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Vegetation classification enables inferring mesoscale spatial variation in plant invasibility

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Abstract

Large-scale control of invasive plants can benefit strongly from reliable assessment of spatial variation in plant invasibility. With this knowledge, limited management resources can be concentrated in areas of high invasion risk. We assessed the influence of spatial environments and proximity to roads on the invasibility of African mustard (*Brassica tournefortii* Gouan) over the 280,000-ha Barry M. Goldwater Range West in southwestern Arizona, USA. We used presence/absence data of *B. tournefortii* acquired from a vegetation classification project, in which lands were mapped to the level of vegetation subassociations. Logistic regression models suggested that spatial environments represented by the subassociations, not proximity to roads, represented the only factor significantly explaining *B. tournefortii* presence. We then used the best model to predict *B. tournefortii* invasibility in each subassociation. This prediction indicates management strategy should differ between the western part and the central to eastern part of the range. The western range is a large spatial continuum with intermediate to high invasion risk, vulnerable to an untethered spread of *B. tournefortii*. Controlling efforts should focus on preventing existing local populations from further expansion. The central and eastern ranges are a mosaic varying strongly in invasion risk. Control efforts can take advantage of natural invasion barriers and further reduce connectivity through removal of source populations connected with other high-risk locations via roads and other dispersal corridors. We suggest our approach as one effective way to combine vegetation classification and plant invasion assessment to manage complex landscapes over large ranges, especially when this approach is used through an iterative prediction–validation process to achieve adaptive management of invasive plants.

Introduction

Managing invasive plants on a mesoscale (e.g., tens to hundreds of kilometers) requires prioritizing strategic locations for monitoring and treatment in order to contain large-scale spread (Epanchin-Niell and Hastings 2010; Giljohann et al. 2011; Roura-Pascual et al. 2010). The probability of having a specific invasive species, defined here as the invasibility of that species, often varies dramatically in space due to spatial environmental heterogeneity (Brummer et al. 2016; Chabrerie et al. 2008). Locations of higher invasibility usually should be given higher priority for monitoring and treatment (Giljohann et al. 2011; Roura-Pascual et al. 2010). Nevertheless, it is often challenging to assess invasibility at a fine spatial resolution over a large extent of space.

This challenge is exemplified by the invasion of African mustard (*Brassica tournefortii* Gouan) (Brassicaceae), a winter annual species of serious invasion concern in arid western North America. Its invasion is especially problematic over the Mojave and Sonoran Deserts, where it is widely distributed (Abella et al. 2009; Li et al. 2015) and negatively impacts native ecological communities (Barrows et al. 2009; Berry et al. 2014; VanTassel et al. 2013). *Brassica tournefortii* can establish over a broad range of physical environments (Li et al. 2015; Winkler et al. 2018), within which it experiences dramatic spatial variation in its density and presence (Berry et al. 2014; Craig et al. 2010; Van Devender et al. 1997). This spatial variation underscores the need for a better prediction of *B. tournefortii* invasibility at large scales and a better understanding of spatial factors influencing its invasibility.

Species distribution models (SDMs) have been increasingly used to predict habitat suitability for, and hence invasibility of, invasive plants (Elith and Leathwick 2009). Based upon regression or machine-learning methods, these models combine density or point occurrence (presence/absence or presence only) data of the invasive species and spatial environmental variables to predict the probability of occurrence of the focal species. In the case of *B. tournefortii*, both density data and presence-only data have been used in SDMs to predict its invasibility over large landscapes (Berry et al. 2014; Sanchez-Flores 2007).

Management Implications

Brassica tournefortii (African mustard) is an introduced winter annual plant species that is negatively impacting native species in arid North America, especially in the Mojave and Sonoran Deserts. Managing this species on a large scale requires directing finite resources to locations favoring its population growth and persistence (i.e., invasibility). We analyzed data collected from a vegetation mapping project to determine factors influencing the invasibility of *B. tournefortii* and to predict its invasibility over 280,000 ha of the Barry M. Goldwater Range (BMGR) West, managed by the U.S. Marine Corps Air Station–Yuma.

First, we showed that *B. tournefortii* invasibility was explained by spatial environments represented by associations of dominant native vegetation, but not by proximity to roads. This finding indicates that while roads may serve as corridors for *B. tournefortii* dispersal, habitat characteristic ultimately determines whether this species can establish in a location. Special attention should be paid to roads intercepting habitats subject to high invasibility of *B. tournefortii*. Local population buildup along roads in these interceptions may lead to whole-habitat invasion.

Second, we predicted a large continuum of space subject to intermediate to high invasibility in the western range, whereas the central and eastern ranges are a mosaic varying strongly in invasibility. This spatial pattern suggests that the western range could see an untethered expansion of *B. tournefortii* and should be prioritized for eliminating nascent and established populations. In the rest of the range, management can take advantage of the abundance of habitats with low invasibility, which can serve as natural invasion barriers. In the central to eastern ranges, management can focus on eliminating well-established local populations of *B. tournefortii* that are connected to other highly invasible locations through dispersal corridors (e.g., roads and watercourses), populations in highly invasible habitats that cover large areas, and isolated populations that thrive locally. Focusing on removal of these three types of populations can further divide the fragmented distribution of *B. tournefortii* on the central and eastern ranges, reducing connectivity between local populations and thus facilitating the containment of *B. tournefortii*.

Overall, recording presence/absence of invasive plants in a vegetation mapping project enabled large-scale prediction of invasibility. This method, when used in an iterative prediction–validation process, can strongly inform adaptive management to contain range-wide plant invasions.

SDMs may not adequately predict an invasive species' distribution if the species' current distribution represents only a subset of the full environmental niche of that species (Elith et al. 2010). This becomes less of a problem for well-established invasive species that are also limited in their adaptation to novel environments. *Brassica tournefortii* is one of these species because of its long invasion history, rapid expansion to fully occupy its climatic niche in North America (Li et al. 2015), and limited potential for adaptation due to low genetic diversity (Winkler 2017).

A more challenging problem of predicting invasibility of well-established invasive plants like *B. tournefortii* on a mesoscale is the lack of high-quality and high spatial resolution environmental data. On a mesoscale, factors such as soil type, soil nutrient availability, and biotic interactions are important in influencing habitat quality for plant species (Chabrerie et al. 2008; Chang et al. 2013; Coudun et al. 2006; Jones et al. 2008; Mackey and Lindenmayer 2001). Unfortunately, reliable, high-resolution data for these environmental variables are often not available (e.g., Brummer et al. 2016). Using surrogates such as topographic variables can lead to misleading predictions. For example, Chang et al. (2013) found that when topography was used as a surrogate for environmental variables, models indicated that the spatial composition of a subtropical broadleaf forest was primarily shaped by dispersal-based processes. On the contrary, when soil variables were used, models suggested that the forest composition was primarily shaped by niche-based processes, in which soil types defined spatial niches. It remains a challenge to acquire sufficient fine-scale environmental variables to predict plant habitat suitability over complex spatial environments.

Here we demonstrate an approach that uses vegetation associations as surrogates for the multitude of environmental variables that might affect plant invasibility. Changes in dominant vegetation composition reflect variation in both abiotic and biotic factors, especially those related to soil properties and biotic interactions (Greig-Smith 1979; HilleRisLambers et al. 2012). Therefore, mapping changes in the association of dominant vegetation on a mesoscale may provide reliable data that indicate spatial variation in essential determinants of plant invasibility.

Other than spatial environmental factors, invasibility of a species also can be influenced by propagule pressure linked to dispersal (Simberloff 2009). Roads can serve as major dispersal corridors for invasive plants. Heightened propagule pressure close to roads can increase invasibility (Jørgensen and Kollmann 2009). Previous studies suggested roads could strongly encourage *B. tournefortii* invasion (Berry et al. 2014; Brooks 2009; Sanchez-Flores 2007), whereas one study questioned this road effect (Craig et al. 2010). It is possible that the effect of roads depends on the habitat through which they pass.

We combined data of *B. tournefortii* presence/absence, vegetation associations, and road locations to evaluate *B. tournefortii* invasibility over the 280,000-ha Barry M. Goldwater Range West (BMGR West) in southwestern Arizona, USA. First, we asked how two variables: spatial environments represented by vegetation subassociations and proximity to roads could be used to predict *B. tournefortii* invasibility. Second, we used spatial prediction of *B. tournefortii* invasibility over this range to highlight areas of elevated invasion concern and those contributing most strongly to large-scale spread of *B. tournefortii* over complex landscapes. We used our findings to inform the management of *B. tournefortii* over the BMGR West. We further discussed the ongoing effort of extending our approach to a greater spatial scale and how to enable adaptive management of invasive plants through an iterative prediction–validation process.

Materials and Methods

Site Description

The BMGR West encompasses nearly 280,000 hectares in southwestern Arizona. It falls entirely within the Lower Colorado River subdivision of the Sonoran Desert (Brown 1982). Elevations range from 56 to 962 m above sea level (m asl). The 85-yr climate data from nearby Yuma Citrus Station (58 m asl) show an average high of 41.2 C in July and an average low of 3.9 C in January.

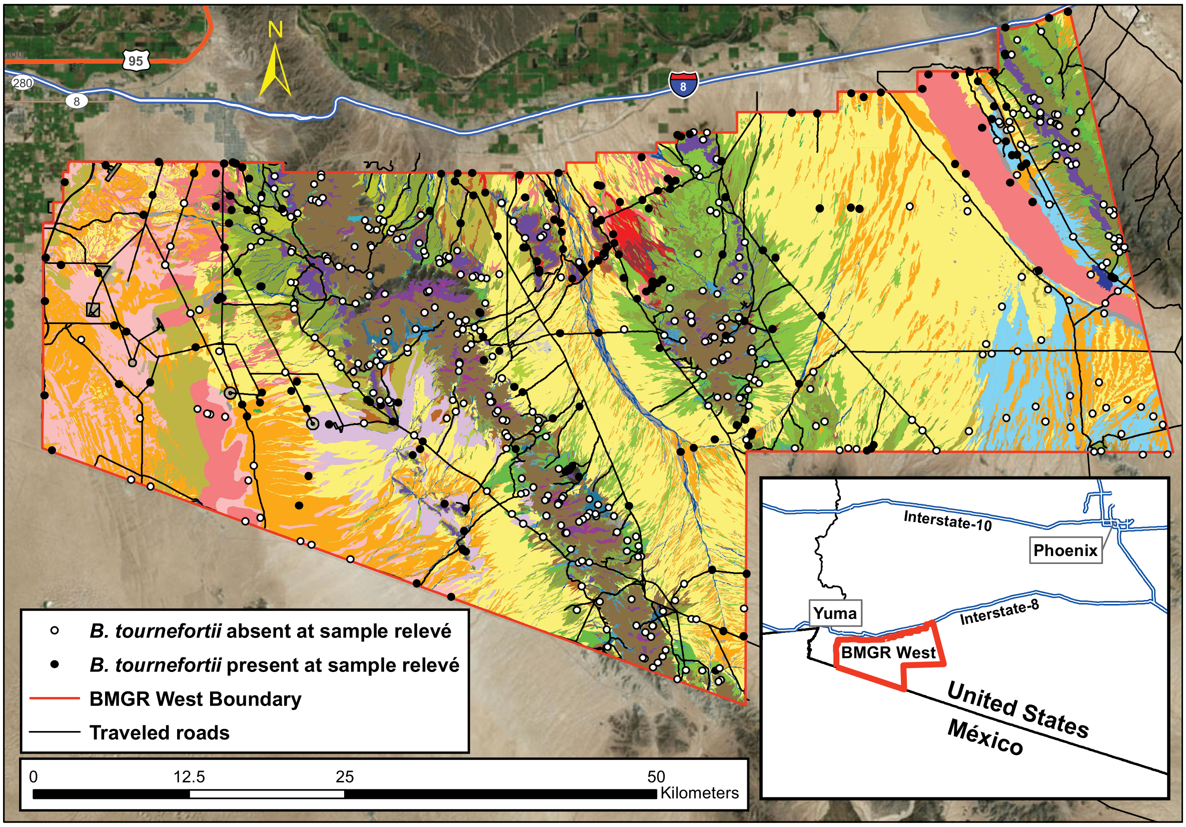

Figure 1. Vegetation classification of the Barry M. Goldwater Range (BMGR) West allowed for inference of spatial variation in *Brassica tournefortii* invasibility. Each unique color represents a vegetation subassociation, the finest level of vegetation type mapped on the BMGR West (see Supplementary Figure S1 for a complete list of subassociation names associated with each color). Vegetation types were determined by sampling vegetation cover in each of the 656 relevés (circles) between 2009 and 2014. *Brassica tournefortii* presence (filled circles) and absence (open circles) were also sampled in these relevés. We used logistic regression models to determine the influence of two factors on the probability of *B. tournefortii* presence: (1) spatial environments represented by subassociations and (2) proximity to traveled roads (black lines). Inset shows the geographic location of BMGR West in southwestern Arizona, USA.

The average annual precipitation of 87 mm is among the lowest in the Sonoran Desert, with a bimodal summer and winter rainy season that supports summer and winter annual plants as well as perennial shrubs, grasses, trees, and cacti, including saguaros [*Carnegiea gigantea* (Engelm.) Britton & Rose] up to 10 m tall. The plant diversity is enhanced by diverse landforms that include mountains, valleys, dunes, ephemeral watercourses, and floodplains.

Brassica tournefortii has a relatively long history of invading the BMGR West. The first specimen of *B. tournefortii* adjacent to BMGR West was collected in 1959 on Yuma Mesa just east of the BMGR West western boundary (K. C. Hamilton, ARIZ 129283 & 130879). No collection appeared on the BMGR in the following decades, likely due to the remoteness of the range. It was not until 1973 that the first *B. tournefortii* specimen was collected on the Mohawk Dunes within the BMGR (D. J. Pinkava, ASU 0026561). Over the winter–spring growing season of 2000 to 2001, high abundance of *B. tournefortii* was recorded over the Mohawk Valley from the BMGR West northern boundary well into the heartland of the range (Malusa et al. 2003), suggesting this species was well established on the range.

Vegetation Classification on the BMGR West

Malusa and Sundt (2015) developed a vegetation classification map of the BMGR West based on remote-sensing imagery and field surveys. They established 656 sample relevés (Minnesota Department of Natural Resources 2013; Mucina et al. 2000) to survey and compare vegetation composition across all distinctive landforms identified through aerial imagery (Figure 1). The presence of *B. tournefortii* was not a factor in choosing relevés.

Within each relevé, the percent canopy cover of perennial vegetation was assessed by a step-point transect (Evans and Love 1957), in which a notch in the toe of the observer's boot was the "point." With each step the observer looked straight down for a bird's-eye view, determining whether the notch intercepted the canopy of a plant. If the canopy was that of a desert tree (typically 2- to 4-m tall), a 1.5-m walking stick was used to extend the point upward.

Other species observed but not intercepted in the step-point transect were recorded, so long as they occurred within the same vegetation type. For example, a species 10 m from the end of a transect would be included as present (but not a "hit") if it were along the bank of an arroyo that was being sampled, but not if it were 10 m outside the arroyo in a different vegetation type. All perennials were recorded, as well as certain annuals of interest, such as *B. tournefortii*. This annual plant was noted as present even if there were only the distinctive skeletal remains of the plant from the previous year.

A transect that began near a road would proceed away from that feature. Transects in habitats defined by watercourses were surveyed along the courses. Transect length varied in proportion to the density of vegetation or difficulty of terrain or both.

The longest were 1,000 steps (about 700 m at 0.7 m step^{-1}) in creosote bush [*Larrea tridentata* (DC.) Coville] monotypes, while the shortest were 100 steps on steep north-facing slopes with mormon tea (*Ephedra viridis* Coville) and in watercourses. The length of each step was kept consistent to the best of the surveyor's ability.

Fifty-one of these relevés were surveyed in 2001, while the rest were surveyed from 2009 to 2014. Those 51 relevés were not included in our analysis because of the concern that the conditions for *B. tournefortii* invasion then would be too different from those in 2009 to 2014.

Using this vegetation survey data and following the U.S. National Vegetation Classification (Federal Geographic Data Committee 2008; Jennings et al. 2009, USNVC 2018), Malusa and Sundt (2015) defined the alliance and association levels of vegetation based on the dominant species and their associates, with the dominant species having the highest percent cover. For example, there is an association of *Larrea tridentata*–burrobush [*Ambrosia dumosa* (A. Gray) Payne], which in turn is part of the higher-level *L. tridentata* alliance. Subassociations, typically based on landform and indicator species, were also mapped. For instance, *L. tridentata*–*A. dumosa* may occur in several subassociations, including gravelly ridges with ocotillo (*Fouquiera splendens* Engelm.), on moving sands with desert palafox (*Palafoxia arida* B.L. Turner & Morris), or on stony hills with California fagonbush (*Fagonia laevis* Standl.). All but one subassociation were surveyed by multiple relevés. The completed map shows seven alliances, 25 associations, and 42 subassociations across the BMGR West. Barrens (<1% total vegetation cover) and disturbed areas (e.g., roads) were mapped but not sampled further.

Determining Factors That Influence Brassica tournefortii Invasibility

We used logistic regressions to model a dependent variable (presence/absence of *B. tournefortii*) and two independent variables: distance to a road and vegetation subassociation. The number of relevés representing each subassociation was proportional to its mapped extent on the BMGR West, ranging from a single relevé from the 7 ha of the honey mesquite (*Prosopis glandulosa* Torr.) bosque subassociation to 51 relevés from the 56,943 ha of the *L. tridentata*–*A. dumosa* subassociation. This skewed sample compelled us to exclude or combine subassociations to obtain a total of 29 vegetation subassociations or their combinations (hereafter also called "subassociations") to represent distinct spatial environments for the statistical analysis.

First, five subassociations, ranging from 7 to 288 ha, were *excluded* from the analysis because they were (1) represented by five or fewer relevés and (2) did not share dominant species or landforms with another subassociation (Supplementary Table S1). In other words, these are unique subassociations with very small sample sizes, as in the case of the desertholly [*Atriplex hymenelytra* (Torr.) S. Watson]–*Ambrosia dumosa*–wand holdback (*Hoffmannseggia microphylla* Torr.) shrublands.

Second, 13 subassociations, ranging from 217 to 1446 ha, were *combined* into six groups (Supplementary Table S1). Subassociations in the same group (1) belonged to the same association, (2) shared dominant species or landforms or both, and (3) held similar proportions of relevés with *B. tournefortii*. Proportions were considered similar if they were not marginally significantly different ($p > 0.1$) according to a Fisher's exact test. For example, the 4 relevés for "teddybear cholla [*Cylindropuntia bigelovii* (Engelm.) F.M. Knuth] on bajadas with >1% tree cover" were combined with the 10 relevés for "*C. bigelovii* on bajadas with <1% tree cover" for a total of 14 relevés.

We used ArcGIS (v. 10.5.1, Esri, Redlands, CA) to determine the distance of each relevé to the nearest road. Projection used for GIS layers was NAD_1983_StatePlane_Arizona_West_FIPS_0203. Using a Microsoft Access (Redmond, WA) database, we first created feature classes that represented the starting locations of all relevés (Figure 1). We added a road layer provided by the U.S. Marine Corps that included 37 km of paved and 983 km of unpaved roads on the range. Roads were plain to see on satellite imagery, which allowed us to improve the accuracy of the road layer in ArcGIS by including an additional 173 km of unpaved roads that are mostly the result of U.S. Border Patrol activity over the last 15 yr, including construction of a pedestrian fence and vehicle barrier along the international frontier. The Near Analysis Tool was used to calculate the perpendicular distance (in meters) from each relevé starting point to the nearest road. The natural log of the distance was used in the regression to restore the normality of the distribution of this variable.

To determine whether each of the two independent variables was significantly associated with the presence/absence of *B. tournefortii*, we performed logistic regressions in R (v. 3.4.4) using the *glm* function (R script and data available at https://osf.io/5tkd6/; DOI: 10.17605/OSF.IO/5TKD6). We performed likelihood ratio tests to compare the full model with an alternative model, in which one of the independent variables was dropped. The generalized variance-inflation factors adjusted for degrees of freedom ($\text{GVIF}^{1/(2\cdot\text{df})}$) was smaller than 1.1 for both independent variables (estimated using the *vif* function in the CAR package, v. 3.0; Fox and Weisberg 2011), suggesting negligible influence of collinearity between the two variables on model inferences (Zuur et al. 2010).

The uneven spatial distribution of our relevés over the range meant that they could be clustered or dispersed, leading to spatial autocorrelation (Supplementary Appendix S1). To evaluate the influence of spatial autocorrelation, we performed further logistic regressions using the *corrHLfit* function in the SPAMM package (v. 2.3.0; Rousset and Ferdy 2014). Regressions performed by this function, which accounts for autocorrelation, give the same overall conclusions and predictions as the basic models (Supplementary Appendix S1). Therefore, we present in the main text results inferred by the basic logistic regression models.

Spatial Assessment of Brassica tournefortii Invasibility

We estimated invasibility as the probability of *B. tournefortii* presence in a subassociation (P_{invasion}) predicted by the most-parsimonious logistic model. This probability equates the proportion of relevés with *B. tournefortii* present in a specific vegetation subassociation (see "Results and Discussion"). We obtained the 95% confidence interval (CI) of each probability as the modified Jeffreys interval for a binomial proportion. This interval has far more satisfactory coverage than the commonly used Wald CI, especially when sample sizes are small (Brown et al. 2001). Based on the spatial distribution of each subassociation and its predicted invasibility of *B. tournefortii*, we produced a 1:380,000 map in ArcGIS indicating the spatial variation in *B. tournefortii* invasibility over the BMGR West.

Table 1. Likelihood ratio tests of logistic regression models determine that spatial environments represented by vegetation subassociations, but not proximity to roads, were significantly associated with the presence/absence of *Brassica tournefortii*.[a]

Models in comparison	Deviance	Degrees of freedom	Probability>χ^2
Full model vs. model in which proximity to road was dropped	0.180	1	0.671
Full model vs. model in which subassociation was dropped	214	28	$<10^{-7}$

[a] Each likelihood ratio test compares the full model, in which both explanatory variables were included, with an alternative model, in which one of them was dropped.

Results and Discussion

Factors Influencing Brassica tournefortii Presence

Likelihood ratio tests based on logistic regression models suggested that vegetation subassociation was the only factor significantly associated with *B. tournefortii* presence/absence ($\chi^2_{28} = 214, p < 10^{-7}$; Table 1). In general, subassociations subject to high invasibility ($P_{\text{invasion}} > 0.5$) of *B. tournefortii* are on flat terrain (fans, dunes, floodplains, etc.), whereas those subject to low invasibility ($P_{\text{invasion}} < 0.25$) are on mountainous terrain (Figure 2). This association pattern was further supported by a significant negative correlation between *B. tournefortii* presence and the steepness of relevés ($\chi^2_1 = 0.27.96$, $p = 1.24 \times 10^{-7}$; Table A3 in Supplementary Appendix S1).

Our models indicated that proximity to roads was not significantly associated with *B. tournefortii* presence ($\chi^2_1 = 0.180$, $p = 0.671$; Table 1). This result implies that while roads may serve as corridors for *B. tournefortii* dispersal, habitat characteristic ultimately determines whether this species can establish in a location. Proximity to roads, nevertheless, may have positive influence on *B. tournefortii* density within the species' favorable habitat (Berry et al. 2014). As dispersal corridors, roads can increase propagule pressure of invasive plants, which can lead to increased invasive plant density (Levine 2000; Simberloff 2009). Precipitation runoff from roads enhances soil moisture along the road's margin, improving conditions for germination and successful recruitment of annual weeds such as *B. tournefortii*. Certain types of road berms, which resemble sandy soil habitat associated with high invasibility of *B. tournefortii*, can enhance recruitment of *B. tournefortii* (Brooks 2009). Therefore, road-edge management can influence plant invasibility of roadside habitat (Craig et al. 2010). Special attention should be paid to roads intercepting habitat with high invasibility of *B. tournefortii*. Local population buildup along roads in these interceptions may lead to whole-habitat invasion.

Our finding agrees with other observations that sandy soils are associated with high *B. tournefortii* population growth, rather than rocky shallow soils on more steep terrain (Berry et al. 2014; Brooks 2009; Van Devender et al. 1997). There are exceptions to this general pattern. For example, brittlebush (*Encelia farinosa* A. Gray ex Torr.)–*Larrea tridentata* on dark rocks (typically basalt) is subject to a relatively high invasibility ($P_{\text{invasion}} = 0.429$; Figure 2). Seemingly similar spatial environments could also differ substantially in *B. tournefortii* invasibility. The best example is the difference between *L. tridentata* monotype and *L. tridentata*–*A. dumosa* subassociation with predicted invasibility of *B. tournefortii* of 0.572 and 0.257, respectively.

Managing Invasion According to Spatial Assessment of Invasibility

The predicted *B. tournefortii* invasibility indicates a large continuum of space subject to intermediate to high invasibility ($0.4 < P_{\text{invasion}} < 0.8$) in the western part of the BMGR West, whereas the central and eastern ranges are a mosaic varying strongly in *B. tournefortii* invasibility ($0 \leq P_{\text{invasion}} \leq 1$) (Figure 3). This habitat distribution pattern suggests that the western range could see an untethered expansion of *B. tournefortii* if this species is able to establish farther into those moderately to highly invasible habitats. Land managers need to focus on removing nascent populations and preventing further growth of established local populations on the western range.

In comparison, the expansion of *B. tournefortii* on the central and eastern ranges will be limited by the strong spatial variation in the species' invasibility. Some of the subassociations most invasible by *B. tournefortii* occur in this part of the range (e.g., *Ambrosia dumosa*–big galleta [*Pleuraphis rigida* Thurb.] on fans with a $P_{\text{invasion}} = 1$), but they are also frequently intercepted by areas of low or intermediate invasion risk ($0 \leq P_{\text{invasion}} < 0.25$) that act as natural invasion barriers. Reducing habitat connectivity can be the most cost-effective approach to limit invasion (Blackwood et al. 2010). Following this general principle, land managers can take advantage of these natural barriers and focus on eliminating the following types of populations in descending order of priority: (1) well-established local populations of *B. tournefortii* that are connected to other highly invasible locations ($P_{\text{invasion}} > 0.5$) through dispersal corridors (e.g., roads and watercourses), (2) populations in highly invasible subassociations ($P_{\text{invasion}} > 0.5$) that cover large areas (e.g., Mohawk Dunes in the eastern range), and (3) isolated populations that thrive locally. Focusing on removal of these three types of populations can further divide the fragmented distribution of *B. tournefortii* on the central and eastern ranges, reducing connectivity between local populations and thus facilitating the containment of *B. tournefortii* in this part of the BMGR West.

Future Directions

Our study predicted a general spatial pattern of *B. tournefortii* invasibility over the 280,000-ha BMGR West. Our prediction provides an initial base for land managers to focus their controlling efforts in areas most vulnerable to large-scale invasion of a high-impact exotic plant. It is necessary to continue the monitoring and demographic surveys of *B. tournefortii* over the BMGR West so as to create an iterative process (Dietze et al. 2018) to improve the accuracy of our prediction, while providing timely information to land mangers so they can adjust the selection of priority areas for managing this invasive species. One caveat of our findings is that some subassociations have relatively high uncertainty of *B. tournefortii* invasibility, as indicated by their large CIs (Figure 2). This increased uncertainty was caused by small sample sizes. We will establish additional relevés in these subassociations (while minimizing their spatial autocorrelation) in the iterative process, to reduce this uncertainty.

We showed that vegetation mapping can enable mesoscale inference of spatial variation in plant invasibility. By measuring presence/absence of invasive plant species while mapping vegetation associations representing distinct environments, one can acquire valuable data for inferring spatial patterns of invasibility over a large extent of space. This approach strikes a balance between the details required to define spatial environments and their

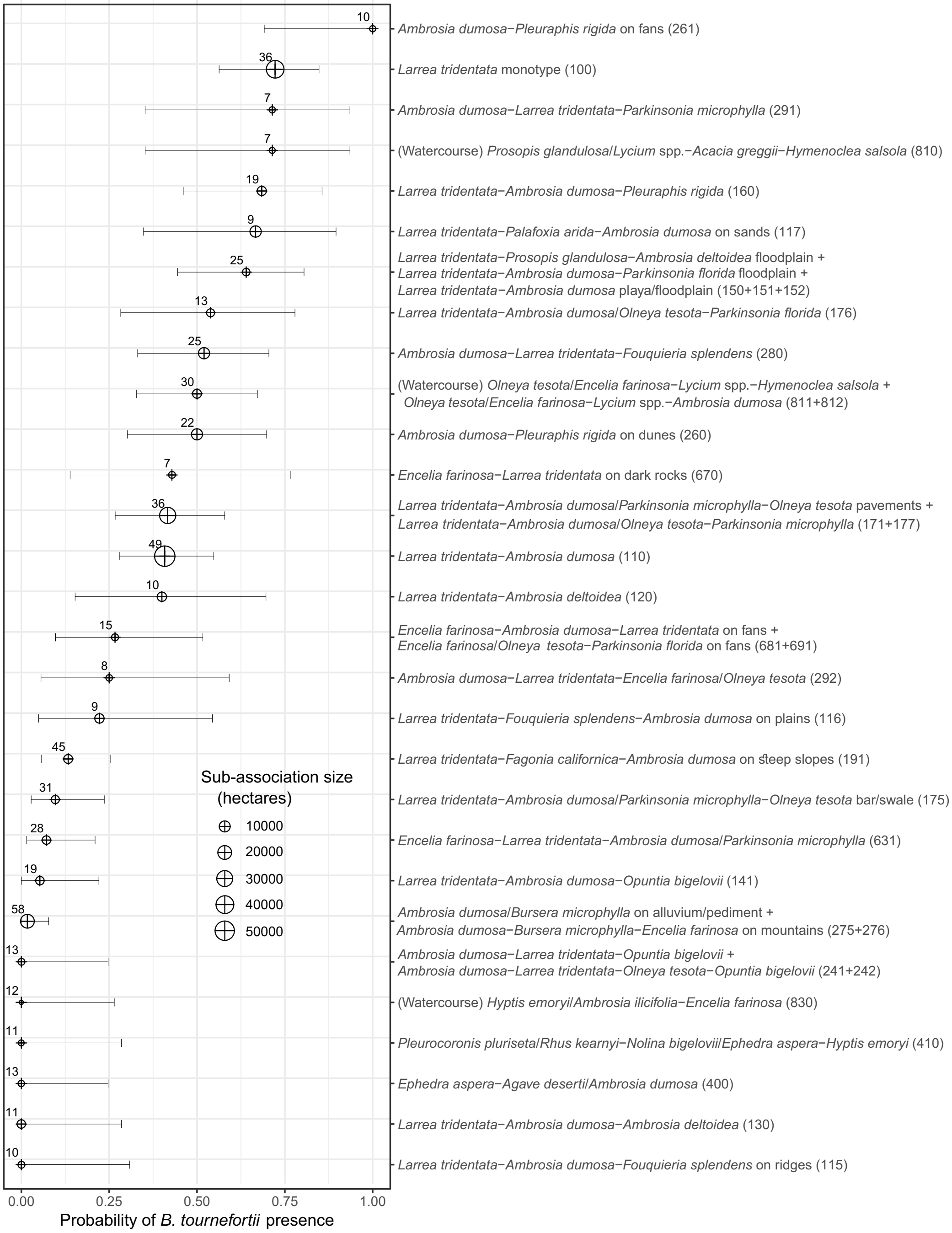

Figure 2. The inferred probability of *Brassica tournefortii* presence (invasibility) in spatial environments represented by vegetation subassociations. Logistic regression models inferred that vegetation subassociations, but not proximity to roads, explained the probability of *B. tournefortii* presence, and the predicted probability equated the observed probability (i.e., the proportion of relevés with *B. tournefortii* presence in a subassociation). Circle sizes indicate sizes of the subassociations. The name of a subassociation is followed by the subassociation code used in Malusa and Sundt (2015). The first digit of the three-digit code distinguishes vegetation alliances; the second digit distinguishes vegetation associations; and the third digit distinguishes vegetation subassociations. Bars indicate the 95% confidence intervals of the observed probabilities based on the modified Jeffreys intervals (Brown et al. 2001).

vulnerability to plant invasion and the large spatial scales required to produce meaningful predictions for managing range-wide plant invasion.

As the same protocols were followed to complete vegetation classification of the BMGR East and Cabeza Prieta National Wildlife Refuge bordering the BMGR West, there soon will be a continuous vegetation classification map covering approximately 1 million hectares in southwestern Arizona. With additional data of *B. tournefortii* presence/absence acquired from these highly comparable mapping projects, we will be able to assess *B. tournefortii* invasibility to an even greater spatial extent. This endeavor, along with the iterative process of producing and validating invasibility predictions on the ground, creates an important decision-making tool for managing *B. tournefortii* invasion across jurisdiction boundaries in southwestern Arizona. Our approach can be adopted and refined more commonly to

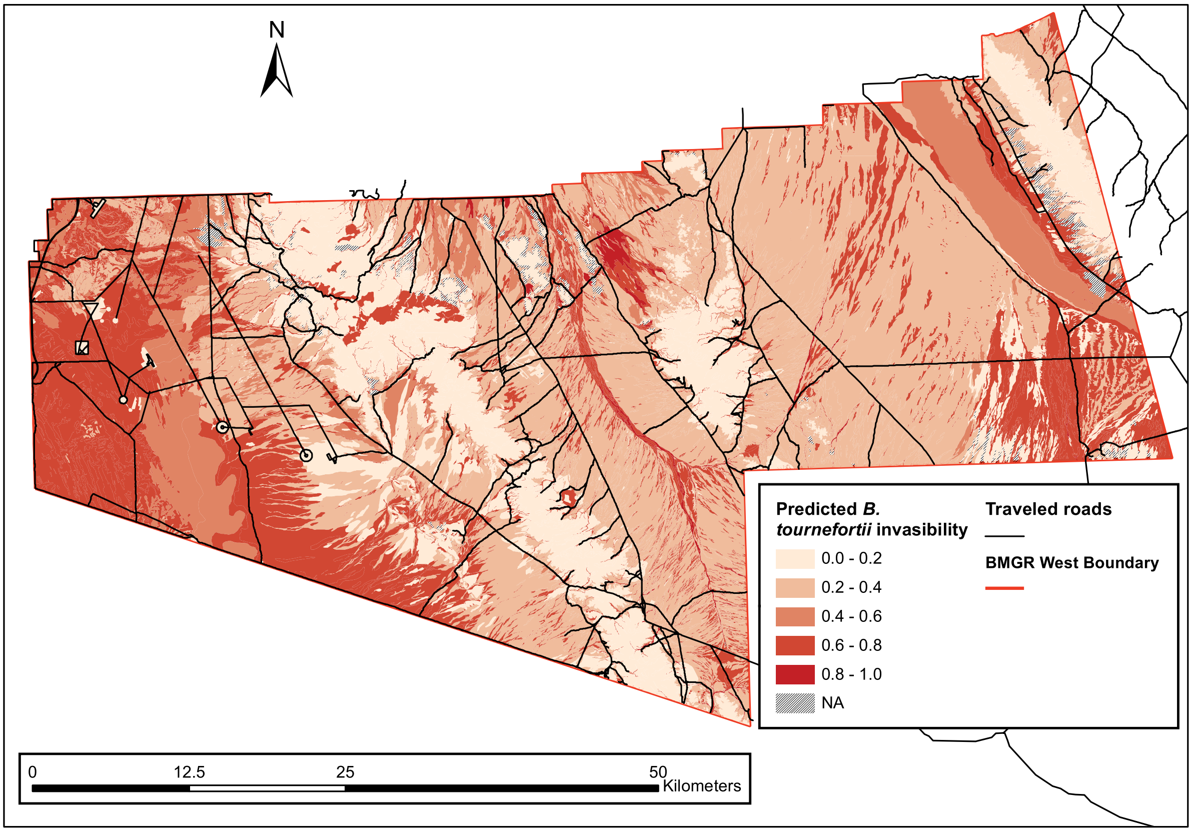

Figure 3. Spatial assessment of predicted invasibility of *Brassica tournefortii* shows distinct spatial patterns of invasion risk over the BMGR West. The western range consists of a large continuum of space with intermediate to high *B. tournefortii* invasibility ($0.4 < P_{\text{invasion}} < 0.8$) and may experience an untethered spread of *B. tournefortii* if the species can expand farther over that space. The central and eastern range are a mosaic varying strongly in *B. tournefortii* invasibility. Some of the most invasible habitats occur there, but are frequently intercepted by space of low invasion risk (those with $0 \leq P_{\text{invasion}} < 0.25$).

simultaneously complete vegetation classification and spatial assessment of plant invasion, both of which are becoming increasingly essential for conservation management on large scales (Chytrý et al. 2011; Epanchin-Niell and Hastings 2010; Giljohann et al. 2011; Roura-Pascual et al. 2010).

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Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/inp.2019.23

References

Abella SR, Spencer JE, Hoines J, Nazarchyk C (2009) Assessing an exotic plant surveying program in the Mojave Desert, Clark County, Nevada, USA. Environ Monit Assess 151:221–230

Barrows CW, Allen EB, Brooks ML, Allen MF (2009) Effects of an invasive plant on a desert sand dune landscape. Biol Invasions 11:673–686

Berry KH, Gowan TA, Miller DM, Brooks ML (2014) Models of invasion and establishment for African mustard (*Brassica tournefortii*). Invasive Plant Sci Manag 7:599–616

Blackwood J, Hastings A, Costello C (2010) Cost-effective management of invasive species using linear-quadratic control. Ecol Econ 69:519–527

Brooks ML (2009) Spatial and temporal distribution of non-native plants in upland areas of the Mojave Desert. Pages 101–124 in Webb RH, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, Miller DM, eds. The Mojave Desert: Ecosystem Processes and Sustainability. Reno: University of Nevada Press

Brown LD, ed (1982) Biotic Communities of the American Southwest–United States and Mexico. Tucson: University of Arizona. 342 p

Brown LD, Cai TT, DasGupta A (2001) Interval estimation for a binomial proportion. Stat Sci 16:101–117

Brummer TJ, Taylor KT, Rotella J, Maxwell BD, Rew LJ, Lavin M (2016) Drivers of *Bromus tectorum* abundance in the western North American sagebrush steppe. Ecosystems 19:986–1000

Chabrerie O, Verheyen K, Saguez R, Decocq G (2008) Disentangling relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest. Divers Distrib 14:204–212

Chang L-W, Zelený D, Li C-F, Chiu S-T, Hsieh C-F (2013) Better environmental data may reverse conclusions about niche- and dispersal-based processes in community assembly. Ecology 94:2145–2151

Chytrý M, Schaminée JHJ, Schwabe A (2011) Vegetation survey: a new focus for applied vegetation science. Appl Veg Sci 14:435–439

Coudun C, Gégout J-C, Piedallu C, Rameau J-C (2006) Soil nutritional factors improve models of plant species distribution: an illustration with *Acer campestre* (L.) in France. J Biogeogr 33:1750–1763

Craig DJ, Craig JE, Abella SR, Vanier CH (2010) Factors affecting exotic annual plant cover and richness along roadsides in the eastern Mojave Desert, USA. J Arid Environ 74:702–707

Dietze MC, Fox A, Beck-Johnson LM, Betancourt JL, Hooten MB, Jarnevich CS, Keitt TH, Kenney MA, Laney CM, Larsen LG, Loescher HW, Lunch CK, Pijanowski BC, Randerson JT, Read EK, Tredennick AT, Vargas R, Weathers KC, White EP (2018) Iterative near-term ecological forecasting: needs, opportunities, and challenges. Proc Natl Acad Sci USA 115:1424–1432

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods Ecol Evol 1:330–342

Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst 40:677–697

Epanchin-Niell RS, Hastings A (2010) Controlling established invaders: integrating economics and spread dynamics to determine optimal management. Ecol Lett 13:528–541

Evans RA, Love RM (1957) The step-point method of sampling: a practical tool in range research. J Range Manage 10:208–212

Federal Geographic Data Committee (2008) National Vegetation Classification Standard. Version 2. FGDC-STD-005-2008. Reston, VA: Federal Geographic Data Committee

Fox J, Weisberg S (2011) An R Companion to Applied Regression. 2nd ed. Thousand Oaks CA: Sage. 472 p

Giljohann KM, Hauser CE, Williams NSG, Moore JL (2011) Optimizing invasive species control across space: willow invasion management in the Australian Alps. J Appl Ecol 48:1286–1294

Greig-Smith P (1979) Pattern in vegetation. J Ecol 67:755–779

HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM (2012) Rethinking community assembly through the lens of coexistence theory. Annu Rev Ecol Evol Syst 43:227–248

Jennings MD, Faber-Langendoen D, Loucks OL, Peet RK, Roberts D (2009) Standards for associations and alliances of the U.S. National Vegetation Classification. Ecol Monogr 79:173–199

Jones MM, Tuomisto H, Borcard D, Legendre P, Clark DB, Olivas PC (2008) Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. Oecologia 155:593–604

Jørgensen RH, Kollmann J (2009) Invasion of coastal dunes by the alien shrub *Rosa rugosa* is associated with roads, tracks and houses. Flora Morphol Distrib Funct Ecol Plants 204:289–297

Levine JM (2000) Species diversity and biological invasions: relating local process to community pattern. Science 288:852–854

Li YM, Dlugosch KM, Enquist BJ (2015) Novel spatial analysis methods reveal scale-dependent spread and infer limiting factors of invasion by Sahara mustard. Ecography 38:311–320

Mackey BG, Lindenmayer DB (2001) Towards a hierarchical framework for modelling the spatial distribution of animals. J Biogeogr 28:1147–1166

Malusa J, Halvorson B, Angell D (2003) Distribution of the exotic mustard *Brassica tournefortii* in the Mohawk Dunes and Mountains, Arizona. Desert Plants 19:31–36

Malusa J, Sundt P (2015) Vegetation of the Barry M. Goldwater Range West, Marine Corps Air Station–Yuma, Arizona. Tucson: School of Natural Resources and the Environment, University of Arizona. 308 p

Minnesota Department of Natural Resources (2013) A Handbook for Collecting Vegetation Plot Data in Minnesota: The Relevé Method. 2nd ed. St. Paul: State of Minnesota, Department of Natural Resources. 64 p

Mucina L, Schaminée JHJ, Rodwell JS (2000) Common data standards for recording relevés in field survey for vegetation classification. J Veg Sci 11:769–772

Roura-Pascual N, Krug RM, Richardson DM, Hui C (2010) Spatially-explicit sensitivity analysis for conservation management: exploring the influence of decisions in invasive alien plant management. Divers Distrib 16:426–438

Rousset F, Ferdy J (2014) Testing environmental and genetic effects in the presence of spatial autocorrelation. Ecography 37:781–790

Sanchez-Flores E (2007) GARP modeling of natural and human factors affecting the potential distribution of the invasives *Schismus arabicus* and *Brassica tournefortii* in "El Pinacate y Gran Desierto de Altar" Biosphere Reserve. Ecol Model 204:457–474

Simberloff D (2009) The role of propagule pressure in biological invasions. Annu Rev Ecol Evol Syst 40:81–102

[USNVC] U.S. National Vegetation Classification (2018) United States National Vegetation Classification Database. Version 2.02. Washington, DC: Federal Geographic Data Committee, Vegetation Subcommittee

Van Devender TR, Felger RS, Búrquez A (1997) Exotic plants in the Sonoran Desert region, Arizona and Sonora. Pages 1–6 in Proceedings of the California Exotic Pest Plant Council Symposium. Berkeley: California Exotic Pest Plant Council

VanTassel HLH, Hansen AM, Barrows CW, Latif Q, Simon MW, Anderson KE (2013) Declines in a ground-dwelling arthropod community during an invasion by Sahara mustard (*Brassica tournefortii*) in aeolian sand habitats. Biol Invasions 16:1675–1687

Winkler DE (2017) Effects of Climate Change on Protected and Invasive Plant Species. Ph.D dissertation. Irvine: University of California, Irvine eScholarship. 472 p

Winkler DE, Gremer JR, Chapin KJ, Kao M, Huxman TE (2018) Rapid alignment of functional trait variation with locality across the invaded range of Sahara mustard (*Brassica tournefortii*). Am J Bot 105:1188–1197

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14