 2017) and data describing the elevation and the standard deviation of both the elevation and slope of each pixel (a measure of the 'roughness' of the terrain) derived from a digital elevation model for the region (Consultative Group on International Agricultural Research Consortium for Spatial Information, 2017). Although the bioclimatic variables based on 1970–2000 climate normals predate our field measurements, we expect the spatial patterns of variation in climate to be largely unchanged and that most of the observed plant populations became established in prior decades. Disturbance was characterized using a measure of the human footprint within each pixel and the fire history of the pixel. Data describing the normalized human footprint within a pixel ranged from 0 to 100 and was based upon values of the Human Influence Index version 2 (HII), which describes human population density, human land use and infrastructure, and the degree of human access to an area via transportation corridors and coastline within a pixel during the period from 1995 to 2004 (Wildlife Conservation Society and Center for International Earth Science Information Network 2005). A binary variable indicated whether each pixel occurred within the boundaries of a wildfire recorded between 1984 and 2016 (Monitoring Trends in Burn Severity, 2017), as fire is often positively associated with plant invasions (D'Antonio and Vitousek, 1992; Hobbs and Huenneke, 1992; Keeley et al., 2003). When aggregating fire history data in the construction of lower-resolution rasters, the presence of a wildfire in any of the aggregated pixels within a larger pixel was taken to indicate the presence of a historical wildfire in the aggregated pixel. Due to the complexity of incorporating data describing the intensity of wildfire events, particularly where multiple wildfires had been recorded across years within an area, we did not include a descriptor of burn severity among our abiotic predictors.

The biotic environment in each pixel was characterized using modeled descriptors of forest stand conditions in each pixel including the basal area of live trees, stand age, the quadratic mean diameter of stands, and canopy cover (Landscape Ecology, Modeling, Mapping and Analysis 2014). Standard deviations of each metric were also included as an estimate of variability within each pixel in order to provide an estimate of the 'patchiness' of forest conditions, which can indicate the degree to which disturbance may have affected forest stands within an area. These biotic variables describe potential competitive relationships with overstory trees for resources such as light and soil nutrients. Many invasive plants are shade intolerant and may be incapable of growing under dense forest canopy cover (Martin et al., 2009). In addition, stand age and size may serve as a proxy for the time since stand-replacing disturbance, with younger stands or smaller trees representing forests which have been more recently disturbed.

2.3. Model dataset construction

We paired abiotic, biotic, and disturbance data for each presence or absence record for each of the five focal species at each of the five examined resolutions (extract, raster package, Hijmans, 2017). Absence records that likely resulted from dispersal limitation were removed from datasets at each resolution in accordance with methods outlined in Hattab et al. (2017; Appendix 2), which allowed us to better model the potential distribution of the focal species. The number of presence and absence records retained after spatial thinning and the removal of likely dispersal-limited absences for each species at each resolution is presented in Appendix 3. For each species at each resolution, we selected a subset of explanatory variables to be considered for inclusion in distribution models based upon their explanatory power in univariate logistic regressions and their lack of strong multicollinearity with other selected explanatory variables ($r \leq |0.7|$ *sensu* Dormann et al., 2013). From this preliminary set of explanatory variables, we further narrowed the set of

terms to be included in the models by ranking potential predictors according to their normalized importance values in generalized linear models for the presence of each focal species at each resolution. Normalized importance values for predictors were calculated by determining the correlation between the model prediction using the original data values and the prediction using randomly drawn data values and subtracting the value of that correlation from one. If predictor randomization has a large impact on the prediction generated by the model, this indicates that the predictor contributes a relatively large amount to model predictions and therefore has a higher importance value than a predictor with a lower impact. To determine the relative contribution of biotic predictors across resolutions, we first built SDMs for each species at each resolution using solely abiotic and disturbance-related predictors (*hereafter,* abiotic models) and then built SDMs using abiotic, disturbance-related, and biotic predictors (*hereafter,* full models). We then compared the accuracy of abiotic and full models at each resolution to determine the how the contribution of biotic predictors to model accuracy changed across resolutions. We retained the same number of predictors in both the abiotic and full models for each species at a given resolution to ensure that differences in model fit were due to differences in the variables included in the models rather than a result of a greater number of predictors in the full models. While disturbances impact both the abiotic and biotic environment experienced by a species at a fine spatial scale, we included disturbance-related predictors in the abiotic models (rather than categorizing them as biotic predictors to be included solely in the full models) so as to provide a conservative estimate of the contributions of biotic predictors to model fit when comparing abiotic and full models across resolutions.

Some efforts at predicting the invasive range of a species utilize occurrence records and associated environmental data from both the introduced and the native ranges in an attempt to more comprehensively describe the potential distribution of the invasive species (Jiménez-Valverde et al., 2011), although this practice can yield biased results if the niche is not conserved between the native and introduced ranges (Srivastava et al., 2019; *e.g.,* Ibáñez et al., 2009). We did not include data from the native ranges of the focal species in our models for several reasons. First among these is that support for niche conservatism between the native range and the introduced range is equivocal (Guisan et al., 2014): environmental conditions associated with presence in the native range may not be reflective of those favoring presence in the introduced range, particularly for long-standing invasions spanning a wide breadth of environmental conditions such as those examined here (Liu et al., 2020; Nguyen and Leung, 2022). Second, the definition of presence utilized in our dataset (≥3% cover) could not be applied to records queried from the native range, as data describing cover are rarely recorded along with occurrence records. Using a different definition of presence for records from the native range than is used in the introduced range may bias predictions of environmental conditions supporting presence at ≥ 3% cover. Third, some of the predictor data used to describe the environment associated with presence or absence records in the invasive range were not available for the native range. Relying upon a subset of our environmental predictors to describe environmental conditions suitable for the presence of the species in the native range could yield inaccurate descriptions of conditions suitable for occurrence in the introduced range. Finally, the long history of focal species presence in the introduced range means that environmental conditions under which they are observed in the study area likely represent a fairly comprehensive description of conditions suitable for their occurrence in this region.

2.4. SDM construction and evaluation

All SDMs were built using the biomod2 package (version 3.5.1; Thuiller et al., 2021) in R (version 4.1.0; R Core Team, 2021). For all SDMs, we used an ensemble approach to avoid biasing model outcomes through the use of a single algorithm and to take advantage of the strengths associated with the use of several algorithms (Araújo and New, 2007). These ensemble SDMs comprised four algorithms, which included two regression methods, (1) generalized linear models (GLM; McCullagh and Nelder, 1989), and (2) generalized additive models (GAM; Hastie and Tibshirani, 1986; 1990), and two machine learning methods, (3) boosted regression trees (BRT; Elith et al., 2008), and (4) random forest (RF; Breiman, 2001), each of which was run 5 times (*sensu* Thuiler et al., 2021). We evaluated the fit of models constructed using each algorithm using 5-fold split-sample cross-validation in which 80% of the original data were used for model construction and the remaining 20% for model evaluation, with evaluation data containing 20% of both presence and absence records. Model runs were evaluated based upon the area under the curve of the receiver operating characteristic (AUC; Swets et al., 1988; Hanley and McNeil, 1982) and the true skill statistic (TSS; Allouche et al., 2006) for each of the 5 model runs to account for limitations inherent to the metrics when viewed in isolation (Shabani et al., 2018). When constructing the ensemble SDM, we retained only model runs whose TSS values exceeded 0.4 and weighted the influence of each model on ensemble SDM predictions as a function of its TSS value. We evaluated ensemble SDM fit using AUC and TSS and generated response plots detailing the influence of variation in model terms on predicted probability of the occurrence of each species at each resolution.

To determine if the inclusion of biotic predictors in SDMs impacted model fit when all species were considered together, we used one-tailed T tests at each resolution to establish whether the difference in TSS values between the full and abiotic models for each individual species (ΔTSS) was significantly greater or less than zero. We also tested for consistent changes in ΔTSS across resolutions and species by performing a multiple linear regression in which ΔTSS was included as the response variable and resolution, species, and an interactive resolution*species term were included as predictors.

3. Results

3.1. Correlates of invasive species infestations

The full set of predictors included in each abiotic and full model, relative importance values for each predictor, variable response plots, and prediction maps for full and abiotic ensemble SDMs for each species at each resolution are presented in Appendix 3. The names of predictor variables included in each SDM, their standardized importance values, and the general relationship between the variable and predicted probability of presence of an infestation by each focal species are presented in Fig. 2. Standardized importance values for each predictor were calculated according to the formula $IV_x = IV_x / \sum_{i=1}^{n} IV_i$, where SIV_x is the standardized importance value of predictor ×, IV_x is the raw importance value of predictor x in the model and $\sum_{i=1}^{n} IV_i$ represents the sum of raw importance values for all predictors in the model. Standardizing importance values allowed for comparisons among models.

In a strict sense, SDMs predict the probability of a species' presence (in this case, the presence of an infestation at ≥3% cover) under a particular set of environmental conditions. This prediction is sometimes referred to as a prediction of habitat suitability under those environmental conditions. We refer to the outputs of our SDMs as predictions of habitat suitability for infestations of focal species when discussing our results below.

Habitat suitability for infestations of *Bromus diandrus* was predicted to be higher in areas with a pronounced annual dry period (lower precipitation in the driest quarter of the year in full models constructed at resolutions of 1 km to 5 km and in the driest month of the year for the full model at the 10 km resolution), higher mean annual temperature, highly variable canopy cover, and more consistent ages of the dominant trees in forest stands. The relationships between habitat suitability and mean annual temperature and precipitation in the driest quarter or

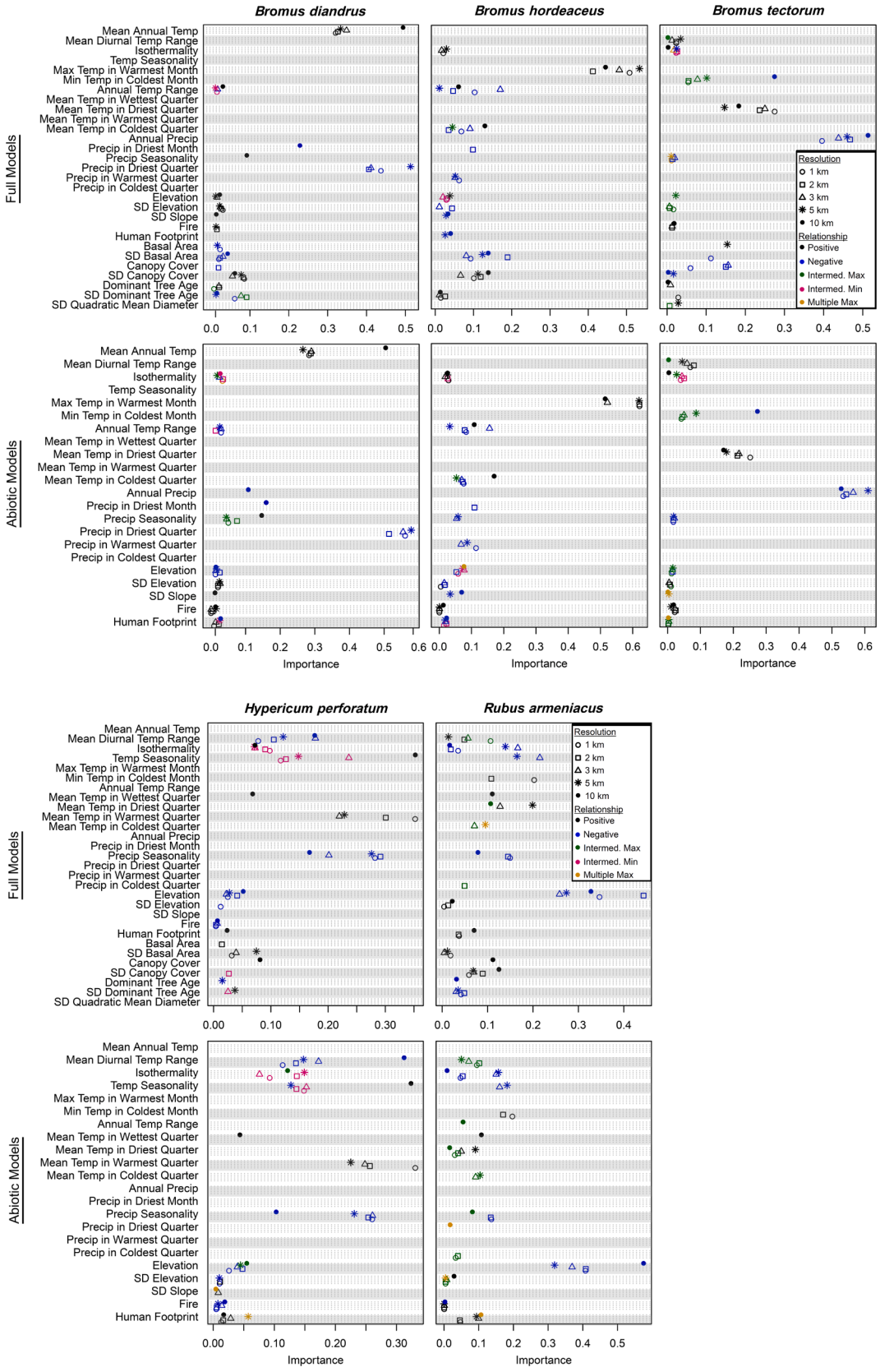

Fig. 2. The standardized importance for predictors of habitat suitability differed among species and between full and abiotic models within species. Importance varied with spatial resolution for many variables within a species and model type. Model resolution is denoted according to symbol shape and fill and the relationship between the predictor and habitat suitability is denoted by symbol color (positive slope, negative slope, unimodal or intermediate maximum, bimodal or intermediate minimum, or multiple maxima or flat). Detailed variable response plots and raw importance values are presented in Appendix 3.

month of the year were similar in abiotic models, wherein higher precipitation seasonality was also positively associated with suitability.

In both full and abiotic models for *Bromus hordeaceus* infestations, higher habitat suitability was predicted for areas with a high maximum temperature in the hottest month and low mean temperatures in the coldest quarter of the year in models built at resolutions of 1 km to 5 km. Somewhat counterintuitively, lower annual temperature ranges (the difference between the maximum temperature in the warmest month and minimum temperature in the coldest month of the year) were also positively associated with habitat suitability in these models. Relationships between habitat suitability and these predictors differed in 10 km resolution models, where habitat suitability was predicted to increase slightly with increasing mean temperature in the coldest quarter of the year and greater annual temperature ranges. In full models at all

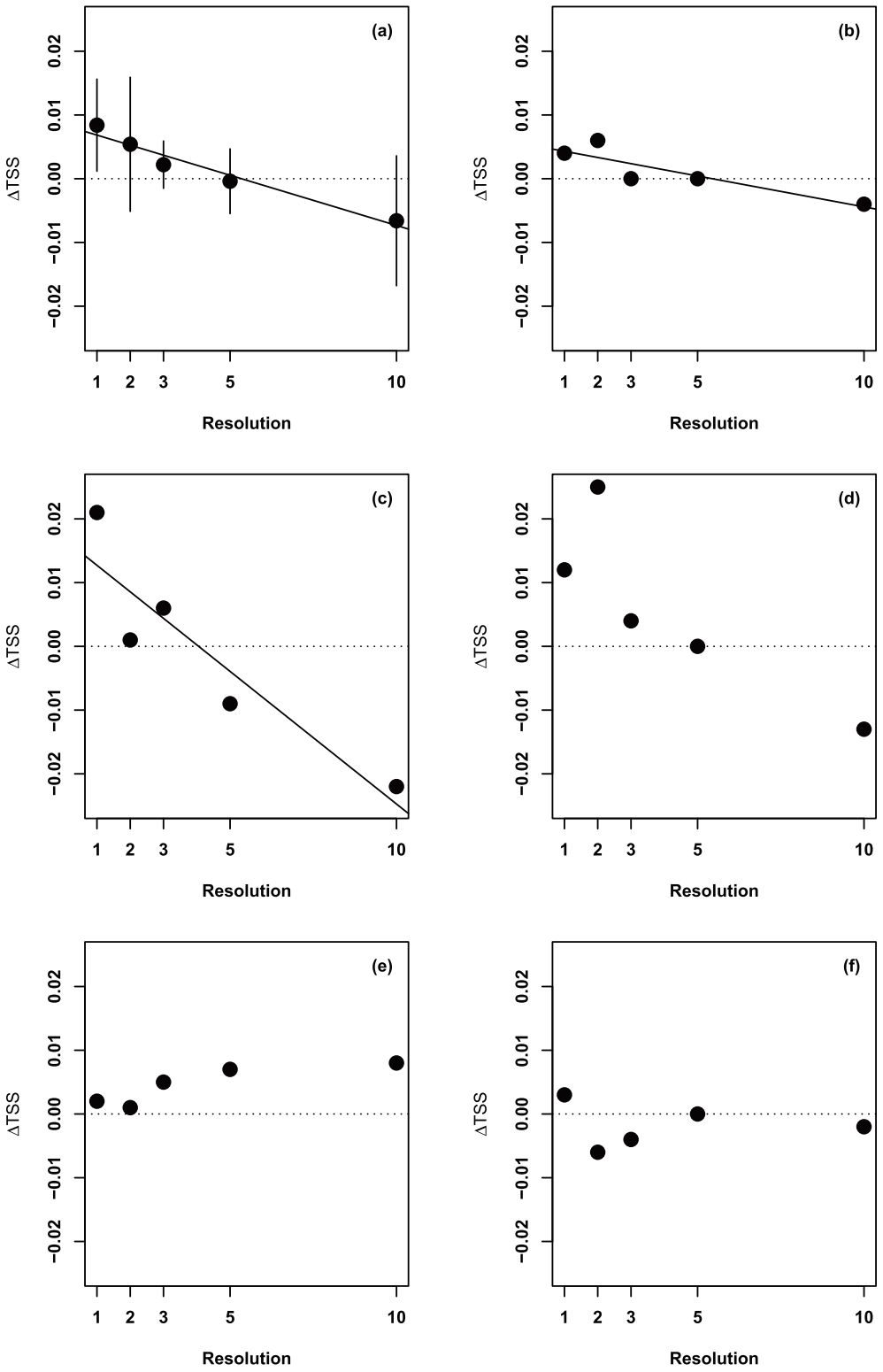

Fig. 3. ΔTSS by resolution for models of infestations of the focal species (a) Mean (±2 S.E.) of all focal species, (b) *Bromus diandrus*, (c) *Hypericum perforatum*, (d) *Bromus hordeaceus*, (e) *Rubus armeniacus*, and (f) *Bromus tectorum.*

resolutions, habitat suitability was predicted to increase in areas with less variability in the basal area of live trees but greater variability in canopy cover.

Habitat suitability for infestations of *Bromus tectorum* was predicted to increase in areas characterized by low annual precipitation, high mean temperatures in the driest quarter of the year and low minimum temperatures in the coldest month of the year, and higher diurnal temperature ranges in both full and abiotic models. No biotic predictor was consistently included in all full models across resolutions, but habitat suitability for *B. tectorum* infestations was negatively associated with canopy cover in full models at resolutions of 1 to 3 km and negatively associated with basal area of live trees at the 5 km resolution.

Habitat suitability for *H. perforatum* infestations was predicted to be greater in areas characterized by low precipitation seasonality and narrower diurnal temperature ranges, and to decrease in areas with intermediate levels of both isothermality and temperature seasonality. In full and abiotic models constructed at 1 to 5 km resolutions, habitat suitability was also predicted to peak where the mean temperature of the warmest quarter of the year was quite high. Important biotic predictors of habitat suitability in full models differed among resolutions, but the standard deviation of the basal area of live trees was positively correlated with habitat suitability at resolutions of 1, 3, and 5 km (Fig. 2).

Predicted habitat suitability in both full and abiotic models for infestations of *Rubus armeniacus* tended to be greatest in low-elevation areas with low annual variation in precipitation and temperature but greater diurnal temperature variation. Habitat suitability was also predicted to be higher in areas with a larger human footprint value across most models. In full models, habitat suitability was negatively associated with variation in the ages of dominant trees at resolutions of 1 to 5 km and positively associated with variation in the canopy cover of forest stands across all examined resolutions. In models at 10 km resolution, greater mean canopy cover and younger stand age were also positively associated with habitat suitability.

3.2. Contributions of biotic predictors to SDM fit across resolutions

Both full and abiotic ensemble SDMs showed excellent performance across the resolutions examined in this study according to their AUC and TSS scores; metrics of SDM fit declined with decreasing resolution (Table A3.2). Although ΔTSS did tend to decline with increasing resolution when all species were considered together (Fig. 3a), only SDMs built at a 1 km resolution showed ΔTSS values that differed significantly from 0, indicating a consistent improvement in SDM fit when biotic predictors were included in SDMs at this resolution but not at any other resolution (Table 1). Multiple linear regression revealed that the relationship between ΔTSS and resolution varied significantly among species (Resolution: $F_{1,15} = 21.6$, $P < 0.001$; Species: $F_{4,15} = 1.8$, $P = 0.19$, Resolution*Species: $F_{4,15} = 7.9P = 0.001$). Models for infestations of *Bromus diandrus* and *Hypericum perforatum* both showed a significant negative relationship between ΔTSS and model resolution ($F_{1,3} = 10.9$, $P = 0.046$, *Adj.* $R^2 = 0.71$ and $F_{1,3} = 16.3$, $P = 0.027$, *Adj.* $R^2 = 0.79$, respectively; Fig. 3b-c). Models for *Bromus hordaceus* infestations showed a marginally significant negative relationship between ΔTSS and model resolution ($F_{1,3} = 8.7$, $P = 0.059$; Fig. 3d), and those for *Rubus armeniacus* infestations showed a marginally significant positive relationship between ΔTSS and resolution ($F_{1,3} = 8.6$, $P = 0.061$; Fig. 3e). No significant relationship existed between ΔTSS and model resolution for models of *Bromus tectorum* infestation ($F_{1,3} = 0.01$, $P = 0.92$; Fig. 3f).

Table 1
Results of one-tailed T-tests for ΔTSS ≠ 0. Resolutions for which ΔTSS is significantly different from 0 are indicated with an asterisk (*).

Model Resolution	H_0	Mean	S.E.	*T*	d.f.	*P*
1 km*	μ>0	0.0084	0.0036	2.32	4	0.04
2 km	μ>0	0.0054	0.0053	1.03	4	0.18
3 km	μ>0	0.0022	0.0019	1.19	4	0.15
5 km	μ<0	−0.0004	0.0025	−0.16	4	0.44
10 km	μ<0	−0.0066	0.0051	−1.30	4	0.13

4. Discussion

A common assumption in constructing large-scale species distribution models is that abiotic constraints have a far larger impact than biotic constraints at the resolutions typical of these models, and that the exclusion of biotic predictors does not significantly affect model performance due to the more local scale at which biotic constraints primarily operate (Willis and Whittaker, 2002; Pearson and Dawson, 2003; Wien, 2011). However, the validity of this practice, particularly for determining the environmental forces that may constrain species distributions, has been increasingly questioned (Anderson, 2017; Godsoe et al., 2017b; Godsoe and Harmon, 2012; Guisan and Thuiller, 2005; Mod et al., 2016; Wisz et al., 2013). In this study, we found that including proxies for biotic interactions consistently improved the fit of SDMs for infestations of several invasive species in Western US forests in models built at the highest resolution we examined. However, including biotic predictors did not improve the accuracy of models built at 2 km to 10 km resolutions across all focal species. The contribution of biotic variables to SDM fit tended to change from positive to slightly negative with decreasing model resolution, albeit with significant variation in this pattern among the focal species. Our results allow us to determine which attributes of the abiotic and biotic environment may predispose forested areas to infestation by common invasive species and describe how the relative importance of these attributes may change across resolutions.

4.1. Correlates of invasive species infestations

The environmental predictors chosen for inclusion in our SDMs and their relationships with habitat suitability for focal species infestations often mirrored previously-observed associations between environmental attributes and invasions by the focal species. Along with the high values of SDM accuracy metrics, this bolsters confidence in our models' ability to describe the environmental conditions under which each of these focal species is likely to establish an infestation throughout the study area. It also and allows us to speculate regarding the drivers underlying relationships between environmental attributes and habitat suitability for infestations of each species.

In general, the invasive *Bromus* species we included in our study are most likely to invade and become dominant in areas where they can outcompete native species for limited resources by germinating and growing vegetatively in the autumn and pre-emptively utilizing water to reproduce earlier in the growing season than perennial native grasses (Harris, 1967; Aguirre and Johnson, 1991; Knapp, 1996; Booth et al., 2003; Chambers et al., 2016; but see Bradford and Lauenroth, 2006). Our SDMs for *B. diandrus*, *B. hordeaceus*, and *B. tectorum* infestations all showed higher habitat suitability in areas with relatively high temperatures in the warmest or driest quarters of the year, indicating hot summer conditions that might allow these invaders to outcompete native species for limited water during the warmest part of the growing season. Negative relationships between predicted habitat suitability and annual precipitation (*B. tectorum*) or precipitation in the driest quarter of the year (*B. diandrus*) also point towards the propensity of these species to invade areas where competition for water may favor the aforementioned life history strategy. Positive associations between habitat suitability and lower mean temperature in the coldest quarter of the year (*B. hordeaceus*) or minimum temperature in the coldest month of the year (*B. tectorum*) may be related to the tendency of these species to thrive in areas with continental rather than coastal climates. Several studies have suggested that *B. tectorum* is most strongly limited by its need for a pulse of precipitation in the autumn to spring and a dearth of

precipitation in the late spring to summer (Mack and Pyke, 1983; 1984; Thill et al., 1984; Knappm 1996; Booth et al., 2003; Bradford and Lauenroth, 2006; Williamson et al 2020), but we did not observe this pattern in our SDMs for infestation by this species. It is possible that these environmental conditions promote the initial establishment of *B. tectorum* but are less important determinants of its ability to become dominant in a recipient community, which may explain why these predictors were not important in our models for *B. tectorum* infestation. Although *B. diandrus* is capable of growing under intact tree canopies (Marañón and Bartolome, 1989, 1993, 1994; Rice and Nagy, 2000), invasive *Bromus* species are often quite shade intolerant (Pierson et al., 1990; Marañón and Bartolome, 1993; Chambers et al., 2016). Our SDMs captured the tendency of these species to establish infestations in areas where competition for light is likely to be minimal due to either disturbance or a lack of overstory shading: full models for at least some resolutions in each species showed higher habitat suitability in forest stands with consistently low canopy cover, consistently young trees, and/or consistently low basal area. In addition, habitat suitability was positively associated with both fire and larger human footprint values in all abiotic models for infestations of each of the *Bromus* species we examined, an observation in keeping with the tendency of invasions by some *Bromus* species to be augmented by both anthropogenic and natural disturbance (D'Antonio and Vitousek, 1992; Gundale et al., 2008; Monty et al., 2013).

Relationships between environmental predictors and habitat suitability in SDMs for *Hypericum perforatum* infestation also matched those described in previous studies relating environmental attributes to invasion by this species. For example, our SDMs for *H. perforatum* infestation showed a positive association between habitat suitability and temperature seasonality, concurring with a previous study which demonstrated that invasions by this species were more likely in areas with broader annual temperature ranges across a portion of our study area (Gray, 2005). *H. perforatum* may also outcompete more shallow-rooted native species for limited water resources during the dry season (Tisdale et al., 1959), which could explain why our SDMs predicted higher suitability for *H. perforatum* infestations in areas where the mean temperature of the warmest quarter of the year was quite high if higher temperatures exacerbate water limitation. We also found that the standard deviation of the basal area of live trees was positively correlated with predicted habitat suitability for *H. perforatum* infestations in SDMs constructed at 1, 3, and 5 km resolutions (Table 1), which may be reflective of the tendency of this species to occur in disturbed settings within forested systems rather than under intact canopies (Tisdale et al., 1959; Spies, 1991; Parks et al., 2005) due to shade intolerance (Parendes and Jones, 2000). This interpretation assumes that variation in basal area of live trees is reflective of a history of patchy disturbances at the resolutions examined in this study.

Habitat suitability for infestations of *Rubus armeniacus* was positively associated with lower elevation, an outcome which agrees with documented patterns of *R. armeniacus* occurrence across elevational gradients (Ohmann and Spies, 1998; Gray, 2005). This species commonly occurs in warm, reliably moist sites characterized by temperate or Mediterranean climates (Ohmann and Spies, 1998; Sarr and Hibbs, 2007; Gaire et al., 2015), which was reflected in our SDMs as higher habitat suitability in areas with higher minimum temperatures in the coldest month of the year and lower precipitation seasonality. As with variation in the basal area of live trees, higher variation in canopy cover may be indicative of disturbance within pixels; the positive relationship between habitat suitability for infestations of *R. armeniacus* and the standard deviation of canopy cover may reflect the tendency of this species to occur in disturbed areas (Hoshovsky, 2000; Caplan and Yeakley, 2006), as seedlings are known to be largely incapable of surviving under heavily shaded conditions (Amor, 1974; Gaire et al., 2015).

4.2. Contribution of biotic predictors to SDM fit across resolutions

Including biotic predictors in our SDMs for infestation by the focal species only significantly improved model fit across all species at the highest resolution we examined (1 km), a result that diverges somewhat from the assumption that the impacts of biotic interactions are not detectable in regional-scale SDMs constructed at the resolutions investigated here. However, this finding is in keeping with a growing number of studies spanning a variety of taxa that have demonstrated an important role for biotic predictors in modeling landscape or regional distributions at resolutions similar to those examined in this study (Wisz et al., 2013; *e.g,* plants: Meineri et al., 2012; Nieto-Lugilde et al., 2015; Duffy and Johnson, 2017; invertebrates: Giannini et al., 2013; González-Salazar et al., 2013; Silva et al., 2014; Simões and Peterson, 2018; reptiles: Gherghel et al., 2018; birds: Heikkinen et al., 2007; Luoto et al., 2007; de Araújo et al., 2014; Belmaker et al., 2015; Freeman and Mason, 2015; and mammals: González-Salazar et al., 2013; Leach et al., 2016; Lewis et al., 2017). Investigations of this kind in invasive plants are relatively rare, and their conclusions remain equivocal. A handful of studies have demonstrated that the inclusion of data describing land cover (Collingham et al., 2000; Cabra-Rivas et al., 2016) can improve models for the distributions or abundance of invasive plants built at resolutions of 2 km to 10 km. While we found that including predictors describing biotic environmental conditions consistently improved the fit of regional-scale models for infestations of the focal species at a 1 km resolution, this was not the case for models built at resolutions of 2 to 10 km. This outcome is more in keeping with those of Fraterrigo et al. (2014), who found that including descriptors of interspecific competition did not significantly impact the accuracy of regional scale models for the distribution of an invasive grass. Our finding that including biotic predictors did not significantly improve SDMs at resolutions of 2 km to 10 km may be explained as a product of the spatial scale at which variation in biotic predictors remained detectable and meaningful, the types of biotic predictors included in our SDMs, and/or the ability to distinguish the influences of biotic interactions from those of abiotic conditions in our SDMs.

Fraterrigo et al. (2014) explained the lack of a significant influence of biotic interactions when modeling the distribution of an invasive grass by appealing to the Eltonian Noise Hypothesis (ENH; Soberón and Nakamura, 2009). The ENH posits that the scale at which biotic interactions affect species' distributions is so local that the impacts of biotic interactions simply appear as 'noise' at the resolutions typical of most large-scale SDMs. In keeping with the ENH, biotic predictors in our SDMs may have become increasingly uninformative as pixels were aggregated at 2 km to 10 km resolutions due to increasing 'noisiness' within each pixel, while a 1 km resolution was sufficiently fine-grained to capture some of the relevant variation in the biotic environment that affected species' distributions. This possibility would also explain why the contribution of biotic predictors to models (ΔTSS) tended to decline across increasing pixel sizes when all species were considered together, although this pattern was not consistent across all species we examined.

The fact that ΔTSS remained consistently positive in SDMs for infestations of *Rubus armeniacus* constructed at all resolutions indicates that the primary biotic predictor in full models, the standard deviation in canopy cover, remained informative for this species even when aggregated across relatively large areas. This was not the case for models of *B. diandrus and B. hordeaceus* infestations, where full models also contained this predictor across resolutions. This apparent discrepancy may be explained by the level of variation present in this predictor in areas that were abiotically suitable for infestation by each species. Abiotic conditions for the presence of infestations of both *Bromus* species were only predicted to be suitable in close proximity to non-forested areas where variation in the standard deviation of canopy cover was relatively minimal and aggregation at resolutions >1 km may have yielded a high degree of homogeneity in the predictor across this abiotically-suitable portion of the landscape, rendering the standard

deviation of canopy cover an uninformative predictor at these resolutions. In contrast, infestations of *Rubus armeniacus* tended to occur in disturbed patches within more heavily-forested systems; abiotically-suitable areas tended to have more variability in the standard deviation of canopy cover which may not have become as homogeneous with aggregation to lower resolutions and may therefore have remained informative at these resolutions.

Another reason that biotic predictors may not have significantly improved the accuracy of our SDMs at resolutions of 2 km to 10 km is that the particular forest stand characteristics described by the biotic predictors included in our SDMs did not represent the strongest biotic checks on the landscape-scale distributions of infestations of the focal species. Although these types of predictors have been shown elsewhere to significantly improve SDMs for plants (Ibáñez et al., 2009; Nieto-Lugilde et al., 2015; Cabra-Rivas et al., 2016), other interactions may more strongly influence the distribution of infestations of our focal species. For example, the species richness or phylogenetic diversity of recipient communities may be correlated with the presence and performance of invasive species at some scales (Stohlgren et al., 2005; Iannone et al., 2016; Nunez-Mir et al., 2017; Peng et al., 2019; Mungi et al., 2021). Including the distribution of known facilitative or antagonistic species may also improve large-scale SDMs (*e.g,* Bullock et al., 2000; Heikkenen *et al.,* 2007; de Araújo et al., 2014), but *a priori* identification of strong competitors or facilitators of invasive species is difficult (Sexton et al., 2009; Louthan et al., 2015). The fact that our biotic predictors represent antagonistic rather than facilitative interactions may also make their effects less detectable at coarse resolutions; the effects of facilitative interactions are thought to be more readily detectable at large spatial scales (Heikkenen *et al.,* 2007; Araújo and Rozenfeld, 2014; Belmaker et al., 2015). Furthermore, our approach of including terms describing the fire history and human footprint in each cell in the category of abiotic predictors likely provided a very conservative estimate of influence of biotic interactions on the distributions of infestations of the focal species across the study region, as the disturbances represented by these two predictors affect facets of both the abiotic and biotic environment.

A third possible explanation for our finding that biotic predictors do not improve SDMs at resolutions lower than 1 km^2 is that collinearity among our abiotic and biotic predictors or context dependence in the outcome of biotic interactions precluded detection of their contributions to SDMs. This context-dependence in the influence of biotic interactions on species' distributions is well-documented in other plants (Bullock et al., 2000; Moeller et al., 2012; Fraterrigo et al., 2014; Baer and Maron, 2018) and aligns with predictions that abiotic context may dictate the influence of biotic interactions in constraining species' distributions (MacArthur, 1972; Louthan et al., 2015). Moreover, the addition of variables describing land cover may not significantly improve the accuracy of SDMs due to strong associations between land cover and climate (Thuiller et al., 2004). The issue of collinearity among abiotic and biotic conditions and context-dependence in the effects of biotic interactions has spurred increased skepticism of inferring the mechanisms underlying species' distributions from SDMs constructed using solely abiotic predictors, regardless of model accuracy (Godsoe et al., 2017a; Wisz et al., 2013; *e.g,* Meineri et al., 2012). Such may be the case for our focal species: biotic attributes commonly included in the full models for our focal species such as the mean or variability of canopy cover may have been at least partially accounted for in abiotic models if correlated abiotic predictors were present in those models.

5. Conclusions & future directions

In this study, we demonstrated that the inclusion of biotic predictors related to forest stand characteristics significantly improved the accuracy of species distribution models for the regional distribution of infestations of five common invasive species in Western U.S. forests when models were built at a 1 km resolution, but this improvement was not sustained at lower resolutions. This pattern is partially in keeping with the predictions of the Eltonian Noise Hypothesis, but a true investigation of the applicability of the ENH would require the availability of data describing both the abiotic and biotic environment at scales ranging from meters to tens of kilometers. As such data are largely unavailable, it is difficult to discern the precise scales at which biotic and abiotic attributes of the environment constrain species distributions. Our results agree with a growing body of literature suggesting that the scale at which biotic interactions influence species' distributions is larger than previously thought. Nevertheless, the fact that our SDMs constructed at resolutions of 2 km to 10 km were not consistently improved by the addition of biotic predictors, abiotic models at all resolutions displayed excellent accuracy, and even our SDMs at a 1 km resolution were only slightly improved by the addition of biotic predictors supports the validity of constructing regional-scale SDMs that do not include biotic predictors at coarse resolutions.

Our study is the first of which we are aware to address the question of scale-dependence in the predictors of infestations of invasive plants in forested systems. The outcomes presented here may provide information regarding both the aspects of the biotic and abiotic environment likely to be associated with infestations of our focal species, as well as suggestions for the most accurate manner in which to predict where invasions may occur in forested systems of the Western U.S.

6. Data availability

Data including fuzzed plot locations and invasive species records are available from the Forest Inventory and Analysis database (https://www.fia.fs.fed.us/tools-data/index.php).

CRediT authorship contribution statement

Kathryn C. Baer: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Project administration. **Andrew N. Gray:** Conceptualization, Resources, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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