LETTER

Local-scale biotic interactions embedded in macroscale climate drivers suggest Eltonian noise hypothesis distribution patterns for an invasive grass

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Abstract

A hierarchical view of niche relations reconciles the scale-dependent effects of abiotic and biotic processes on species distribution patterns and underlies most current approaches to distribution modeling. A key prediction of this framework is that the effects of biotic interactions will be averaged out at macroscales – an idea termed the Eltonian noise hypothesis (ENH). We test this prediction by quantifying regional variation in local abiotic and biotic niche relations and assess the role of macroclimate in structuring biotic interactions, using a non-native invasive grass, *Microstegium vimineum*, in its introduced range. Consistent with hierarchical niche relations and the ENH, macroclimate structures local biotic interactions, while local abiotic relations are regionally conserved. Biotic interactions suppress *M. vimineum* in drier climates but have little effect in wetter climates. A similar approach could be used to identify the macroclimatic conditions under which biotic interactions affect the accuracy of local predictions of species distributions.

Keywords

Biotic effects, competition, facilitation, hierarchical Bayesian models, macroclimate, niche theory, spatial scale, species distribution modeling.

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INTRODUCTION

Understanding what determines species distributions has long been the focus of ecological study, but the topic is attracting renewed interest because of its relevance for predicting the geographies of species invasions and range shifts in response to rapid environmental change (Peterson *et al.* 2011). A persistent problem is explaining how abiotic and biotic factors affect the distributions of species across spatial scales.

Contemporary niche theory (Hutchinson 1957; Bruno *et al.* 2003) suggests that Eltonian niches (Elton 1927), which are based on spatially fine-grained variables related to biotic interactions and resource-consumer dynamics, are important for structuring species distributions at broad scales. However, species distributions often are predicted exclusively from Grinellian niches (Grinnell 1917), which are based on largely coarse-scaled, non-interacting abiotic variables. Soberon (2007) proposed that niche relations are hierarchical in nature, such that macroscale environmental conditions determine all possible suitable areas that meet the physiological requirements of a species (i.e., the Grinnellian niche), whereas biotic interactions determine the subset of these areas that remain suitable after accounting for species interactions and impacts of species on limiting resources (i.e., the Eltonian niche). That is, species interact at fine scales but habitat heterogeneity within a landscape moderates the broad-scale consistency of such interactions, producing variation in biotic effects at intermediate scales (Lawton 1999). Consequently, the effects of biotic interactions are expected to be averaged out at broader scales – an idea termed the Eltonian noise hypothesis (ENH; Soberón & Nakamura 2009). Although a hierarchical niche

relations framework greatly enhances understanding of niche relations across spatial scales, empirical examples of hierarchical niche relations remain few, and examples exist where biotic interactions appear to limit species' distributions as much or more than macroscale environmental conditions (Bullock *et al.* 2000; Leathwick & Austin 2001; Araújo & Luoto 2007; Gotelli *et al.* 2010; de Araújo *et al.* 2013).

Vegetation theory posits (Tilman 1982; Austin 1990) and field studies corroborate (Bullock *et al.* 2000; Leathwick & Austin 2001) that biotic interactions vary along environmental gradients. The resource theory of competition (Tilman 1982), for example, suggests that the availability of a limiting resource can influence competitive outcomes. Environmental filtering can also alter the role of local biotic processes in determining community interactions. Under strong environmental filtering, deterministic processes, including biotic interactions, strongly affect community patterns, whereas they are much less important under weak environmental filtering (Chase 2007). Likewise, the stress-gradient hypothesis (SGH; Bertness & Callaway 1994) proposes that the level of environmental stress determines whether neighbouring species will compete against or facilitate each other (Callaway & Walker 1997). Unlike resource competition theory, SGH predicts that facilitation will prevail in stressful environments. However, when a limited resource is the fundamental stress factor, facilitation will only occur if neighbours increase the availability of this resource; otherwise, competitive interactions will dominate (Maestre *et al.* 2009). Hence, along a climatic gradient, competition is expected to dominate species interactions where moisture is low because the water consumption of neighbouring species exacerbates water-related stress, whereas

facilitation is expected to dominate where there is more moisture and the availability of another limiting resource is increased by the presence of neighbouring species (Maestre & Cortina 2004).

If macroscale environmental variables such as climate modulate local niche processes, then relationships between species fitness and spatially fine-grained niche variables may differ across space. Indeed, it is a common finding that local niche relations vary across geographic space (Broennimann et al. 2007; Murphy & Lovett-Doust 2007), yet few studies have explicitly investigated relationships between macroscale environmental variables, local niche processes, and species fitness. Consequently, it is generally unknown whether local niche relations vary at regional scales and what, if anything, structures these relations. Understanding the potential hierarchy of controls on species niches is critically important for species distribution modelling and may help to resolve contradicting evidence for the Eltonian noise hypothesis (Araújo & Luoto 2007).

In this study, we use hierarchical generalised linear models implemented within a Bayesian framework and empirical estimates of plant performance to examine regional variation in local niche relations and test the hypothesis that macroclimate structures local niche relations for a non-native invasive grass, M. vimineum, in its introduced range. We address two specific questions: (1) is there regional variation in the relationships between the performance of M. vimineum and local abiotic and biotic covariates and (2) does macroclimate explain regional variation in these relationships? A Bayesian approach to inference allowed direct estimation of parameter uncertainty and thereby enabled us to quantify regional variation in niche relations. Hierarchical linear models enabled us to explicitly investigate regional shifts in niche processes and hierarchically structured relationships between macroclimate and potential niche relations at the local scale.

The decision to use M. vimineum as a model organism for this study was motivated by several factors. First, niche variation has previously been documented for non-native species in their introduced range (Broennimann et al. 2007). Several processes, including release from abiotic or biotic constraints (Mitchell et al. 2006), the availability of empty niches (Hierro et al. 2005), and their ability to evolve rapidly in their introduced range (Buswell et al. 2011), can promote niche shifts by non-native invaders. Second, M. vimineum is widespread, having invaded forests in 25 states in the USA. This invasion scale allowed us to investigate potential differences in local population processes across a broad gradient of macroclimatic conditions. Third, local niche relations have been quantified for M. vimineum throughout its native and introduced ranges, providing an excellent basis for comparison with our results. Finally, a common garden experiment conducted in a single location in the introduced range of M. vimineum indicated that the provenance of North American populations of M. vimineum had no effect on their relationship with abiotic and biotic variables (Flory et al. 2011). This finding suggests that local niche relations may be similar when broad-scale environmental conditions are held constant, but leaves open the question of whether regional niche variation exists and is structured by broad-scale environmental conditions.

METHODS

Study design and data collection

This study took place across four eastern deciduous forest sites where M. vimineum has invaded (see Appendix S1 for details about the study species). Plots were established at Whitehall Experimental Forest (Athens-Clarke County, GA, USA), Chattahoochee National Forest (Habersham County, GA, USA) and Coweeta Hydrologic Laboratory (Macon County, NC, USA) in 2009 (n = 12 plots at each site) and at Shawnee National Forest (Pope and Saline Counties, IL, USA) in 2011 (n = 10 plots). These sites, which are broadly representative of the variation in the invaded range of the plant, span three ecoregions and vary in climate and elevation (Table S1).

Within each site, plots were established at discrete invasion boundaries to collect information on M. vimineum growth and local abiotic and biotic variables. Each plot contained three 25 × 25 cm subplots spaced along a three meter transect. From June to August, M. vimineum above-ground biomass was collected from each subplot. Biomass was dried at 65 °C and weighed in the lab. Using identical methods, we also collected the above-ground biomass of all other herbaceous species in each subplot as a proxy for interspecific interactions. Despite being an indirect measure, biomass production by neighbouring individuals is widely used to reveal the outcome of interspecific interactions (Tilman & Wedin 1991; Campbell & Grime 1992), and has previously been shown to correlate with invader effects on native plant communities. For example, between 2009 and 2011, M. vimineum coverage of previously uninvaded plots (adjacent to invaded plots) increased from 0 to 16% and the patch boundaries expanded on average by almost 3 m. Concurrently, native herbaceous coverage dropped by 34% (Warren et al. 2013). Biomass data were pooled across subplots. Four local abiotic covariates were measured before biomass was harvested and averaged across the three subplots. Although all the abiotic variables have a fine-grained spatial structure, light and soil texture represent static environmental conditions, whereas soil moisture and pH interact with vegetation and are dynamic. Soil moisture was measured as volumetric water content, using a Hydrosense Soil Moisture System (Campbell Scientific Inc., Logan, UT, USA) or a Decagon 5TM Soil Moisture Sensor (Decagon Devices Inc., Pullman, WA, USA). Percent photosynthetically active radiation reaching a plot was calculated by measuring light in the plot and in a nearby reference site with an open canopy. One 10-cm deep soil core was collected from each subplot for pH and texture analysis. We measured pH using a benchtop pH meter (1 : 1, soil : H_2O by volume). Soil texture was analysed using a standardised hydrometer method. Given that soil texture values varied collinearly across the gradient (data not shown), we only used percent clay content in our analysis.

Macroclimate covariates were obtained from the National Oceanic and Atmospheric Administration's National Climatic Data Center and based on measurements collected at the weather stations nearest to our plots. Due to the unavailability of temperature and precipitation data from one station, both the Suches, GA and Camp Merrill, GA stations were

used to get regional data for Chattahoochee. The stations at Athens-Ben Epps Airport, Coweeta Experimental Station, and Dixon Springs Agricultural Center were used for climate data at Whitehall, Coweeta, and Shawnee (respectively). We used data from May to August of the year the biomass was harvested to reflect the growing season conditions at each site. Climate variables were chosen *a priori* and consisted of the following: number of days with maximum temperatures over 32.2 °C (DT90), number of days with equal to or > 2.54 cm of precipitation (DP01), and mean temperature (MNTM).

Statistical models

In order to quantify regional variation in the local niche relations of *M. vimineum* and examine the role of macroclimate for structuring this variation, hierarchical generalised linear models were implemented within a Bayesian framework. Our basic approach to fitting models to evaluate the evidence for regional variation in local niche relations was as follows. For each abiotic and biotic covariate, we initially constructed two hierarchical linear models, in each case using *M. vimineum* biomass as the response variable. In one model, we specified a single, regional slope parameter for the covariate being considered to represent the hypothesis of no variation in the regional biomass–covariate relationship across study sites. In the other model, we specified site-specific slope parameters for the covariate being considered to represent the hypothesis that local niche relations vary by site. Spatial structure in the data and unmeasured site effects were implicitly accounted for by including a random site effect.

In all models, *M. vimineum* biomass (y_{ij}) is represented with a log-normal distribution because it is bound by zero with a fat tail:

$$y_{ij} \sim \text{lognorm}(\mu_{ij}, \sigma^2),$$

where σ^2 is the residual error and μ_{ij} is the location parameter for the i-th plot at the j-th site. Because we are using a log-normal distribution for the data, the expected value for y_{ij} is expressed as $e^{\mu + (\sigma^2)/2}$ and incorporates both the location and scale parameter.

We formulated the two models by using a different equation for the location parameter (μ_{ij}). The regional-slope model fits one slope for all of the sites and adds a single random site effect (α_j):

$$\mu_{ij} = \beta_0 + \beta_1(x_{ij} + \alpha_j),$$

where x_{ij} is a local environmental variable. The site-specific slope model fits site-specific slopes and defines these slopes with a constant (λ) and random site effect (α_j):

$$\mu_{ij} = \beta_0 + \beta_{1j}(x_{ij})$$

$$\beta_{1j} = \lambda + \alpha_j$$

The random site effects are modelled as normal with a mean of zero and variance [$\alpha_j \sim \text{norm}(0, \tau^2)$]. Because the sample size at the site level is small ($n_{site} = 4$), the prior on τ^2 was defined as $\tau \sim \text{uniform}(0, 10)$ to minimise the influence

of the prior on the posterior distribution as described by Gelman (2006).

The regional and site-specific slope models were compared using the Deviance Information Criterion (DIC), which is calculated using model deviance plus penalties for extra parameters (Spiegelhalter *et al.* 2002). Model comparison based on DIC is analogous to that based on Akaike's Information Criterion from classical statistics, in that models that differ in their DIC values by < 5 are considered equally supported by the data (Spiegelhalter *et al.* 2002). This approach enabled us to determine whether the *M. vimineum* performance data were better fit with models that had one parameter representing a uniform relationship with the covariate across sites, or site-specific parameters representing locally varying relationships.

After identifying the best model representing each individual biomass–covariate relationship, we constructed multivariate models that included the significant predictors and the appropriate interaction terms to better describe the performance of *M. vimineum*. We compared model DIC scores to determine which models explained the most variance without being over fit. For relationships that varied regionally (i.e., those better fit with a site-specific slope model), we determined if macroclimate variables could explain the variation in our site-specific slopes. To assess this, we incorporated the macroclimate variables (C_j) in our site-specific slope model by expanding our definition of β_{1j} to include a linear relationship to climate:

$$\beta_{1j} = \lambda_0 + \lambda_1(C_j + \alpha_j)$$

To ensure that the models were not over fit, we compared the DIC scores of the models that incorporated macroclimate with those that did not. We also checked for significant relationships between β_{1j} and the macroclimate variables by looking at the credible intervals around λ_1; that is, the interval over which 95% of the density of a posterior probability distribution falls. All models were fit using R software (R Development Core Team 2014) and OpenBUGS (Spiegelhalter *et al.* 2007), which uses Markov Chain Monte Carlo (MCMC) sampling methods to characterise the posterior distributions of the model parameters. At each iteration of the MCMC, parameter estimates are used to predict species response (i.e., *M. vimineum* biomass), such that predictions are conditional on the observed responses and estimated parameters. Inclusion of this step allows propagation of uncertainty associated with all parameters to influence prediction.

RESULTS

Local relations between *M. vininuem* performance and abiotic covariates were similar across the region. For light and percent clay, the two non-interactive abiotic variables, differences in the regional and site-specific slope model DIC scores are < 1, which suggests that both types of models are equally supported by the data (Table S2). In the regional model, the response of *M. vimineum* to light is positive (Fig. 1a; mean $\beta_{1,Regional} = 0.027$; > 95% confidence in positive relationship). Site-specific slope estimates for light relations suggest a positive response of *M. vinenium* to light at Chattahoochee and Coweeta (mean $\beta_{1,Chattahoochee} = 0.030$, mean β_1,

Coweeta = 0.041; > 99% confidence in positive relationship) and a non-significant, positive trend at the other sites (Fig 1a). For percent clay, the regional relationship between *M. vimineum* biomass and percent clay is negative (Fig 1b; mean $\beta_{1,Regional}$ = −0.049; > 95% confidence in negative relationship). Site-specific slope estimates show a negative response of *M. vimineum* at Shawnee and Whitehall (mean $\beta_{1,Whitehall}$ = −0.061, mean $\beta_{1,Shawnee}$ = −0.063; > 99% confidence in negative relationship) and a non-significant, negative trend at Chattahoochee and Coweeta (Fig 1b). There is no relationship between *M. vimineum* performance and the two interactive abiotic variables, pH (Fig. 1c) and soil moisture (Fig. 1d).

In contrast, there is strong evidence for regional variation in the local relations of *M. vimineum* performance and the measured biotic covariate. The DIC of the site-specific slope model relating *M. vimimeum* biomass to the biomass of other

herbaceous species was smaller compared to the DIC of the regional model (difference in DIC = 6.2), suggesting that this relationship varies by site (Table S2). Moreover, site-specific slope estimates varied in magnitude and sign (Fig. 1e). At Shawnee and Whitehall, the two sites that are farthest apart, the slope for the relationship between *M. vimineum* biomass and the biomass of other herbaceous plants is negative (mean $\beta_{1,Shawnee}$ = −0.092 and mean $\beta_{1,Whitehall}$ = −0.11; 90% confidence in negative relationship at Shawnee and > 95% confidence in negative relationship at Whitehall) (Fig. 2). The slope for the relationship at Coweeta, however, is positive (mean slope = 0.015; > 95% confidence in positive relationship), and, at Chattahoochee, there is no relationship between the biomass of *M. vimineum* and other herbaceous species (Fig. 2).

Comparing the fit of all possible multivariate models that include the three covariates with significant relationships to
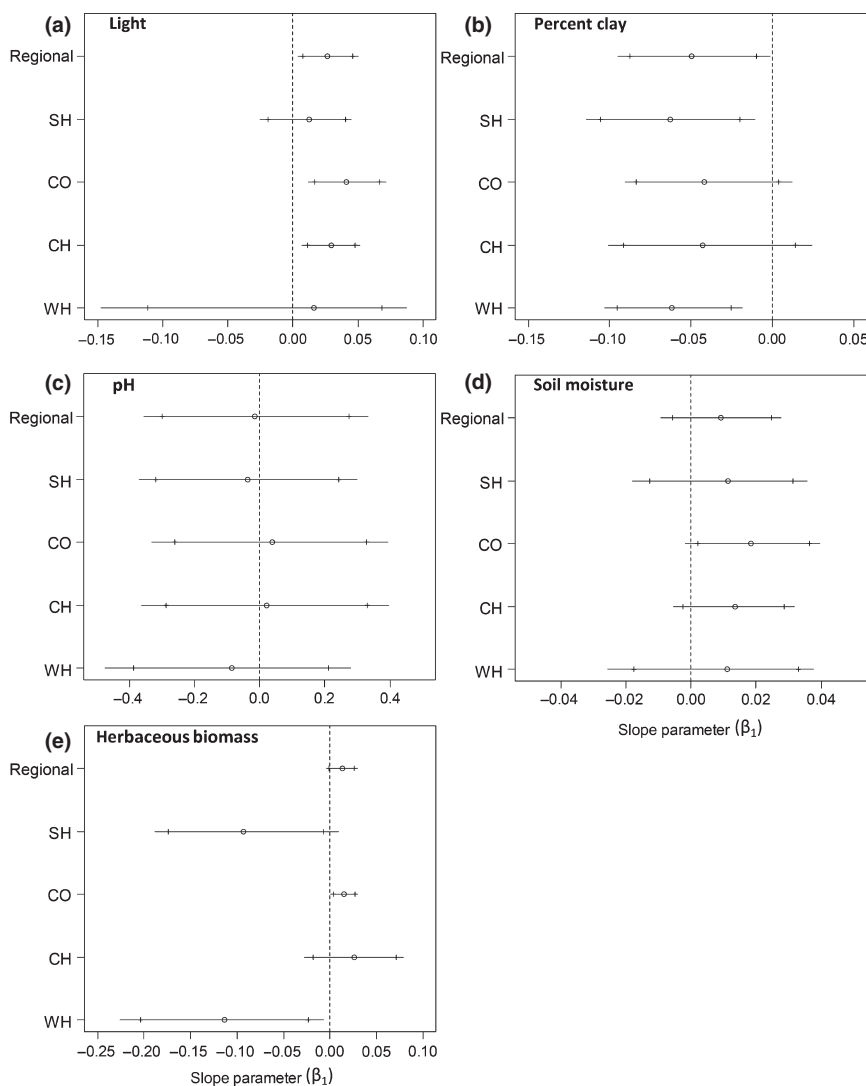

Figure 1 Slope estimates for the regional and site-specific slope models relating *M. vimineum* biomass with (a) light, (b) percent clay, (c) pH, (d) soil moisture and (e) herbaceous biomass. The open circles represent the means and the horizontal lines are the 95% credible interval with hashes at the 90% credible interval. 'Regional' refers to the slope estimate for the regional model. Refer to Table S1 for site names.
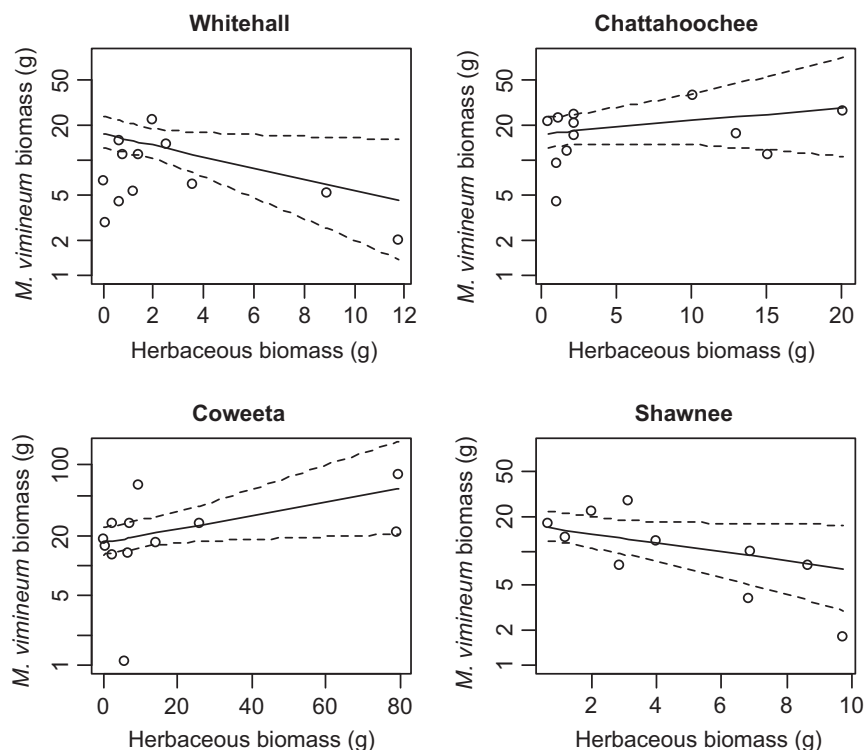
Figure 2 The relationship between *M. vimineum* and other herbaceous biomass for each site. The solid line is the expected relationship predicted by the model and the dashed lines are the 95% credible interval around this estimate.

M. vimineum biomass (light, percent clay, and herbaceous biomass) and their interactions, we find that the five best supported models include herbaceous biomass modelled by site (Table S3). All six supported models include a weak negative interaction between herbaceous biomass and light, suggesting that biotic interactions become more negative as light increases (Table S4). In two of these models, the interaction varies by site, and is more negative by an order of magnitude at the drier sites (Whitehall and Shawnee).

We used the best performing and most parsimonious one-level multivariate model (i.e., the first and third models listed in Table S3) to explore the role of macroclimate in structuring local biotic effects. In both cases, the two-level model that included the number of days with precipitation ≥ 2.54 (DP01) performed better than the one-level model. The model with mean growing season temperature (MNTM) was also competitive (Table S5). The models indicate that there is a significant positive relationship between β_{1j} (i.e., site-specific slope estimates relating *M. vimineum* and herbaceous biomass) and growing season precipitation (Fig. 3a; Table S6), and a significant negative relationship between β_{1j} and a growing season mean temperature (Fig. 3b; Table S6). The effect of local light availability on *M. vimineum* biomass is relatively constant at the regional scale (Table S6).

DISCUSSION

The ENH (Soberón & Nakamura 2009) posits that ecological interactions and species effects on resources determine distri-

butions at fine spatial scales, whereas coarse-scaled abiotic factors (e.g., precipitation and temperature) determine distributions at broader scales – where the effects of species interactions are lost as statistical noise (but see Araújo & Luoto 2007). We quantified regional variation in the local niche relations of a non-native invasive plant, and we found substantial variation in the magnitude and sign of the plant's local biotic interactions at the regional scale, and much less variation in its local response to non-interactive abiotic variables at the regional scale. Hence, our results support the ENH, in that *M. vimineum*'s abiotic niche requirements appear conserved at the regional scale, while its local biotic interactions vary greatly at this scale.

Our results indicate that *M. vimineum*'s response to biotic effects shifted across the macroclimatic gradient. At the warmest and driest sites (Shawnee and Whitehall), a negative relationship between *M. vimineum* and herbaceous biomass suggests heightened interspecific competition, consistent with Flory & Clay's (2010) findings that *M. vimineum* had more pronounced negative effects on tree seedlings after drought years via a considerable biomass increase. In contrast, we found a positive relationship between herbaceous and *M. vimineum* biomass at the coolest and wettest sites (Coweeta and Chattahoochee). It is well documented that *M. vimineum* increases soil nitrogen (N) availability by stimulating microbial activity (Ehrenfeld *et al.* 2001; Fraterrigo *et al.* 2011), and evidence suggests that other plants can benefit from this increased N availability (Fraterrigo *et al.* 2011). However, moisture strongly regulates this effect, which may explain why *M. vimineum* facilitated the growth of neighbour-
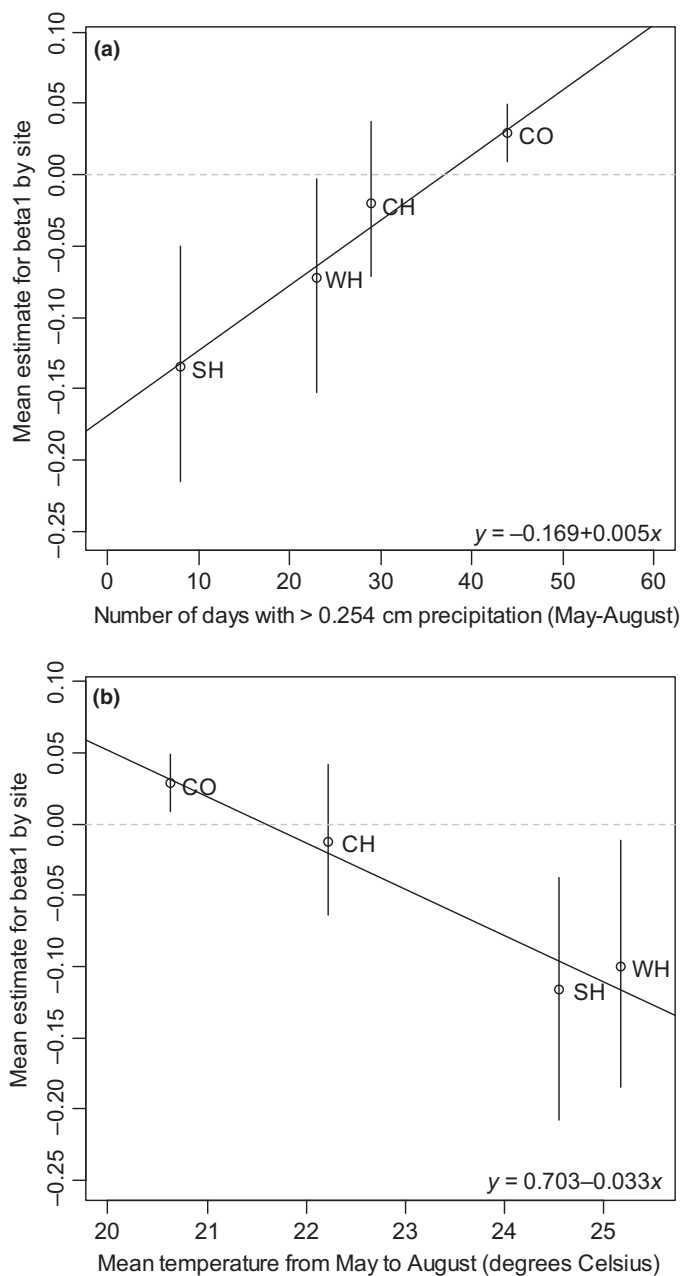
Figure 3 The relationship between β_{1j} (i.e., the estimated slopes for site-specific relationships between *M. vimineum* and herbaceous biomass) and macroclimate variables: (a) number of growing season days with precipitation ≥ 2.54 cm and (b) mean growing season temperature.

ing herbaceous species where moisture was high but suppressed growth where moisture was low. Additionally, *M. vimineum* can initially shade out residents species, suggesting a strong role for light availability in mediating biotic interactions.

Supporting this idea, at the local scale, biotic interactions exhibited the opposite pattern along light gradients, such that the negative relationship between *M. vimineum* and herbaceous biomass intensified with increasing light, though the negative relationship was stronger in the drier sites (Table S4). *Microstegium vimineum* has unique photosyn-

thetic capacities (Horton & Neufeld 1998), relative to forest herbs, which confer heightened fitness in shady habitats (Brewer 2011). Our findings suggest that this competitive advantage depends on moisture conditions, however, which are primarily determined by macroclimate and much less by local-scale differences in soil moisture (Fig. 1, Table S6). According to SGH, contingency in plant–plant interactions often follows environmental gradients in a manner that positive interactions dominate in stressful abiotic conditions and negative interactions dominate in benign or favourable conditions (Bertness & Callaway 1994), but depending on the system, the species and the approach, such patterning can be reversed (see Brooker *et al.* 2008; Maestre *et al.* 2009).

More generally, our results suggest the need to carefully distinguish between interactive and non-interactive abiotic variables (Soberon 2007). The local response of *M. vimineum* to non-interactive abiotic variables was consistent at the regional scale, whereas interactive abiotic variables did not predict performance. Hutchinson referred to non-interactive, non-consumable environmental variables as scenopoetic (Hutchinson 1978), and others have advocated for using this terminology when operationalising niche definitions (Soberón & Nakamura 2009).

Whereas biotic effects were locally contingent, biotic response to climate was predictable at the regional scale. The most parsimonious explanation for this pattern is that biotic interactions vary in strength with landscape heterogeneity (Thompson 2005). The small effect sizes associated with biotic interactions (Table S4) suggest that these interactions create noise within the milieu of macroscale distributions, but do not necessarily limit those distributions at broad scales (Soberón & Nakamura 2009; Peterson *et al.* 2011). Instead, macroclimate appears to impose the most control on species distributions (Sexton *et al.* 2009), a dynamic well-recognised by biogeographers but not so much by ecologists (Wiens 2011). As such, species niche relations appear much conserved at broad scales so that they demonstrate consistent climatic requirements across large, heterogeneous areas (Lawton 1999; Soberón & Nakamura 2009; Wiens 2011).

Invasive species, including *M. vimineum* (Novy *et al.* 2013), can evolve rapidly and exhibit high phenotypic plasticity in novel habitat (Buswell *et al.* 2011; Davidson *et al.* 2011), so that we might expect high variance in *M. vimineum* macroclimate responses at our scale of measurement. However, rapid evolution and plasticity in invasive plants generally do not prompt shifts in abiotic requirements to the degree they do in biotic interactions, such as rapid shifts from herbivore defense to greater biomass and seed production. Moreover, if we consider invasive species an accidental test of ecological theory (Sax *et al.* 2005), invasive species generally exhibit abiotic/biotic niche patterns consistent with the Eltonian noise hypothesis. At local scales, invasive species can extirpate native species, but extinction due to invasive species is less common at the macroscale level (Powell *et al.* 2013). We find consistent patterns with *M. vimineum* as biotic interactions appear noisy and contingent at local scales, but climate responses are highly conserved at the macroscale.

Certainly, biotic interactions also influence species distributions at the macroscale level (for review, see Wisz *et al.* 2013), but the core question for assessing and predicting species distributions is whether biotic influences override abiotic signals at macroscales. If biotic interactions vary systematically with broad-scale drivers as observed for *M. vimineum*, then they remain embedded in macroscale environmental signals and may be influential for only a subset of environmental conditions, where biotic and abiotic effects diverge, such as at range edges. Otherwise, biotic interactions may be accounted for implicitly in species distribution models via their relationship with broad-scale drivers. The ENH does not undermine the importance of biotic interactions, just delineates their scale of detectable influence, though it cannot distinguish between a lack of macroscale influence or a climate-embedded macroscale influence.

Much focus on the influence of climate vs. biotic interactions at macroscale centers on competitive interactions, such that species may be constrained at broad scales by better or dominant competitors (Gotelli *et al.* 2010; le Roux *et al.* 2012; Pellissier *et al.* 2013). However, such constraints are often consistent with broad-scale climate patterns. Although including biotic interactions may improve species distribution predictions (Araújo & Luoto 2007; Meier *et al.* 2010; le Roux *et al.* 2012), it is possible that biotic factors better reflect multiple on-the-ground climate conditions than one or two coarse-scale climate parameters. Ultimately, it may be more useful to consider biotic interactions a stress or resource similar to abiotic predictors (Jones *et al.* 2012; Warren *et al.* 2014).

Microstegium vimineum is still infilling its invaded range (Warren *et al.* 2013), so the complete picture of its biotic interactions and range limitations are yet to be seen; moreover, we use a coarse evaluation of biotic interactions that may not capture the full strength of positive vs. negative interactions. Still, insights can be drawn from coarse-scale patterns in species assemblies (Diamond 1975), and our results suggest that the invasive grass *M. vimineum* exhibits its strongest biotic niche relations (in impacting and/or being impacted by other herbaceous species) at local scales, whereas macroclimate controls its biotic niche relations at regional scales. As a result, we can expect reasonable success in macroscale prediction of this species' range shifts with climate and invasion in novel habitats, yet scaling down to local dynamics might be troublesome at best, impossible at worst.

AUTHORSHIP

JMF designed the study, SW and RJW collected data, SW analysed data, and all the authors wrote the manuscript.

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