Received: 19 August 2021 | Revised: 14 January 2022 | Accepted: 28 January 2022

DOI: 10.1002/ecy.3697

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Community invasion resistance is influenced by interactions between plant traits and site productivity

Claire M. Tortorelli[1] | **Becky K. Kerns**[2] | **Meg A. Krawchuk**[1]

[1]Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon, USA

[2]Pacific Northwest Research Station, Corvallis Forestry Sciences Lab, USDA Forest Service, Corvallis, Oregon, USA

Correspondence
Claire M. Tortorelli
Email: claire.tortorelli@oregonstate.edu

Funding information
Joint Fire Science Program, Grant/Award Number: USDA USFS Project #16-1-01-21; National Science Foundation, Grant/Award Number: Graduate Research Fellowship to CT; Oregon Native Plant Society, Grant/Award Number: Field Research Grant

Handling Editor: Daniel Charles Laughlin

Abstract

Plant communities are predicted to be more resistant to invasion if they are highly productive, harbor species with similar functional traits to invaders, or support species with high competitive potential. However, the strength of competition may decrease with increasing abiotic stress if species more heavily invest in traits that confer stress tolerance over competitive ability, potentially influencing community trait–resistance relationships. Recent research examining how community traits influence invasion resistance has been predominantly focused on single vegetation types, and results between studies are often conflicting. Few studies have evaluated the extent to which abiotic factors and community traits interact to influence invasion along vegetation gradients. Here, we use an in situ seed addition experiment to examine how above- and below-ground plant traits and vegetation type interact to influence community resistance to invasion by a recently introduced annual grass, *Ventenata dubia*, along a productivity gradient in eastern Oregon, USA. To measure invasion resistance, we evaluated *V. dubia* biomass in seeded subplots with varying trait compositions across three vegetation types situated along a productivity gradient: scab-flats (sparsely vegetated dwarf-shrublands), low sage-steppe, and ephemeral wet meadows. Trait–resistance relationships were highly context dependent. In wet meadows (the most productive sites), resistance to invasion increased with increasing resident biomass and as community weighted mean trait values for specific leaf area, fine-to-total root volume, and height become more similar to *V. dubia*'s trait values, although these relationships were relatively weak. We did not find evidence that neighboring species influenced invasion resistance in less productive vegetation types, in contrast to our expectations that facilitative interactions may increase with decreasing productivity as posited by the stress-gradient hypothesis. Unlike *V. dubia*, which heavily invaded all three vegetation types, introduced species with similar trait values, including *Bromus tectorum*, were not abundant throughout the study area demonstrating *V. dubia*'s unique ability to take advantage of available resources. Our results illustrate how community traits and site productivity interact to influence community resistance to invasion and highlight that communities with lower overall biomass and few functionally similar species to *V. dubia* may be at the greatest risk for invasion.

KEYWORDS
biological resistance, context-dependent interaction, trait similarity, *Ventenata*, invasion, invasive annual grass, limiting similarity, niche, productivity gradient, sage-steppe, trait complementarity, trait hierarchy

INTRODUCTION

Community resistance to invasion by introduced species is influenced by interactions with biotic and abiotic characteristics of the recipient community. These resistance factors are not mutually exclusive, and the strength and direction of biophysical interactions may vary across gradients in resource availability and environmental stress (Chesson, 2000; Von Holle & Simberloff, 2005). Studies of plant communities that investigate the local biotic factors influencing invasion, such as resident biomass and functional trait composition, often focus on a single biophysical setting or vegetation type and may neglect to consider how local biotic factors interact with abiotic site conditions and resource availability, such as available soil moisture (Byun et al., 2018). Understanding how above- and belowground community traits and environment interact to influence invasion resistance is important for predicting potential impacts associated with introduced species, targeting management efforts, and developing generalizable invasion frameworks.

Multiple community assembly hypotheses have been developed to explain how community traits contribute to community assembly, biotic interactions, and invasion resistance in plant ecology. Of these, three key hypotheses have emerged, which we examine here. Community productivity is posited to lead to higher competitive potential and invasion resistance as productive communities more completely utilize resources and leave fewer resources available for invaders (Gaudet & Keddy, 1988; Lulow, 2006). We refer to this hypothesis hereafter as the "productivity-resistance hypothesis." However, community functional trait composition may be a stronger predictor of invasion resistance than biomass alone if some traits increase community competitive potential more than others. The limiting similarity hypothesis posits that ecologically similar species with similar trait values have greater niche overlap and compete more strongly for limited resources than dissimilar species (Kunstler et al., 2012; MacArthur & Levins, 1967), hereafter the "trait similarity hypothesis." Alternatively, the competition–trait hierarchy hypothesis predicts that competitive ability is directionally ranked, with differences in traits related to competition reflecting disparities in fitness and competitive ability (Kunstler et al., 2012), hereafter the "trait hierarchy hypothesis."

Under the trait similarity hypothesis, communities composed of species with similar trait values to invaders are expected to compete more strongly for resources in shared niches, resulting in greater invasion resistance than communities with dissimilar traits. Functional similarity between resident species and potential invaders has been found to increase community resistance to invasion in some cases; however, findings between studies are often inconsistent (Price & Pärtel, 2013). Invasion resistance through trait similarity can be maintained by different mechanisms with distinct ecological assumptions that can be measured different ways, potentially contributing to conflicting findings (Gallien et al., 2014). Competition with invaders may be driven by several species and influenced by each species' relative abundance or may be driven by only those species that are most similar to the invader, irrespective of their abundance (Thuiller et al., 2010). However, all indices of trait similarity may be poor predictors of invasion resistance if there is an insufficient degree of niche overlap present, or if invasion is more strongly influenced by other processes such as fitness differences (Hess et al., 2020).

Trait hierarchies may influence invasion resistance when trait variations between resident and introduced species reflect competition and fitness differences rather than niche overlap. Many recent studies have found such hierarchies to be stronger drivers of community resistance to invasion than trait similarity (Lai et al., 2015; Sheppard, 2019). For example, species with traits that confer high competitive potential for limited surface soil resources, such as high specific root length, low root-to-shoot biomass, and low leaf nitrogen concentration, suppressed invader growth more strongly than species with similar trait values to an invader in a Californian serpentine grassland (Funk & Wolf, 2016).

Despite the expanding body of literature exploring relationships between community traits and invasion resistance, inconsistencies across studies have slowed the development of generalizable community trait–resistance frameworks (Garbowski et al., 2020; Hess et al., 2020; Price & Pärtel, 2013). Such inconsistencies may be in part attributed to context dependencies driven by interactions

between community trait–invasion relationships and abiotic conditions.

Environmental stress has been shown to alter the strength and direction of species interactions and plant community-invasion resistance relationships. Competitive interactions are predicted to be weaker in less productive communities (Grime, 1979), and may shift from competitive to facilitative in stressful environments when neighboring species ameliorate physical environmental conditions as predicted by the "stress-gradient hypothesis" (Bertness & Callaway, 1994; Hacker & Gaines, 1997). That is, resident biomass, community-trait similarity, and trait-hierarchies may contribute more strongly to community invasion-resistance in low-stress, resource rich environments than in stressful environments with limited resources. The presence of resident species may even facilitate invasion in high-stress environments if the characteristics of the community or species helps to ameliorate abiotic stressors (Lucero et al., 2019; Von Holle, 2013; Zarnetske et al., 2013).

Additionally, the relative importance of community traits in conferring invasion resistance and the strength of trait–resistance relationships may differ depending on environmental conditions and resource availability (Conti et al., 2018; Funk, 2021). Traits related to high rates of resource acquisition such as high height and specific leaf area (SLA) may contribute strongly to community resistance in low-stress and resource-rich-environments, while traits associated with stress tolerance and conservative resource use, such as low SLA and low leaf nitrogen may be more important in high-stress and resource-limited communities (Funk & Wolf, 2016).

The relatively recent invasion of a Eurasian annual grass, *Ventenata dubia*, in North America's Inland Pacific Northwest provides an important and relevant opportunity to disentangle contrasting community assembly and invasion hypotheses. The rapid expansion of *V. dubia* into previously uninvaded natural areas (Tortorelli et al., 2020) and its potential to alter ecosystem processes through changing fuel characteristics and fire behavior have contributed to this species' high management concern (Kerns et al., 2020). Despite its high-risk profile, relatively little is known regarding the factors influencing community susceptibility or resistance to *V. dubia* invasion, or how community–resistance relationships vary across vegetation types. Understanding how community traits and site conditions interact to influence resistance to this aggressive invader can aid the development of targeted management approaches while helping to build generalizable resistance frameworks.

Here, we use an in-situ field experiment to test how three community assembly hypotheses predict resistance to *V. dubia* invasion, and how trait–resistance relationships vary with biotic and abiotic context. We examine how (1) resident biomass, (2) trait similarity, and (3) trait hierarchy influence invasion resistance in three distinct vegetation types situated along a vegetative productivity gradient (Figure 1).

MATERIALS AND METHODS

Study area

The study was conducted over summer 2019 through 2020 in the Ochoco National Forest of eastern Oregon's Blue Mountains, USA. The mixed conifer forest ecosystems of the Blue Mountains are situated on an expansive lava plateau positioned just east of the Cascade Mountains. The forests are intermixed with large patches of shallow, basaltic soils supporting ephemeral wet meadows and xeric dwarf-shrublands. This area receives between 19 and 52 cm of precipitation per year, with the majority falling between November and June (Western Regional Climate Center, 2021). Precipitation during the sampling season was slightly higher than average, with more rain falling in the late summer and early fall (Appendix S1).

Vegetation gradient

Study sites included three non-forest vegetation types embedded within the larger forested landscape that are frequently invaded by *V. dubia*: ephemeral wet meadows, low sage-steppe, and scab-flats (Figure 2). The vegetation types have distinct floral compositions that vary along a productivity gradient likely driven by differences in soil depth and available soil moisture (Table 1). Ephemeral wet meadows are the most productive and have the deepest soils of the three vegetation types (Paulson, 1977). These sites are characterized by a perched water table and saturated soils in spring and early summer, allowing them to support wetland obligate species including *Juncus* spp. and *Camas quamash* (Johnson & Swanson, 2005). Of the two dwarf-shrubland vegetation types, scab-flats are the least productive with foliar cover typically under 20% and very shallow soils (Johnson & Swanson, 2005; Paulson, 1977). These rocky sites support low cover of *Artemisia rigida*, the shallow-rooted bunchgrass *Poa secunda*, and various annual and perennial forbs. Low sage-steppe falls between the wet meadows and scab-flats along the productivity gradient. This vegetation type has moderate foliar cover and deeper, better draining soils than scab-flats that support characteristic *Artemisia arbuscula* and deep-rooted perennial bunchgrasses, including *Pseudoroegneria spicata*, along

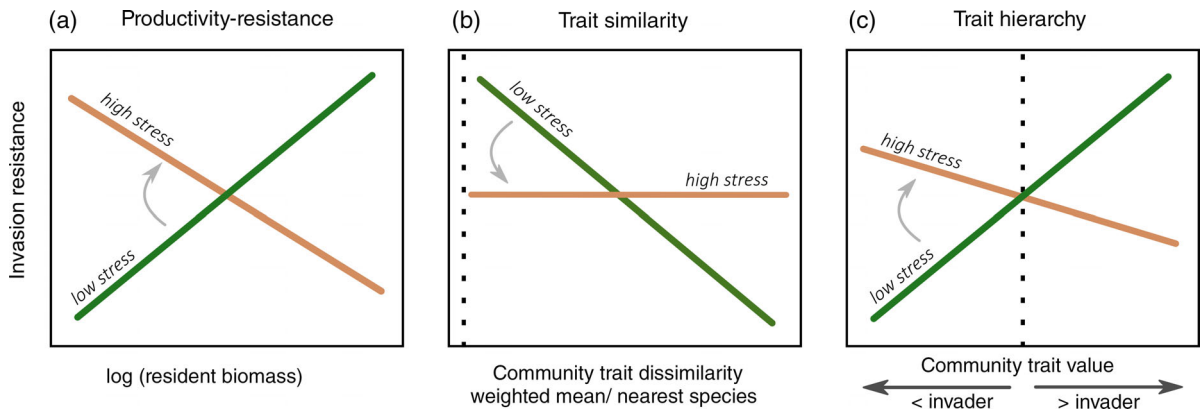

FIGURE 1 Three community assembly hypotheses and potential interactions with environmental stress. (a) **Productivity–resistance** relationships are predicted to be positive in low-stress environments where competition between resident species and invaders is strongest. However, productivity–resistance relationships may become negative in high-stress environments if residents ameliorate stressful abiotic conditions and facilitate invasion. (b) Invasion resistance is expected to decrease with increasing **trait dissimilarity** in low-stress environments where competition for resources is predicted to be strongest, but these relationships may be less pronounced as abiotic stress increases and competition between species weakens. (c) The **trait hierarchy** hypothesis posits that invasion resistance will either increase or decrease as community trait values exceed those of the invader, depending on the trait. The direction of the trait-resistance relationship may be influenced by environmental conditions

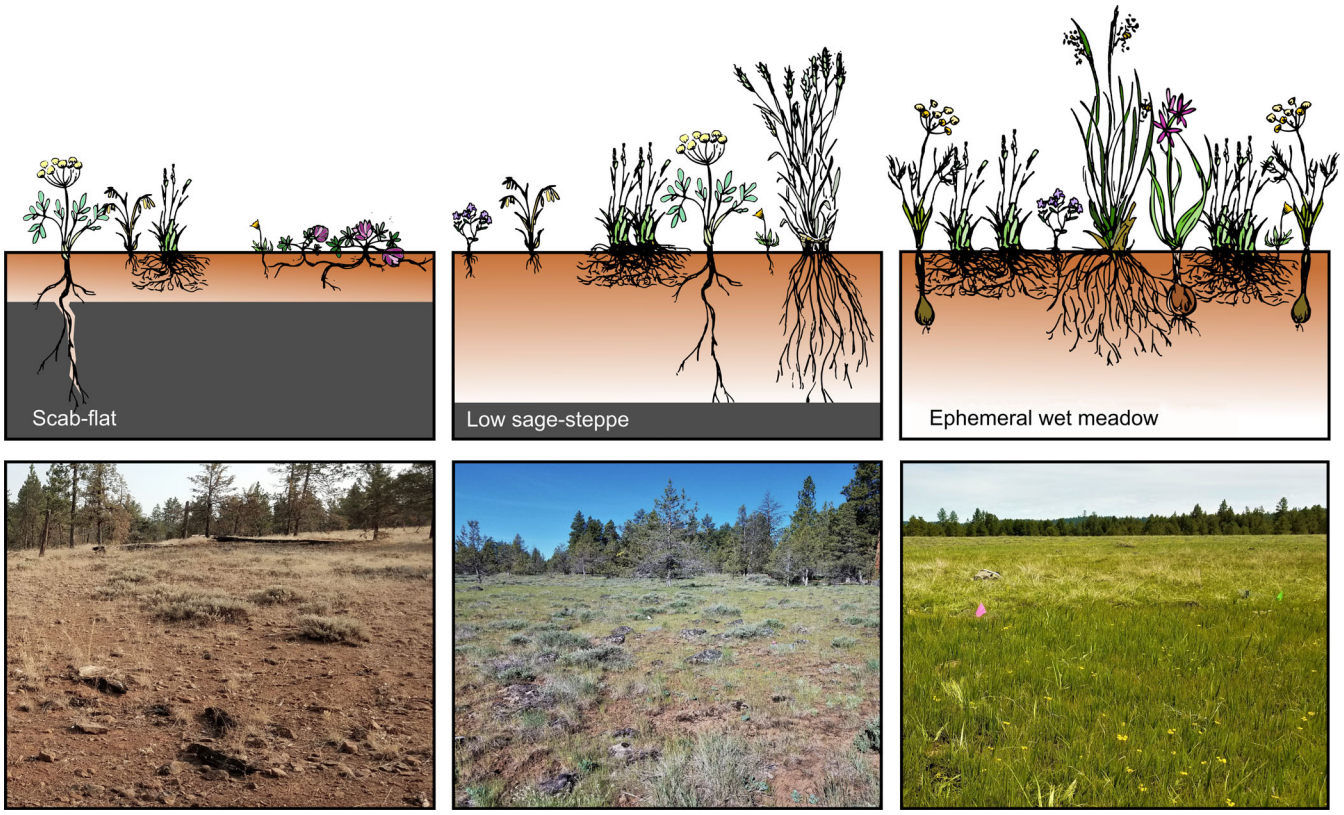

FIGURE 2 Sampled communities were distributed across a productivity and soil moisture gradient consisting of three vegetation types: scab-flats, low sage-steppe, and ephemeral wet meadows

with various annual and perennial forbs (Paulson, 1977). The three vegetation types often exist in close proximity to one another and are exposed to harsh growing conditions and similar climatic extremes.

We chose the three vegetation types to represent a vegetative productivity gradient based on plant associations and soil descriptions from the Ochoco National Forest Soil Resource Inventory (Paulson, 1977) and

TABLE 1 Soil depth, soil moisture availability, mean foliar cover, mean resident biomass, and mean species richness for three vegetation types

Vegetation type	Soil depth (cm)	Water-holding capacity	Foliar cover (%)	Resident biomass (g)	Species richness
Ephemeral wet meadow	50–150	Very low to moderate	53.9 (41.0, 70.9)	8.5 (4.8, 15.0)	9.0 (5, 16)
Low sage-steppe	39–45	Very low to low	25.9 (19.6, 34.3)	4.1 (2.3, 7.2)	5.5 (3, 9)
Scab-flat	<25	Very low	17.9 (13.4, 23.9)	1.9 (1.1, 3.4)	5.2 (3, 8)

Notes: Soil characteristics are estimated from Ochoco National Forest soil categories and species associations from Paulson (1977). Mean foliar cover (with 95% CI in parentheses), resident biomass (with 95% CI in parentheses), and species richness (with minimum and maximum in parentheses) are summarized from our study data (Appendix S2).

consultation with local soil and vegetation experts. We examined the extent to which the sampled vegetation types represented a true productivity gradient, and found that mean biomass differed between the three vegetation types with wet meadows being the most productive, followed by low sage-steppe and scab-flats (Table 1; Appendix S2).

Experimental design and implementation

We conducted an in situ experiment to measure community resistance to invasion by *V. dubia* across the three vegetation types, using a seed addition experiment to control propagule pressure and invasion intensity. Over June through August 2019, we installed five experimental blocks across the study region consisting of one plot in each of the three vegetation types. Distance between blocks ranged from 4.2 to 17.4 km. Each plot contained seven randomly selected subplots (20 × 20 cm) that varied naturally in species and functional trait composition. Subplots were arranged in a grid positioned so that all subplots fell within the target vegetation type. In total, we installed 105 subplots (5 blocks × 3 vegetation types/plots × 7 subplots). Distances between neighboring subplots ranged from 1 to 3 m.

We chose to conduct the experiment at a neighborhood scale (20 × 20 cm) to focus the study on interactions between *V. dubia* and its immediate neighboring species. Given *V. dubia*'s slight structure and minute root system, we expected interactions to be strongest at relatively small spatial scales. However, the restricted subplot size resulted in lower species richness and trait diversity present in local communities, and may not accurately represent trait compositions in larger communities. Species richness in subplots ranged from 4 to 17 species (Table 1). We limited the study to investigate interactions between *V. dubia* and herbaceous forbs and grasses because shrubs were not present in all plots and to avoid removing ecologically important *Artemisia* spp. when collecting biomass for testing the productivity–resistance hypothesis. Accordingly, subplots were located at least 50 cm from the edge of the nearest dwarf-shrub canopy. At the plot level, dwarf-shrub cover ranged from 5% to 15% in low sage-steppe and scab-flats. Sample plots were installed in currently invaded areas to ensure that *V. dubia* was adapted to the environmental conditions of each plot and to avoid spreading *V. dubia* into uninvaded areas. In subplots where *V. dubia* was already established, community composition and biomass may have been influenced by the invader. In a previous observational field study, we found that *V. dubia* cover increased with decreasing Shannon Diversity (Tortorelli et al., 2020). However, whether diversity was reduced by invasion or diversity conferred invasion resistance was unknown.

Subplots were prepared by removing any existing *V. dubia* then adding a measured aliquot of seed to minimize the effects of natural variability in *V. dubia* propagules at each subplot. Existing *V. dubia* was hand pulled from inside subplots and from a 25-cm buffer surrounding each subplot to reduce natural recruitment of *V. dubia*. Disturbance from hand pulling was minimal. The seed was collected from just outside each plot in early August, combined, hand cleaned, weighed into equal portions, and tested for viability with a tetrazolium chloride test at the Oregon State University seed lab. Seeds were 91% viable. We broadcast seeds into subplots at a rate of ~500 seeds (0.41 g) per subplot (12,500 seeds/m^2) in late August 2019, because *V. dubia* is a cool season, C_3 annual, known to germinate in the fall (Wallace et al., 2015). Seed amounts were chosen to represent a realistic high level of invasion assuming that individuals generally produce 15–35 seeds per plant (Wallace et al., 2015) and we observed hundreds of individual plants in the most heavily invaded subplots prior to seeding. We seeded at a high invasion level to increase potential biotic interactions within the subplots and to dampen the effect of the residual seed bank between subplots. We expected the effect of residual seed bank to be

relatively low given the short seed bank lifespan of *V. dubia* (<3 years; Wallace et al., 2015). However, to measure natural *V. dubia* recruitment, we installed an additional three subplots at each plot ($n = 45$) as "unseeded controls" in which we removed *V. dubia* from all subplots but did not add *V. dubia* seed (Appendix S3). We installed 10-cm high cages around each subplot composed of steel wire hardware cloth with 3-mm openings at the time of seeding to limit seeds from blowing out or into subplots.

We revisited all subplots in late June 2020 to measure percent foliar cover of plant species and harvest all above-ground biomass in each subplot. *Ventenata dubia* biomass and non-*V. dubia* (resident) biomass were separated, dried at 55°C for 42 h, and weighed to the nearest 0.01 g. This study was conducted over a single growing season and care should be taken when generalizing results to years with climatic conditions that differ from those that occurred over the sapling period. Higher fall precipitation observed over the sample period (Appendix S1) may have increased the germination success of fall-germinating annual grasses (including *V. dubia*) relative to spring-germinating native annual forbs compared to an average year.

Species functional traits

We sampled and calculated above- and belowground functional traits from 37 of the most abundant species present in the subplots (Appendix S4: Table S1). To reduce the total number of species included in the analysis down to 37, we excluded species if their foliar cover was consistently <0.5% or they occurred in fewer than three subplots (2% of subplots). To quantify the trait potential of each species in conditions where competitive strategies are most clearly expressed, we collected samples between May and July 2020 from reproductive individuals, either in flower or in seed, from the least stressful environment possible. Most species were collected from wet meadows ($n = 31$; Appendix S4: Table S2). Many species, including *V. dubia*, displayed trait plasticity across the vegetation types with individuals appearing generally more robust in wet meadows than in low sage-steppe or scab-flat plots. Thus, our trait metrics may overestimate trait values in less productive sites for traits that are more strongly expressed in more productive sites.

We focused on seven functional traits related to competitive ability, potential growth rate, carbon capture, nitrogen acquisition, resource allocation, and root longevity (Table 2) following protocols presented in Cornelissen et al. (2003). For aboveground traits, two young, fully expanded leaves per individual were harvested, scanned for leaf area using Easy Leaf Area software (Easlon & Bloom, 2014), dried, weighed to calculate specific leaf area (SLA), and analyzed for percent leaf nitrogen concentration (Central Analytical Laboratory, Corvallis, OR, USA).

For belowground and whole plant traits, four to seven individuals per species were harvested by digging up the entire root system, when possible (Appendix S4: Table S2). Roots were washed, dried, and scanned using the WinRHIZO image analysis system to determine total root length, root diameter, and fine-to-total root volume ratio (<2 mm; Regent Instruments Inc., 2019). Above and belowground biomass was separated for each species, dried at 55°C for 48 h, and weighed to calculate root-to-shoot ratio (R. Species trait values were averaged across individuals and log transformed. Log-transformed trait values were mean centered and scaled by standard deviation to obtain standardized trait values for each species for comparisons (hereafter "trait values"). Community weighted mean (CWM) trait values were calculated for each subplot as the mean trait value weighted by proportional foliar cover of each species present.

Calculating community metrics

We used the following "community metrics" to calculate community resident biomass and trait values for each of the proposed assembly hypotheses, following Gallien et al. (2014) and Catford et al. (2019). To characterize the community in relation to the first hypothesis, productivity-resistance, we calculated the resident biomass metric as the sum of all aboveground biomass (excluding *V. dubia*) in each subplot as an indication of community productivity.

We applied two different metrics to characterize the second hypothesis, trait similarity, to account for differences in the relative importance of the entire community versus only the most similar species in conferring invasion resistance (Gallien et al., 2014; Thuiller et al., 2010). The weighted mean dissimilarity metric, also known as absolute trait distance, was calculated as the absolute value of the difference between the CWM trait values (excluding *V. dubia*) and *V. dubia*'s trait values for each of our seven functional traits at each subplot; ($|\overline{\text{CWM}} - V.\ dubia|$). This metric indicates the degree of dissimilarity and potential niche overlap between *V. dubia* and the established community for each trait (Lai et al., 2015). Communities with high weighted mean dissimilarity likely have less niche overlap with *V. dubia* than communities with low weighted mean dissimilarity. To indicate potential niche overlap between *V. dubia* and the functionally closest neighbors (Gallien et al., 2014), we calculated the nearest species dissimilarity metric as the difference between the trait value of the species that have

TABLE 2 Trait descriptions and abbreviations

Trait	Abbreviation	Description	Functional significance
Height	Height	Height from soil surface to tallest photosynthesizing material in situ	Light interception (+) (Gaudet & Keddy, 1988)
Leaf nitrogen	Leaf N	Percent of nitrogen in leaf tissue	Photosynthetic rate (+) (Cornelissen et al., 2003)
Specific leaf area	SLA	Leaf area/leaf mass (cm^2/g)	High resource use and growth in herbaceous species (+) (Cornelissen et al., 2003)
Root-to-shoot ratio	R:S	Root mass/shoot mass	Associated with stress tolerance (+) and resource allocation (Mokany et al., 2006)
Fine-to-total root volume ratio	F:T root V	Fine root volume/total root volume	Reflects rate of nutrient uptake (+) (Roumet et al., 2006)
Root diameter	Root D	Average root diameter (mm)	Reflects rate of nutrient uptake (−) (Roumet et al., 2006)
Root length	Root L	Total length of roots (cm)	Associated with nutrient and water uptake (+) (Roumet et al., 2006)

Note: (+) and (−) indicate direction of relationships between trait values and functions.

trait values directly above ($\overline{a}$) and below ($\overline{b}$) those of *V. dubia* for each functional trait and at each subplot; ($\overline{a} < V.\ dubia < \overline{b}$; nearest species dissimilarity $= \overline{b} - \overline{a}$). Additional information on calculating nearest species dissimilarity is presented in Appendix S3.

To characterize the third hypothesis, trait hierarchy, we calculated the hierarchical distance metric as the difference between the CWM trait values and *V. dubia*'s trait values for each functional trait at each subplot; $\left(\overline{\text{CWM}} - V.\ dubia\right)$. Negative values indicate that the CWM was lower than *V. dubia*'s trait value and positive values indicate that the CWM was higher than *V. dubia*'s trait value. The metric indicates directional fitness differences between communities and *V. dubia* according to the trait-hierarchy hypothesis (Catford et al., 2019; Lai et al., 2015).

Statistical analysis

Examining species and community traits

We examined trait similarity between resident species and *V. dubia* using nonmetric multidimensional scaling (NMS) ordinations with species in trait space. To examine how the community trait distribution and trait potential (from the most productive vegetation type) differed between vegetation types, we plotted subplots in CWM trait space by vegetation type. NMS ordinations were performed using the Bray-Curtis distance measure with two dimensions and random starting locations (Bray & Curtis, 1957). Species and community trait values were log-transformed (to account for them being log-normally distributed), standardized, and shifted by the minimum value of each trait so that all values were positive because Bray-Curtis dissimilarities cannot be calculated for negative values. To further examine the extent to which CWM trait similarity to *V. dubia* varied by vegetation type, we calculated Euclidean distance between CWM and *V. dubia* trait values for each subplot and compared distances between vegetation types (Appendix S5: Table S1, Figures S1 and S2).

Community traits × vegetation gradient effect on invasion resistance

We tested the effect of our community metrics (resident biomass, weighted mean dissimilarity, nearest species dissimilarity, and hierarchical distance) on invasion resistance using linear mixed effects models. Each model examined the response of *V. dubia* biomass to a single community trait (e.g., height-hierarchical distance) and interaction with vegetation type as a factor. Biomass measurements were log-transformed to meet the assumptions of linear modeling. Random intercepts were included for plots nested within experimental blocks. We explored different options for modeling community trait values including reducing trait dimensionality using multivariate distance metrics (Appendix S5: Table S1). However, we chose to base our analysis on individual trait models to avoid issues with collinearity among traits (Appendix S5: Figure S3), to retain high interpretability (e.g., compared to reducing dimensionality using a multi-trait community metric, multivariate distance estimates, or ordination axes), and to maintain appropriate model sizes considering our blocked sampling

design and inclusion of an interaction. To identify which assembly hypotheses best explained invasion resistance, we compared goodness-of-fit between individual models using pseudo marginal r^2 (Nakagawa & Schielzeth, 2013).

Statistical analyses were performed in R version 4.0.3 using the package *lme4* (Bates et al., 2015) for model fitting and performance (Lüdecke et al., 2021). The package *r2glmm* (Jaeger, 2017) was used for computing marginal r^2 following Nakagawa and Schielzeth (2013) and corrected Akaike information criterion corrected for sample size (AIC_c) values were calculated from *MuMIn* (Barton, 2020). *Emmeans* was used for slope comparisons (Russell, 2021). We used the package *car* for testing interaction effects using type II Wald χ^2 tests (Fox & Weisberg, 2019) and *vegan* for NMS ordinations (Oksanen et al., 2019).

RESULTS

Comparison of species functional and community traits

Overall, *V. dubia*'s trait values were most similar to neighboring annual and shallow-rooted perennial graminoids, including two introduced annual grasses, *Bromus tectorum* and *Bromus arvensis* (Figure 3). These introduced grasses were not abundant throughout the study area, with a combined average cover of <4% (Figure 3). On average, *V. dubia* had slightly shorter roots and lower root diameter compared to other introduced annual grasses and lower root-to-shoot ratio, root diameter, and leaf N and higher fine-to-total root volume and SLA compared to most native residents (Figure 3; Appendix S4: Table S2). The most abundant resident species throughout our subplots was *P. secunda* with average cover of 7.5%.

Community weighted mean trait values were highly variable among subplots and within vegetation types (Appendix S5: Figure S4). There was considerable overlap in CWM trait values between vegetation types. However, on average, wet meadows had higher root diameter and shorter total root length, low sage-steppe had slightly higher fine-to-total root volume and height, and scabflats had higher root-to-shoot ratio and lower SLA than other vegetation types (Appendix S5: Figure S4). Stress for the species and subplot two-dimensional NMS solutions were 0.13 and 0.11, respectively. Euclidean distances calculated between *V. dubia* and CWM trait values were highly variable between subplots (Appendix S5: Figure S2). While mean Euclidean distance did not strongly differ between vegetation types, subplots in scabflats generally had slightly higher Euclidean distances than those in low sage-steppe or wet meadows and the lowest Euclidean distances were recorded from subplots in low sage-steppe (Appendix S5: Figure S2).

The range of CWM trait values across all subplots generally fell entirely above or below *V. dubia*'s trait

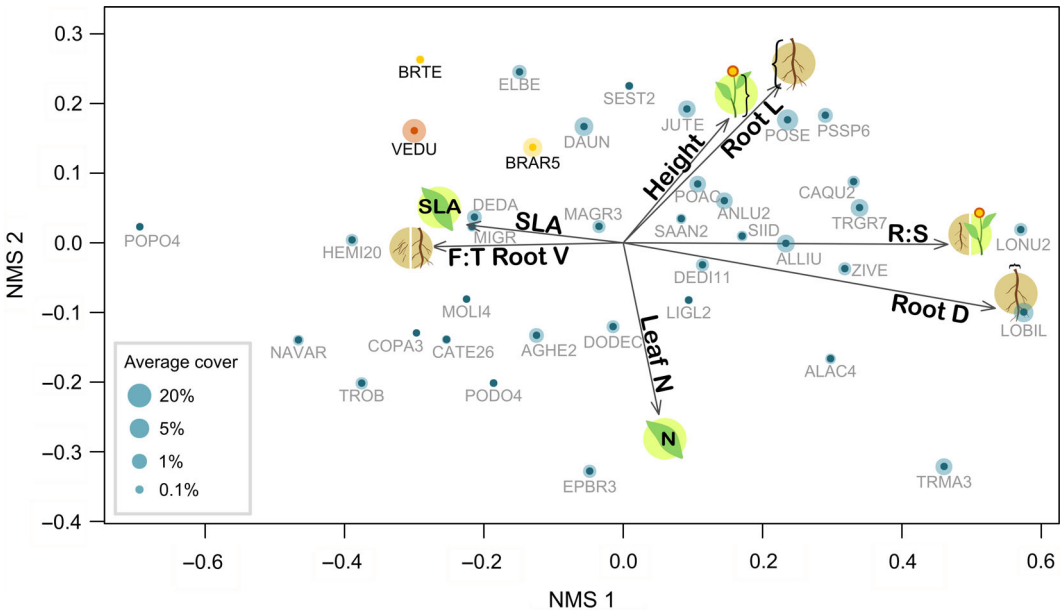

FIGURE 3 Nonmetric multidimensional scaling (NMS) ordination of species in trait space. *Ventenata dubia* (VEDU) is represented by a red point. Introduced annual grasses, *Bromus tectorum* (BRTE) and *Bromus arvensis* (BRAR5) are indicated by yellow points. Native species are represented by blue points. Points are scaled exponentially by their average foliar cover across all subplots. Species are represented by their USDA plant code (Appendix S4: Table S1). F:T Root V, fine-to-total root volume ratio; Leaf N, leaf nitrogen; R:S, root-to-shoot ratio; Root D, root diameter; Root L, root length; SLA, specific leaf area

values depending on the trait, rather than some subplots having higher values and some lower. This is indicated by the presence of only negative or positive hierarchical distance values represented for a single trait. *Ventenata dubia* generally had higher height, SLA, and fine-to-total root volume and lower leaf N, root-to-shoot ratio, root diameter, and root length than CWM trait values (Figure 4c).

Community metrics × vegetation gradient effect on invasion resistance

Ventenata dubia biomass responses to community metrics were variable and highly context dependent. When considering all vegetation types, community metrics were generally weak predictors of *V. dubia* biomass (marginal r^2 for all models <0.1; Appendix S6: Table S1). The strongest predictors of *V. dubia* biomass were SLA-weighted mean dissimilarity, SLA-hierarchical distance, and resident biomass (marginal r^2 = 0.081, 0.081, and 0.077, respectively; Figure 4). We found no evidence of an effect of nearest species dissimilarity on *V. dubia* biomass for any trait.

The strength and direction of community-metric–*V. dubia* relationships often depended on vegetation type. Community metric–*V. dubia* relationships were stronger in wet meadows than scab-flats or low sage-steppe for resident biomass and for all traits except root-to-shoot rati and root length for weighted mean dissimilarity and

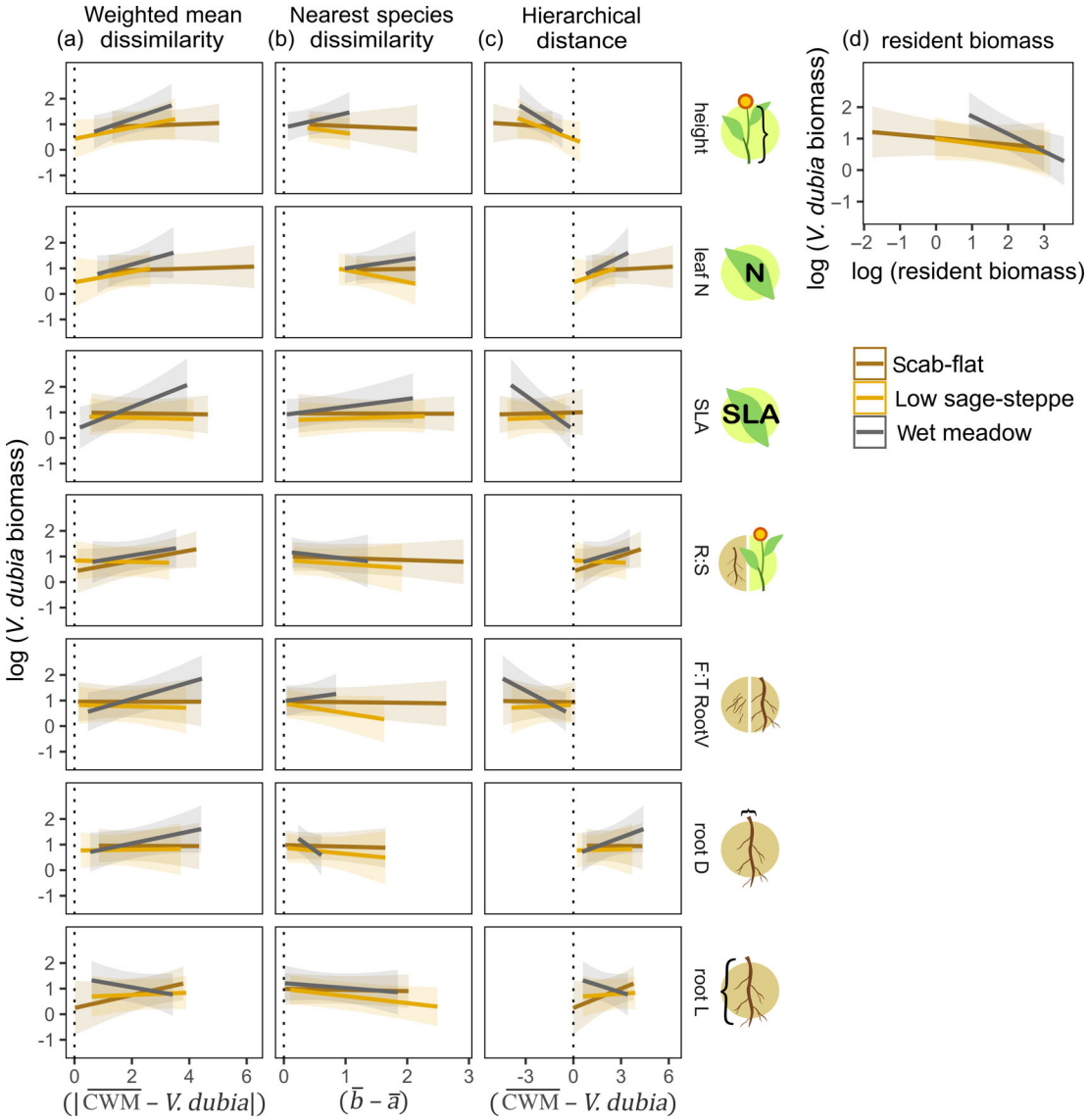

FIGURE 4 *Ventenata dubia* biomass response to (a) community weighted mean (CWM) dissimilarity, (b) nearest species dissimilarity, and (c) hierarchical distance community trait values, and (d) resident biomass across three vegetation types spanning a productivity gradient. F:T Root V, fine-to-total root volume ratio; leaf N, leaf nitrogen; R:S, root-to-shoot ratio; root D, root diameter; root L, root length; SLA, specific leaf area

hierarchical distance metrics. While the strength of many trait-vegetation type interactions was uncertain given high variance in the data, we found evidence that vegetation type interacted with SLA hierarchical distance ($\chi^2 = 4.95$, $p = 0.08$), SLA weighted mean dissimilarity and ($\chi^2 = 4.90$, $p = 0.09$), and resident biomass ($\chi^2 = 4.06$, $p = 0.13$) to influence *V. dubia* biomass (Appendix S6: Table S2). In wet meadows, *V. dubia* decreased with increasing resident biomass (estimate: −0.56 [95% CI: −0.95, −0.17]) and as CWM fine-to-total root volume, height, and SLA became more similar to *V. dubia* (Figure 4; Appendix S6: Table S3). *Ventenata dubia* also decreased as CWM leaf N and root diameter approached *V. dubia*'s trait value in wet meadows, but these results are uncertain given high variances around the mean. In less productive low sage-steppe and scabflats, we did not find evidence to suggest that resident biomass or community traits strongly influenced *V. dubia* biomass (Figure 4; Appendix S6: Table S3).

DISCUSSION

Community trait–resistance relationships varied by community metric, trait, and vegetation type, with the strongest relationships almost always occurring in the most productive vegetation type, wet meadows. Our findings suggest that community resistance mechanisms and species interactions are highly context dependent and are likely to be strongest in productive sites in concordance with the productivity–resistance hypothesis. However, *V. dubia* successfully invaded and became abundant in communities regardless of vegetation type, community trait composition, or resident biomass, indicating that it may experience relatively little competition and niche overlap with herbaceous neighbors, and the invasibility of communities may be more strongly influenced by unmeasured microsite factors. Despite sharing similar functional traits with *V. dubia*, other annual grasses were not abundant throughout our sample sites, highlighting the novelty of the *V. dubia* invasion. Our findings indicate that *V. dubia*'s success may be driven by additional physiological or other mechanisms distinct from the above- and belowground traits that we included in our analysis.

Resident biomass was one of the strongest drivers of community resistance to *V. dubia*, consistent with the productivity-resistance hypothesis. However, resident biomass only conferred community resistance in wet meadows where site productivity was relatively high. Our findings resonate with past studies that reported stronger effects of biomass on invasion resistance to an introduced perennial forb than individual species' traits (including height, root-to-shoot ratio, and leaf area) in productive wetland communities (Gaudett & Keddy, 1988) and higher community resistance to annual grass invasion in areas with abundant perennial bunchgrasses (Lulow, 2006). Such resistance may be attributed to decreased general resource availability including light, water, soil nutrients, and physical spaces for the invader to establish as community abundance increases (Chambers et al., 2007).

Invasion was lowest when CWM trait values were similar to *V. dubia*'s trait value in the most productive vegetation type, wet meadows, indicating that functionally similar communities may be more resistant to *V. dubia* through greater niche overlap when they also have high biomass, consistent with the trait similarity hypothesis. However, separating the relative importance of trait similarity and trait hierarchy resistance mechanisms is difficult because *V. dubia*'s trait values fell above or below the CWM trait values for each trait in almost every community. For example, it is unclear whether the strong relationships observed between *V. dubia* and SLA in wet meadows was driven by a fitness advantage of species with high SLA or niche differentiation (as species with higher SLA were also more similar to *V. dubia*). The same can be said for relationships with height and fine-to-total root volume. Additionally, the extent to which different traits confer invasion resistance remains unclear. For example, while high SLA and leaf N are commonly associated with competitive potential and resource use, especially in resource rich environments (Cornelissen et al., 2003), some studies have found that species with low SLA and leaf N increase biotic resistance to invaders, including those with higher SLA, particularly in environments with limited resources (Conti et al., 2018; Funk & Wolf, 2016).

In our case, distinguishing between trait similarity and trait hierarchy resistance mechanisms may not be especially relevant for identifying areas at high risk for invasion because *V. dubia*'s trait values nearly always fell outside the range of naturally occurring CWM trait values in these commonly invaded vegetation types. However, for restoration treatments where there is the opportunity to introduce different species to the community, it is important to understand if communities with greater competitive potential (measured through hierarchical distance) compete more strongly with *V. dubia*. Further investigation is needed in vegetation types with a range of CWM trait values that fall above and below *V. dubia*'s trait values (e.g., invaded oak savannahs or Palouse prairies) to address whether trait hierarchies or similarity contribute more strongly to invasion resistance.

Although we were unable to differentiate the effect of trait hierarchies from trait similarities, our findings suggest that community resistance is influenced by multiple

or the most abundant species rather than one or two of the most similar species, since weighted mean dissimilarity was clearly a stronger predictor of community resistance than nearest species dissimilarity. Our results reflect those of Gallien et al. (2014) who reported that community metrics involving the entire community were more successful at measuring competition effects than metrics involving only the most similar species.

The effects of resident biomass, weighted mean dissimilarity, and hierarchical distance on community resistance were almost always strongest in the most productive vegetation type. If effect sizes accurately represent the strength of community–resistance interactions (despite high variability in the data contributing to uncertainty), our results would be consistent with the stress gradient hypothesis, which posits that competitive interactions decrease in strength as environmental stress increases (Bertness & Callaway, 1994; Hacker & Gaines, 1997). The weak trait–resistance relationships present in scab-flats and low sage-steppe may be explained by the overall low cover and biomass, allowing *V. dubia* to take advantage of the abundance of physical space for establishment and resources that may be less available to resident species. Species with similar traits may contribute more to invasion resistance in productive sites where there is greater niche overlap, fewer unused resources, and less physical space available for establishment. We suggest that mixed results observed in many studies evaluating the effect of community trait similarity on community resistance (see Price & Pärtel, 2013) may in part be driven by differences in overall site productivity leading to differences in the competitive potential of resident species.

In contrast to experimental findings from perennial grass invasion along a coastal environmental stress gradient (Zarnetske et al., 2013), we did not find evidence that resident herbaceous biomass facilitated invasion in semi-arid vegetation types with high environmental stress. If this were the case, *V. dubia* would have increased with increasing resident biomass in the least productive scab-flat sites. This may demonstrate that either herbaceous species in these vegetation types are weak facilitators and do little to ameliorate stressful conditions for their neighbors, or that *V. dubia* is not strongly influenced by this particular stress gradient and does not require amelioration to thrive in these environments.

We did not consider the effect of dwarf-shrubs in this study as they were generally sparse in our communities and were not present in all vegetation types. However, where they are present in scab-flats and low sage-steppe they likely play important ecological roles by creating patches of nutrient enrichment beneath their canopies (Bechtold & Inouye, 2007). Recent studies have found facilitative effects of shrubs species on abundance of introduced annuals in otherwise stressful environments (Lucero et al., 2019). Further research is required to understand the effects of shrubs on *V. dubia* establishment and growth.

Ventenata dubia had similar trait values to some resident species, including two introduced invasive annual grasses *B. tectorum* and *B. arvensis*, however these functionally similar graminoids were not abundant across the vegetation gradient, despite maintaining a scattered presence throughout the area for decades and heavily invading nearby *Artemisia tridentata* (big sagebrush) and burned forest communities (Johnson and Swanson 2005). This finding reflects the novelty of *V. dubia*'s invasion into shallow soil communities in which few functionally similar native or introduced species have become abundant (Tortorelli et al., 2020). Furthermore, trait similarities to resident species suggest that standard below- and aboveground traits such as those we present here may not be driving *V. dubia*'s relative success in these areas. Instead, success may be attributed to physiological differences such as cold tolerance, phenology, fecundity, or enemy release (Levine et al., 2004).

This study highlights the importance of testing hypotheses in various contexts by demonstrating that community metrics and site productivity interact to influence invasion resistance. Our findings support community assembly hypotheses by showing that resident biomass and communities with similar SLA, fine-to-total root volume, and height as *V. dubia* conferred some invasion resistance, but only in the most productive vegetation type, and these relationships were rather weak. *Ventenata dubia* successfully invaded communities regardless of resident biomass and community traits demonstrating high invasion potential, particularly in ecosystems that were previously thought to be resistant to annual grass invasion. These findings highlight the novelty of the *V. dubia* invasion, identify communities that are at high risk of invasion (less productive vegetation types and wet meadows with low biomass and few functionally similar species), and contribute to the development of generalizable resistance frameworks that may apply to new invaders and environments.

AUTHOR CONTRIBUTIONS

Claire M. Tortorelli collected data, performed analyses, and wrote the paper. All authors discussed study design, results, and made comments on the manuscript.

ACKNOWLEDGMENTS

We thank Leila Giovannoni, Simone Gibson, and Dustin Gannon for assistance in the field. The Gonzalez-Benecke and Hatten labs helped with trait measurements. We also thank Lauren Hallett for manuscript edits, Ariel

Muldoon and Bruce McCune for statistical guidance, and Gregg Riegel and Jill Welborn for input on study design. We acknowledge that our study area is located within the traditional homelands of the Northern Paiute, Wasco, and Warm Springs people. Today, living descendants of these people are a part of the Confederated Tribes of Warm Springs. Funding for this project was provided through the Joint Science Fire Project (USDA USFS Project no. 16-1-01-21), National Science Foundation Graduate Research Fellowship to Claire M. Tortorelli and The Oregon Native Plant Society.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (Tortorelli, 2022) are available on Zenodo at 10.5281/zenodo.5914948.

ORCID

Claire M. Tortorelli https://orcid.org/0000-0001-9493-9817
Becky K. Kerns https://orcid.org/0000-0003-4613-2191
Meg A. Krawchuk https://orcid.org/0000-0002-3240-3117

REFERENCES

Barton, K.. 2020. "MuMIn: Multi-Model Inference." https://CRAN.R-project.org/package=MuMIn.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using Lme4." *Journal of Statistical Software* 67(1): 1–48. https://doi.org/10.18637/jss.v067.i01.

Bechtold, H. A., and R. S. Inouye. 2007. "Distribution of Carbon and Nitrogen in Sagebrush Steppe after Six Years of Nitrogen Addition and Shrub Removal." *Journal of Arid Environments* 71(1): 122–32. https://doi.org/10.1016/j.jaridenv.2007.02.004.

Bertness, M. D., and R. Callaway. 1994. "Positive Interactions in Communities." *Trends in Ecology and Evolution* 9(5): 191–3. https://doi.org/10.1016/0169-5347(94)90087-6.

Bray, J. C., and J. T. Curtis. 1957. "An Ordination of the Upland Forest Communities in Southern Wisconsin." *Ecological Monographs* 27: 325–49.

Byun, C., S. de Blois, and J. Brisson. 2018. "Management of Invasive Plants through Ecological Resistance." *Biological Invasions* 20(1): 1–15. https://doi.org/10.1007/s10530-017-1529-7.

Catford, J. A., A. L. Smith, P. D. Wragg, A. T. Clark, M. Kosmala, J. Cavender-Bares, P. B. Reich, and D. Tilman. 2019. "Traits Linked with Species Invasiveness and Community Invasibility Vary with Time, Stage and Indicator of Invasion in a Long-Term Grassland Experiment." *Ecology Letters* 22(4): 593–604. https://doi.org/10.1111/ele.13220.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. "What Makes Great Basin Sagebrush Ecosystems Invasible by *Bromus tectorum*?" *Ecological Monographs* 77(1): 117–45. https://doi.org/10.1890/05-1991.

Chesson, P. 2000. "Mechanisms of Maintenance of Species Diversity." *Annual Review of Ecology and Systematics* 31(5): 343–66. https://doi.org/10.1146/annurev.ecolsys.31.1.343.

Conti, L., S. Block, M. Parepa, T. Münkemüller, W. Thuiller, A. T. R. R. Acosta, M. Van Kleunen, et al. 2018. "Functional Trait Differences and Trait Plasticity Mediate Biotic Resistance to Potential Plant Invaders." *Journal of Ecology* 106(4): 1607–20. https://doi.org/10.1111/1365-2745.12928.

Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, et al. 2003. "A Handbook of Protocols for Standardised and Easy Measurement of Plant Functional Traits Worldwide." *Australian Journal of Botany* 51(4): 335–80. https://doi.org/10.1071/BT02124.

Easlon, H. M., and A. J. Bloom. 2014. "Easy Leaf Area: Automated Digital Image Analysis for Rapid and Accurate Measurement of Leaf Area." *Applications in Plant Sciences* 2(7): 1400033. https://doi.org/10.3732/apps.1400033.

Fox, J., and S. Weisberg. 2019. "*An R Companion to Applied Regression, Third edition*. " Thousand Oaks, CA: Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Funk, J. L. 2021. "Revising the Trait-Based Filtering Framework to Include Interacting Filters: Lessons from Grassland Restoration." *Journal of Ecology* 109: 3466–72. https://doi.org/10.1111/1365-2745.13763.

Funk, J. L., and A. A. Wolf. 2016. "Testing the Trait- Based Community Framework: Do Functional Traits Predict Competitive Outcomes?" *Ecology* 97(9): 2206–11. https://doi.org/10.2307/41739278.

Gallien, L., M. Carboni, M. Tamara, and T. Münkemüller. 2014. "Identifying the Signal of Environmental Filtering and Competition in Invasion Patterns - a Contest of Approaches from Community Ecology." *Methods in Ecology and Evolution* 5(10): 1002–11. https://doi.org/10.1111/2041-210X.12257.

Garbowski, M., B. Avera, J. H. Bertram, J. S. Courkamp, J. Gray, K. M. Hein, R. Lawrence, et al. 2020. "Getting to the Root of Restoration: Considering Root Traits for Improved Restoration Outcomes under Drought and Competition." *Restoration Ecology* 28: 1384–95. https://doi.org/10.1111/rec.13291.

Gaudet, C. L., and P. A. Keddy. 1988. "A Comparitve Approach to Predicting Competitive Ability from Plant Traits." *Nature* 334: 33–4.

Grime, J. P. 1979. *Plant Strategies and Vegetation Proccesses*. Chichester: Wiley.

Hacker, S. D., and S. D. Gaines. 1997. "Some Implications of Direct Positive Interactions for Community Species Diversity." *Ecology* 78(7): 1990–2003. https://doi.org/10.1890/0012-9658(1997)078[1990:SIODPI]2.0.CO;2.

Hess, M. C. M. M., E. Buisson, R. Jaunatre, and F. Mesléard. 2020. "Using Limiting Similarity to Enhance Invasion Resistance: Theoretical and Practical Concerns." *Journal of Applied Ecology* 57(3): 559–65. https://doi.org/10.1111/1365-2664.13552.

Jaeger, B. 2017. "R2glmm: Computes R Squared for Mixed (Multilevel) Models." https://CRAN.R-project.org/package=r2glmm.

Johnson, C. G., and D. K. Swanson. 2005. "Bunchgrass Plant Communities of the Blue and Ochoco Mountains: A Guide for Managers." General Technical Report: PNW-GTR-641. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Kerns, B. K., C. Tortorelli, M. A. Day, T. Nietupski, A. M. G. G. Barros, J. B. Kim, and M. A. Krawchuk. 2020. "Invasive Grasses: A New Perfect Storm for Forested Ecosystems?" *Forest Ecology and Management* 463: 117985. https://doi.org/10.1016/j.foreco.2020.117985.

Kunstler, G., S. Lavergne, B. Courbaud, W. Thuiller, G. Vieilledent, N. E. Zimmermann, J. Kattge, and D. A. Coomes. 2012. "Competitive Interactions between Forest Trees Are Driven by Species' Trait Hierarchy, Not Phylogenetic or Functional Similarity: Implications for Forest Community Assembly." *Ecology Letters* 15(8): 831–40. https://doi.org/10.1111/j.1461-0248.2012.01803.x.

Lai, H. R., M. M. Mayfield, J. M. Gay-des-combes, T. Spiegelberger, and J. M. Dwyer. 2015. "Distinct Invasion Strategies Operating within a Natural Annual Plant System." *Ecology Letters* 18(4): 336–46. https://doi.org/10.1111/ele.12414.

Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. "A Meta-Analysis of Biotic Resistance to Exotic Plant Invasions." *Ecology Letters* 7(10): 975–89. https://doi.org/10.1111/j.1461-0248.2004.00657.x.

Lucero, J. E., T. Noble, S. Haas, H. Michael Westphal, S. Butterfield, and C. J. Lortie. 2019. "The Dark Side of Facilitation: Native Shrubs Facilitate Exotic Annuals more Strongly than Native Annuals." *NeoBiota* 44: 75–93. https://doi.org/10.3897/neobiota.44.33771.

Lüdecke, D., D. Makowski, P. Waggoner, I. Patil, and M. S. Ben-Shachar. 2021. "Package 'Performance'." https://cran.r-project.org/web/packages/performance/citation.html.

Lulow, M. E. 2006. "Invasion by Non-Native Annual Grasses: The Importance of Species Biomass, Composition, and Time among California Native Grasses of the Central Valley." *Restoration Ecology* 14(4): 616–26. https://doi.org/10.1111/j.1526-100X.2006.00173.x.

MacArthur, R., and R. Levins. 1967. "The Limiting Similarity, Convergence, and Divergence of Coexisting Species." *The American Naturalist* 101(921): 377–85.

Mokany, K., R. Johnson Raison, A. S. Prokushkin, F. Products, and S. Branch. 2006. "Critical Analysis of Root: Shoot Ratios in Terrestrial Biomes." *Global Change Biology* 12(1): 84–96. https://doi.org/10.1111/j.1365-2486.2005.001043.x.

Nakagawa, S., and H. Schielzeth. 2013. "A General and Simple Method for Obtaining R^2 from Generalized Linear Mixed-Effects Models." *Methods in Ecology and Evolution* 4(2): 133–42. https://doi.org/10.1111/j.2041-210x.2012.00261.x.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchlin, et al. 2019. "R Package: Vegan." https://CRAN.R-project.org/package=vegan.

Paulson, D. J. 1977. *Soil Resource Inventory: Ochoco National Forest*. Prineville, OR: USDA National Forest, Pacific Northwest Region.

Price, J. N., and M. Pärtel. 2013. "Can Limiting Similarity Increase Invasion Resistance? A Meta-Analysis of Experimental Studies." *Oikos* 122(5): 649–56. https://doi.org/10.1111/j.1600-0706.2012.00121.x.

Roumet, C., C. Urcelay, S. Díaz, and C. Roumet. 2006. "Suites of Root Traits Differ between Annual and Perennial Species Growing in the Field." *New Phytologist* 170(2): 357–68. https://doi.org/10.1111/j.1469-8137.2006.01667.x.

Russell, L. V. 2021. "Emmeans: Estimated Marginal Means, Aka Least-Squares Means." https://cran.r-project.org/package=emmeans.

Sheppard, C. S. 2019. "Relative Performance of co-Occurring Alien Plant Invaders Depends on Traits Related to Competitive Ability More than Niche Differences." *Biological Invasions* 21(4): 1101–14. https://doi.org/10.1007/s10530-018-1884-z.

Thuiller, W., L. Gallien, I. Boulangeat, F. de Bello, T. Münkemüller, C. Roquet, and S. Lavergne. 2010. "Resolving Darwin's Naturalization Conundrum: A Quest for Evidence." *Diversity and Distributions* 16(3): 461–75. https://doi.org/10.1111/j.1472-4642.2010.00645.x.

Tortorelli, C. 2022. "cmtortorelli/Invasion-Response-to-Community-Traits-and-Environment: Data and Code to Support the Manuscript "Community Invasion Resistance Is Influenced by Interactions between Plant Traits and Site Productivity" (v1.0.0)." Zenodo. https://doi.org/10.5281/zenodo.5914948.

Tortorelli, C. M., M. A. Krawchuk, and B. K. Kerns. 2020. "Expanding the Invasion Footprint: *Ventenata dubia* and Relationships to Wildfire, Environment, and Plant Communities in the Blue Mountains of the Inland Northwest, USA." *Applied Vegetation Science* 23: 1–13. https://doi.org/10.1111/avsc.12511.

Von Holle, B. 2013. "Environmental Stress Alters Native-Nonnative Relationships at the Community Scale." *Biological Invasions* 15(2): 417–27. https://doi.org/10.1007/s10530-012-0297-7.

Von Holle, B., and D. Simberloff. 2005. "Ecological Resistance to Biological Invasion Overwhelmed by Propagule Pressure." *Ecology* 86(12): 3212–8. https://doi.org/10.1890/05-0427.

Wallace, J. M., P. L. S. Pavek, and T. S. Prather. 2015. "Ecological Characteristics of *Ventenata dubia* in the Intermountain Pacific Northwest." *Invasive Plant Science and Management* 8: 57–71. https://doi.org/10.1614/IPSM-D-14-00034.1.

Western Regional Climate Center. 2021. "Brer Rabbit Oregon RAWS." https://raws.dri.edu/cgi-bin/rawMAIN.pl?orOBRI.

Zarnetske, P. L., T. C. Gouhier, S. D. Hacker, E. W. Seabloom, and V. A. Bokil. 2013. "Indirect Effects and Facilitation among Native and Non-Native Species Promote Invasion Success along an Environmental Stress Gradient." *Journal of Ecology* 101(4): 905–15. https://doi.org/10.1111/1365-2745.12093.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Tortorelli, Claire M., Becky K. Kerns, and Meg A. Krawchuk. 2022. "Community Invasion Resistance is Influenced by Interactions between Plant Traits and Site Productivity." *Ecology* e3697. https://doi.org/10.1002/ecy.3697