12-2017

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Funding information
Wyoming NASA Space Grant Consortium; M.J. Murdock Charitable Trust, Grant/Award Number: 2015205; National Science Foundation, Grant/Award Number: #0841298 and #1202800

Co-ordinating Editor: Miquel De Cáceres

Abstract

Aims: Species distributions are hypothesized to be underlain by a complex association of processes that span multiple spatial scales including biotic interactions, dispersal limitation, fine-scale resource gradients and climate. Species disequilibrium with climate may reflect the effects of non-climatic processes on species distributions, yet distribution models have rarely directly considered non-climatic processes. Here, we use a Joint Species Distribution Model (JSDM) to investigate the influence of non-climatic factors on species co-occurrence patterns and to directly quantify the relative influences of climate and alternative processes that may generate correlated responses in species distributions, such as species interactions, on tree co-occurrence patterns.

Location: US Rocky Mountains.

Methods: We apply a Bayesian JSDM to simultaneously model the co-occurrence patterns of ten dominant tree species across the Rocky Mountains, and evaluate climatic and residual correlations from the fitted model to determine the relative contribution of each component to observed co-occurrence patterns. We also evaluate predictions generated from the fitted model relative to a single-species modelling approach.

Results: For most species, correlation due to climate covariates exceeded residual correlation, indicating an overriding influence of broad-scale climate on co-occurrence patterns. Accounting for covariance among species did not significantly improve predictions relative to a single-species approach, providing limited evidence for a strong independent influence of species interactions on distribution patterns.

Conclusions: Overall, our findings indicate that climate is an important driver of regional biodiversity patterns and that interactions between dominant tree species contribute little to explain species co-occurrence patterns among Rocky Mountain trees.

KEYWORDS

Bayesian modelling, biotic interactions, joint species distribution model, SDM, species distribution, species sorting

1 | INTRODUCTION

While much research effort has recently been focused on resolving the drivers of species distribution patterns, considerable uncertainties remain for many species and systems. Species distributions are underlain by a complex association of local and regional processes including biotic interactions, dispersal limitation and variation in population dynamics driven by responses to fine-scale resource availability, topography, disturbance and broad-scale climate (Cazelles, Mouquet, Mouillot, & Gravel, 2015; Morueta-Holme et al., 2016; Serra-Diaz et al., 2015). These processes may generate species diversity patterns that vary across a wide range of environmental and ecological gradients spanning multiple spatial scales, complicating efforts to disentangle the relative influences of underlying processes (Normand, Zimmermann, Schurr, & Lischke, 2014; Schurr et al., 2012).

Climate has traditionally been understood to be the dominant factor shaping species distributions (Woodward, 1987), as it correlates particularly well with species occurrence patterns observed at a comparable spatial resolution (Boucher-Lalonde, Morin, & Currie, 2012; Morin, Augspurger, & Chuine, 2007). Yet, widespread observations of species occurring in disequilibrium with climate have generated increased interest in the role of alternative processes in shaping species distributions (Araújo, Pearson, & Rahbek, 2005; Blois et al., 2014). Species interactions have perhaps received the most attention in this regard, and have been the focus of significant research interest as a potentially overlooked driver of species distribution patterns and climate disequilibrium (e.g. Araújo & Luoto, 2007; Araújo & Rozenfeld, 2014; Blois et al., 2014; Cazelles et al., 2015; Godsoe & Harmon, 2012; Kissling et al., 2012). Yet, significant uncertainty remains regarding the ability of species interactions, which typically operate at fine spatial resolutions, to exert independent effects on species distributions, which are typically evaluated over coarse spatial resolutions (~1 km^2) and long temporal scales (e.g. correlated with 30-yr climate normal; Pearson & Dawson, 2003; Soberón & Nakamura, 2009). Empirical investigations have thus far found limited evidence for a widespread effect of species interactions on distributions, and have generally demonstrated that interactions are most likely to affect abundance patterns at local spatial scales without scaling up to affect occurrence patterns observed at coarser spatial resolutions (Boulangeat, Gravel, & Thuiller, 2012; Morueta-Holme et al., 2016; Rouget et al., 2001). However, other studies have demonstrated small improvements in species distribution models (SDMs) by incorporating potentially interacting species as model covariates (Araújo & Luoto, 2007; Meier et al., 2010). Inference from studies employing the SDM approach is limited, as unidirectional relationships between pairs of interacting species may reflect a suite of underlying correlated processes, such as missing environmental covariates to which the predictor species responds (Clark, Gelfand, Woodall, & Zhu, 2014; Guisan & Thuiller, 2005; Kissling et al., 2012; Morueta-Holme et al., 2016; Wisz et al., 2013). These issues complicate valid inference and preclude general conclusions regarding the relative influences of species interactions and climate on species distributions, and extend to inference regarding the influence of other community-level processes.

The effects of non-climatic processes may be better evaluated and identified by analysing species co-occurrence patterns rather than independent species distributions (Wisz et al., 2013). Community processes such as species interactions generate correlated responses among interacting species, although correlated responses may also arise from shared or opposing responses to environmental conditions such as climate. Positive species associations may reflect processes such as facilitation (le Roux, Virtanen, Heikkinen, & Luoto, 2012), shared climatic responses (Clark et al., 2014; Ovaskainen, Hottola, & Siitonen, 2010; Pollock et al., 2014) or significant dispersal barriers (Blois et al., 2014; Morueta-Holme et al., 2016), while negative species associations may arise due to competition (Godsoe & Harmon, 2012) or opposing responses to environmental conditions (Boulangeat et al., 2012; Ricklefs & Jenkins 2011). Disentangling the factors underlying species co-occurrence patterns, which are observed at a scale that is consistent with inference on distributions, may enable quantification of the independent influences of climate and non-climatic processes, such as species interactions on species distributions (Ovaskainen et al., 2010; Pollock et al., 2014), and can be accomplished within a Joint Species Distribution Modelling (JSDM) framework.

The JSDM approach exploits residual correlation in species co-occurrence patterns to infer the strength of positive and negative interspecific interactions. Species co-occurrence can be partitioned to represent that explained by species responses to climate, and co-occurrence left unexplained, representing residual dependence between species. When climatic influences are adequately described, residual correlation may indicate the independent influence of species interactions (Clark et al., 2014; Ovaskainen et al., 2010; Pollock et al., 2014). In practice, directly accounting for all potential drivers of co-occurrence patterns is a difficult task. Processes including dispersal (Blois et al., 2014; Urban, Zarnetske, & Skelly, 2013), responses to topographic variation (Serra-Diaz et al., 2015) and disturbance (le Roux, Virtanen, & Luoto, 2013) may generate correlated species responses that vary independently of climate. As with all correlative approaches, the JSDM approach is unable to quantify the precise contributions of every individual process that may contribute to modelled patterns. Yet, when interpreted carefully, JSDM may offer an improved approach to partitioning the effects of climate from those of non-climatic processes, with species interactions representing a particularly likely explanation for correlated species responses. Such approaches are necessary to guide future studies that will enhance understanding of the integrated impacts of local and regional processes on biodiversity patterns (Cazelles et al., 2015).

In this study, we evaluate co-occurrence patterns of ten dominant canopy tree species in the US Rocky Mountains using a JSDM (Pollock et al., 2014) to disentangle co-occurrence patterns arising from climate responses and those indicative of species interactions. Rocky Mountain forests are characterized by steep environmental gradients and distinct elevational zonation of dominant canopy species. While elevational zonation has been traditionally explained by climate (Rehfeldt, Crookston, Warwell, & Evans, 2006; Schrag, Bunn, & Graumlich, 2008), species interactions may give rise to similar patterns and have not been sufficiently evaluated (Graham et al., 2014; Wiens, 2011). Additionally, climate envelopes of many of our focal species show substantial overlap (Bell, Bradford, & Lauenroth, 2014; Rehfeldt et al., 2006), suggesting that climatic gradients are likely not the sole driver of tree distribution patterns in this region. Due to the strong environmental gradients that characterize this study region, Rocky Mountain forests offer a unique opportunity to test hypotheses regarding the relative importance of abiotic and biotic factors across environmental gradients, and to clarify how these hypotheses extend to species distributions. Specifically, the importance of climate relative to competition is generally hypothesized to increase in regions of high abiotic stress (Tilman, 1982; Meier et al., 2010; Ettinger, Ford, &

HilleRisLambers, 2011). We hypothesize that climate will be the dominant driver of species co-occurrence patterns among high-elevation sub-alpine forest species, which meet their upper distribution margins at tree line and experience more extreme climatic conditions, while lower-elevation montane species will exhibit stronger residual correlation than sub-alpine species, indicating the independent influence of non-climatic processes such as biotic interactions on species co-occurrence patterns. We further hypothesize that leveraging the additional information provided by neighbouring species in the JSDM approach will improve predictions of species distributions relative to single species approaches.

2 | METHODS

2.1 | Tree co-occurrence data

Occurrence data, detailing presence and absence locations, were extracted from the U.S. Forest Service's Forest Inventory and Analysis (FIA) database. The FIA database consists of plot-level forest data from a comprehensive survey of forest conditions across the conterminous United States; one field observation plot has been established for approximately every 25 km^2 of forested land. These plots span all forest ownership types and provide the most comprehensive source of presence/absence data on forest species available in the United States (Smith, 2002). To protect plot integrity and private ownership, all publicly available FIA plot coordinates are perturbed within a 0.8-km radius of actual plot locations. Perturbed coordinates do not appear to reduce the performance of species distribution models relative to precise coordinates (Gibson, Moisen, Frescino, & Edwards, 2014).

This study made use of the most recent survey data (2003–2012) for all FIA field observation plots within the US states of Montana, Idaho, Utah, Wyoming, Colorado, New Mexico and Arizona (Figure 1). Presence and absence locations were extracted for ten commonly occurring tree species (Table 1): *Abies lasiocarpa*, *Picea engelmannii*, *Pinus albicaulis*, *Pinus edulis*, *Pinus contorta*, *Pinus flexilis*, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Populus tremuloides* and *Quercus gambelii*. Selected species represent a range of shade tolerances, drought tolerances and habitat preferences and are adapted to a variety of disturbance regimes. In total, 15,365 FIA plots were used to describe presence and absence locations.

2.2 | Climate data

Climate variables were selected to represent seasonal and annual temperature and precipitation, which have a strong demonstrated influence on tree species within our study region (Bell et al., 2014; Rehfeldt et al., 2006). Multiple subsets of these variables with a correlation <0.7 were considered to minimize problems associated with collinearity (Dormann et al., 2013).

All climate data were extracted from the U.S. Forest Service Moscow Forestry Sciences Laboratory downscaled climate data set (MFSL; Rehfeldt, 2006). These data represent climate normals (1961–1990) downscaled to a 30-arc sec resolution (~1 km^2) using thin-plate spline methods (Rehfeldt, 2006). The extent of MFSL data span North America, with increased testing and application of data covering western North America (Rehfeldt et al., 2006). Both the temporal and spatial resolution of these data were deemed consistent with the spatial resolution of FIA plot-level data and the temporal influence of climate on long-living trees. Topographic position, which can be an important influence on species occurrence patterns in the Rocky Mountains (Peet, 1981), was represented by the covariate *TRASP*, a linear transformation of circular aspect (Evans, Oakleaf, Cushman, & Theobald, 2014; Roberts & Cooper, 1989). Data used to calculate *TRASP* were derived from a 30-m USGS digital elevation model, resampled to a 1-km^2 grid using bilinear interpolation to remain consistent with the spatial resolution of climate and occurrence data.

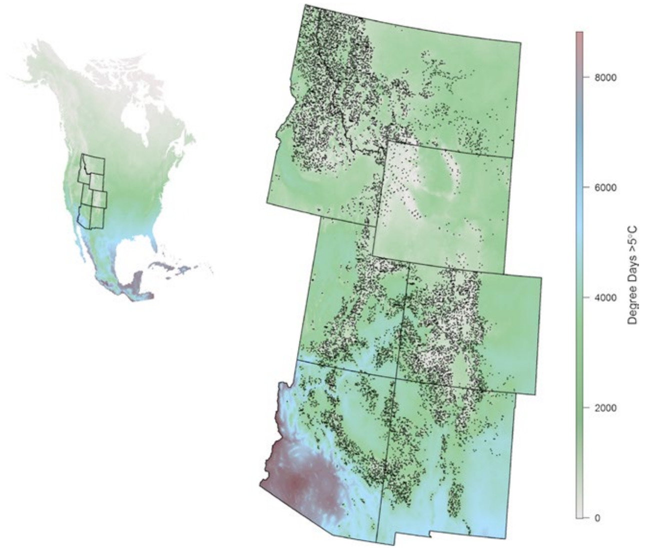

FIGURE 1 The study area spans the US portion of the Rocky Mountain range and encompasses the states of Idaho, Montana, Wyoming, Utah, Colorado, Arizona and New Mexico. 15,265 FIA survey plots were used in this analysis; only locations where study species are present are shown. Maps are displayed using an Albers equal area conic projection

2.3 | Modelling procedure

Species co-occurrence was modelled using the Joint Species Distribution Model (JSDM) approach of Pollock et al. (2014); see Pollock et al. (2014) for a more comprehensive model description and Appendix S1 for additional details. This approach uses a latent variable formulation of a Bayesian hierarchical multivariate probit regression to predict multiple species distributions simultaneously and to disentangle the processes underlying co-occurrence patterns. In the JSDM formulation, continuous climate covariates are related to discrete, binary presence/absence outcomes through a latent variable, which acts in place of a probit link function. The mean of this latent variable determines the probability of occurrence of a given species at a given location, and presence or absence can be inferred by invoking a threshold probability. We set occurrence thresholds individually for each species by calculating the probability that maximized the True

TABLE 1 Ten dominant Rocky Mountain tree species were selected for this study due to their prevalence and life-history traits. Selected species display strong elevational zonation, and most species span much of the latitudinal range of the study area

Species	Common name	*n* (prevalence)	Latitude (decimal degrees)	Elevation (m a.s.l.)
Abies lasiocarpa	Sub-alpine fir	2,622 (0.17)	33.6–48.9	624–3,718
Picea engelmanii	Engelmann spruce	2,567 (0.17)	32.7–48.9	670–3,804
Pinus albicaulus	Whitebark pine	511 (0.03)	42.1–48.9	1,531–3,166
Pinus edulis	Two-needle pinyon	3,362 (0.22)	32.1–41.6	1,157–3,196
Pinus contorta	Lodgepole pine	2,411 (0.16)	37.3–48.9	613–3,709
Pinus flexilis	Limber pine	513 (0.03)	35.2–48.9	1,186–3,709
Pinus ponderosa	Ponderosa pine	2,816 (0.18)	32.0–48.9	426–3,147
Pseudotsuga menziesii	Douglas-fir	4,290 (0.28)	31.4–48.9	426–3,521
Populus tremuloides	Quaking aspen	1,587 (0.10)	32.4–48.9	638–3,718
Quercus gambelii	Gambel oak	1,630 (0.11)	31.4–41.4	1,333–2,987

Prevalence = number of occupied sites/total number of sites.

Skill Statistic (TSS), a measure of model discrimination and performance that ranges from −1 to 1, with values >0 indicating better-than-chance discrimination (Allouche, Tsoar, & Kadmon, 2006). Species in the JSDM are correlated through a multivariate normal distribution, each dimension of which is characterized by independent latent variable distributions related through a variance/covariance matrix. As in standard probit regression, the SD of each latent variable distribution is set to 1 so that the variance/covariance matrix is directly interpretable as a correlation matrix. Regression coefficients are re-scaled by dividing by the SD of the correlation matrix in order to be interpretable as regular probit regression coefficients.

Model selection was accomplished using a multi-staged approach. Due to the extremely high computational demands of this model, fully Bayesian model selection across a large suite of candidate climate covariates was not feasible. To initiate model selection, we fit models with multiple non-correlated sets of climate covariates. For each of these covariate sets, full models were fitted with quadratic terms and interaction terms for each covariate. Fitted models were compared using Posterior Predictive Loss (PPL), a model fit criterion that accounts for goodness-of-fit and penalizes for model complexity and is particularly suitable for use with hierarchical models (Gelfand & Ghosh, 1998). We selected the full covariate set that minimized PPL for further variable selection (Table S1.1 in Appendix S1). To reduce the computational demands of a fully Bayesian variable selection, we fit separate versions of the model with and without covariate interactions to evaluate the potential contribution of complex climate and topography interactions. Both models produced nearly identical inference with regard to climatic and residual correlation, indicating that variable selection does not substantially influence conclusions regarding the relative contributions of climate vs. non-climatic processes (Appendix S1). The full model demonstrated substantially higher performance and was retained for further analysis. Fitted parameter estimates and convergence diagnostics for the full model are given in Appendix S3.

Model discrimination of the fitted JSDM was evaluated using TSS. The relative influences of climate and non-climatic processes were evaluated by comparing the strength of climatic vs. residual correlation for each species. We also compared predictions made using the JSDM to those made without accounting for covariance among species (analogous to an SDM) to determine whether the information contained in co-occurrence patterns can improve predictions of species distributions. Predictions were made only to forested areas, which were identified using the National Forest Type Dataset (Ruefenacht et al., 2008).

3 | RESULTS

The JSDM always showed better-than-chance discrimination (TSS > 0) and moderate performance for all species ($0.411 \le \text{TSS} \le 0.691$; Table 2). High-elevation sub-alpine species were predicted more accurately than lower-elevation montane species (Table 2). Imperfect discrimination was generally due to low specificity, corresponding to over-prediction of occurrence; the JSDM generally predicted broader geographic distributions than are represented by the occurrence data, particularly for low-elevation species such as two-needle pinyon and ponderosa pine (Table S1.2 in Appendix S1). For most species, the JSDM slightly outperformed the single-species approach, although differences in TSS, sensitivity and specificity between the two approaches were minimal (Table 2).

Climatic and residual correlations from the fitted model imply a stronger influence of climate on co-occurrence patterns than non-climatic processes. For nearly all species pairs, correlation due to climate covariates exceeded residual correlation substantially (Figure 2). High-elevation species tended to exhibit positive climatic correlations with one another, indicating shared climate responses, and negative

TABLE 2 The model performed moderately for all species, although performance did not differ substantially when including covariance (JSDM) or without covariance (SDM). TSS values show better-than-chance discrimination for all species (TSS > 0). High-elevation species were generally estimated with greater accuracy than low-elevation species

	TSS	Sensitivity	Specificity	TSS	Sensitivity	Specificity
Species	**With covariance**			**Without covariance**		
Sub-alpine fir[a]	0.647	0.929	0.718	0.638	0.924	0.714
Engelmann spruce[a]	0.577	0.890	0.687	0.562	0.875	0.687
Whitebark pine[a]	0.691	0.910	0.781	0.670	0.886	0.783
Two-needle pinyon[b]	0.565	0.884	0.681	0.535	0.866	0.669
Lodgepole pine[a]	0.537	0.918	0.619	0.542	0.924	0.618
Limber pine[a]	0.456	0.756	0.700	0.412	0.717	0.695
Ponderosa pine[b]	0.444	0.812	0.632	0.446	0.811	0.634
Douglas-fir[b]	0.411	0.772	0.639	0.406	0.771	0.635
Quaking aspen[b]	0.432	0.788	0.644	0.433	0.786	0.647
Gambel oak[b]	0.421	0.827	0.594	0.420	0.826	0.594

[a] High-elevation species.
[b] Low-elevation species.

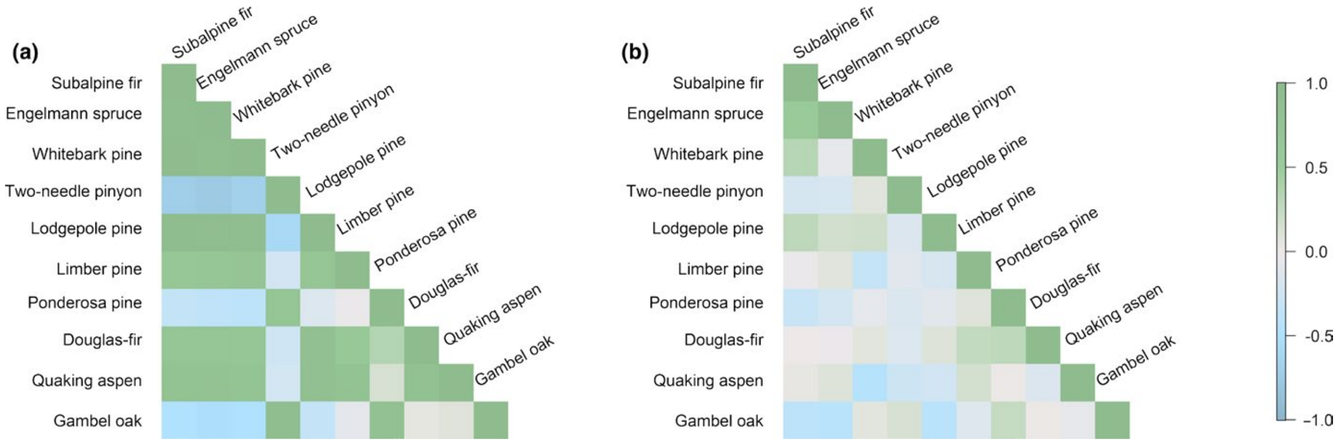

FIGURE 2 Environmental correlation (a) was consistently stronger than residual correlation (b), demonstrating that broad-scale species co-occurrence patterns can be largely explained by climate responses, yet correlations often acted in opposing directions, indicating that local processes may drive variation in co-occurrence patterns across finer spatial scales

climatic correlations with lower-elevation species, indicating divergent climate responses (Figure 2a). Species with weaker climatic correlation (e.g. *Quercus gambelii*, *Pinus ponderosa*) were also predicted less accurately (Table 2), indicating that covariates that were not considered in the model and that do not generate non-random co-occurrence patterns between modelled species may be important in defining the distributions of these lower-elevation species. In contrast to climatic correlations, residual correlations were negative for most species pairs, yet were generally weak relative to climatic correlation (Figure 2b). These patterns indicate that climate and non-climatic processes exert opposing pressures on co-occurrence and that non-climatic processes may contribute to species sorting along finer-scale environmental gradients.

Residual correlation only exceeded an absolute value of 0.5 in the case of *Abies lasiocarpa* and *Picea engelmanii*, two high-elevation sub-alpine species that regularly co-occur and were well predicted by the model (residual correlation = 0.573; Figure 2b). Inclusion of covariance for these species increases the probability of both species occurring together or being absent at the same location and decreases the probability of species occurring separately (Figure S2.1 in Appendix S2).

Predictions of species distributions generated from the JSDM (Figure S2.2 in Appendix S2) reflect model discrimination statistics; high-elevation species (Figure S2.2a–c, e, f in Appendix S2, Table 2) show more constrained and accurate distribution predictions than lower-elevation species (Figure S2.2d in Appendix S2, g–j, Table 2), indicating that alternative factors that were not considered in the fitted model and that do not generate non-random co-occurrence between modelled species may be particularly important in shaping the distributions of montane tree species.

4 | DISCUSSION

Our primary aim in this study was to evaluate the relative influences of climate and non-climatic processes, with particular emphasis on potential species interactions, on co-occurrence patterns of Rocky Mountain trees. The results from the fitted JSDM demonstrate that much of the variation in species co-occurrence patterns can be explained by shared or opposing responses to climate, with little difference in performance between the JSDM and the single-species approach. These findings do not support our initial hypothesis that the inclusion of additional species information would substantially improve predictions relative to a single-species approach. Residual correlations indicate that biotic interactions between these tree species explain little variation in species distribution patterns that arises independently of climate, and also imply that alternative processes capable of generating correlated species responses are not significant drivers of distribution patterns among these species. While these findings do not directly support our initial hypothesis regarding variation in the relative importance of climate and biotic interactions across elevational gradients, lower model performance among lower-elevation montane species does indicate that climate contributes more strongly to the distributions of high-elevation species, and alternative non-climatic processes may operate more strongly at lower elevations. Overall, our findings are in agreement with many other studies that have identified climate as an important driver of North American tree distributions and that have found limited evidence for a strong, independent influence of alternative processes including biotic interactions (reviewed in Copenhaver-Parry, Shuman, & Tinker, 2017).

The factors underlying residual correlation cannot be precisely determined using the JSDM approach, and residual correlation may be explained by any process that generates correlated responses among species, such as biotic interactions or shared dispersal barriers (Morueta-Holme et al., 2016; Pollock et al., 2014). While we only directly considered pair-wise interactions between dominant tree species in our modelling approach, the consistently weak residual correlation relative to environmental correlation we observed between Rocky Mountain tree species indicates that no non-climatic process that can generate correlated responses between these species pairs, including species interactions, appears to have a consistent, significant influence on regional co-occurrence patterns independent of the influence of climate (Figure 2). Pair-wise species interactions have been repeatedly hypothesized to influence species distribution patterns at macroecological scales (Wiens, 2011; Wisz et al., 2013), although direct empirical and mechanistic support remains relatively weak (e.g. Boulangeat et al., 2012; Gutiérrez, Snell, & Bugmann, 2016; Meier, Lischke, Schmatz, & Zimmermann, 2012; Morin et al., 2007; Rouget et al., 2001).

For Rocky Mountain tree species in particular, previous research has demonstrated that weak, local competitive interactions between species exert little influence on tree growth relative to climate (Copenhaver-Parry & Cannon, 2016). Disturbance, which is a ubiquitous feature of Rocky Mountain forests, may further mediate the effects of local interactions on long-lived trees by initiating secondary succession before competitive exclusion can occur (Grime, 1973; Roxburgh, Shea, & Wilson, 2004). Weak residual correlation among species and the small effect of covariance on species co-occurrence may also be attributable to the large spatial extent over which these species were modelled. Rocky Mountain tree species exhibit a high degree of local adaptation across their ranges, generating heterogeneous community dynamics and environmental responses (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008; Gray & Hamann, 2013). For example, *Pinus contorta*, which consists of four subspecies, spans 4000 km in latitude and occupies environments with mean annual temperatures ranging from −5 to 12°C. Local adaptation among *Pinus contorta* populations generates a broad range of environmental responses (Rehfeldt, Ying, Spittlehouse, & Hamilton, 1999). However, individual *Pinus contorta* populations generally exhibit low genetic diversity and narrow realized niches that are strongly impacted by the identity of co-occurring species, which vary across their range (Aitken et al., 2008; Peet, 1981; Rehfeldt et al., 1999). Heterogenous community dynamics and environmental responses in *Pinus contorta* and other tree species may drive variation in co-occurrence patterns among populations that is lost when species responses and co-occurrence relationships are averaged across a coarse scale and large spatial extent.

The strong positive climatic correlations identified for many species pairs in this study, particularly those occupying similar elevation zones (e.g. montane species and sub-alpine species) imply shared climatic requirements. These findings agree with climate envelope models for many of these species, which show substantial envelope overlap across temperature and precipitation gradients (Bell et al., 2014; Rehfeldt et al., 2006). Because trees share many resource requirements, it may at first seem contradictory that these species can occupy climatically similar regions without interacting strongly. The shared environmental responses and lack of strong interactions identified in this study may result from the complex topography of the habitats that these species occupy. Complex terrain influences in mountain landscapes, including cold air drainages, strong elevation gradients and fine-scale slope and aspect effects, may decouple regional climate from climate experienced in situ, generating extreme heterogeneity in local habitat (Dobrowski, 2011). Such heterogeneity coupled with slight differences in species environmental responses and habitat preferences may drive fine-scale segregation in species distributions that are not detectable at the scale at which we evaluated co-occurrence patterns. For example, fine-scale topoclimatic variation in the Colorado Front Range has been shown to generate variable soil moisture conditions that mediate the effects of regional climate on *Pinus contorta* and *Pinus ponderosa*, driving differing responses of these species to moisture availability (Adams, Barnard, & Loomis, 2014). In fact, community-level studies have long documented fine-scale variation in Rocky Mountain tree species spatial patterns with topographic position, most notably related to ridge lines and drainages (Peet, 1981). The existence of weak residual correlation among most species pairs in our study (Figure 2), along with the small effect of covariance on the probability of co-occurrence (Figure S2.1 in Appendix S2), may indicate that habitat features play an important role in defining the fine-scale co-occurrence patterns of Rocky Mountain tree species, but these effects are averaged-out when species co-occurrence patterns are evaluated across coarser spatial resolutions, such as in this analysis. Similarly, weak residual correlation may indicate the averaging-out of species interactions across coarse spatial resolutions (Soberón & Nakamura, 2009). Multiple studies have found that inclusion of other species improves prediction of tree species abundance, but not occurrence (Boulangeat et al., 2012; Clark et al., 2014; Meier et al., 2012; Rouget et al., 2001), indicating that interactions may often be local in nature and insufficient in strength or consistency to impact broad-scale co-occurrence patterns.

Only two of the species evaluated in this study exhibited noteworthy residual correlation: *Abies lasiocarpa* and *Picea engelmanii* (residual correlation = 0.573; Figure S2.1 in Appendix S2). Climatic correlation for this species pair still exceeded residual correlation (climatic correlation = 0.954; Figure 2), but these results suggest that positive interactions in the context of succession might contribute to the broad-scale co-occurrence patterns of these species. *Abies lasiocarpa* and *Picea engelmanii* are well-known to be facilitated at the seedling stage in late seral stands of *Populus tremuloides* (Calder & St. Clair, 2012), *Pinus flexilis* (Donnegan & Rebertus, 1999) and *Pinus contorta* (Kayes & Tinker, 2012) via the provisioning of favourable microsites and nurse plant effects. Our model did not include seedling data, and was thus unable to capture a strong facilitative relationship between *Abies lasiocarpa–Picea engelmannii*, and *Pinus flexilis*, *Pinus contorta* and *Populus tremuloides*, which are likely absent in late successional stands dominated by spruce and fir. Yet, the positive residual correlation between spruce and fir may in actuality reflect simultaneous facilitation of seedlings by adult individuals of early seral species during initial stages of spruce–fir stand development. This is consistent with theoretical evidence that demonstrates that strong positive interactions, such as mutualism and facilitation, are more likely to generate visible effects across coarse spatial resolutions and broad spatial scales than competition (Araújo & Rozenfeld, 2014).

Empirical species distribution modelling approaches, including the JSDM, are limited by their lack of ecological mechanism (Ibáñez et al. 2006). As a result, JSDM climatic correlations might also represent biotic interactions that are themselves strongly correlated with climate. Even if this were the case, substantial variation in species distributions is still left unexplained by the JSDM approach, implying that other processes that do not generate correlated species responses should be addressed. A variety of alternative factors could generate uncorrelated responses between species including interactions with species not included in the JSDM (e.g. herbivores, microbial symbionts, pests, biotic dispersal vectors; Van der Putten, Macel, & Visser, 2010; Lankau, Zhuk, & Ordonez, 2015; Katz & Ibáñez, 2017), interaction modifications and diffuse competition (Inouye & Stinchombe, 2001; Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010), dispersal (Woodall et al., 2009; Zhu, Woodall, & Clark, 2012), human land use (Pearson, Dawson, & Liu, 2004; Thuiller, Araújo, & Lavorel, 2004) or disturbance (le Roux et al., 2013). Disturbance may be an overlooked but particularly important driver. Wildfire shapes landscape vegetation patterns in western North American forests and its suppression during the 20th century may have decoupled some tree species distributions from climatic controls. Fire suppression has had a particularly strong influence on *Pinus ponderosa* (King, Bachelet, & Symstad, 2013; Mast, Veblen, & Linhart, 1998) and *Pinus edulis* (Baker & Shinneman, 2004; Miller & Tausch, 2001) distributions and may explain the lower performance of the JSDM for low-elevation species in this study, and associated low specificity, or over-prediction of species occurrence (Figure S2.2 in Appendix S2).

Overall, our findings bring into question the hypothesized importance of pair-wise species interactions for contributing to broad-scale distribution patterns in Rocky Mountain forests. However, we note several important limitations to inference including the inability of the JSDM to identify the precise factors contributing to residual correlation. We add to this the necessity of fitting the model with a limited number of covariates to eliminate problems associated with collinearity and to achieve computational feasibility. It is possible that some species may respond to a more complex suite of climate covariates than those included in the model, particularly wide-ranging, low-elevation species (Brotons, Thuiller, Araújo, & Hirzel, 2004; McPherson & Jetz, 2007). Collinearity is an important and nearly ubiquitous feature of ecological systems and places a notable constraint on correlative modelling techniques that is not easily overcome (Freckleton, 2011). However, the JSDM performed as well, and in most cases, slightly better than univariate models (analogous to an SDM approach; Table S1.2 in Appendix S1), and also performed similarly to regression tree and spline models, which can accommodate collinearity and complex functional forms (Copenhaver-Parry, Albeke, & Tinker, 2016). Therefore, these limitations are not expected to compromise our main findings. Taken as a whole, our findings indicate the overriding importance of climate on distributions and co-occurrence patterns of Rocky Mountain tree species, yet also highlight the need to consider multiple non-climatic processes, including those that may generate uncorrelated responses, particularly among lower-elevation species. While the question of biotic interactions is by no means entirely resolved, our findings indicate that clarity regarding the underlying drivers of species distributions, especially in Rocky Mountain forests, may be gained by focusing investigations on alternative non-climatic drivers that have not received as much attention as pair-wise species interactions, such as disturbance, dispersal and variation in climate responses across life stages (Copenhaver-Parry et al., 2017). Such clarity is necessary to enable informed and robust predictions of the response of forests to continuing environmental change.

ACKNOWLEDGEMENTS

The authors thank C. Woodall, B. Walters, and S. Albeke for access to data and C. Martinez del Rio, D. Williams, D. Tinker, B. Ewers, S. Albeke and three anonymous reviewers for helpful comments on the manuscript. P.C.P. was supported by a NSF Fellowship (G-K12 Project #0841298), and the MJ Murdock Charitable Trust (#2015205). D.B. was supported by NSF PRFB (#1202800) and the USDA Forest Service Pacific Northwest Research Station. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of NSF or the USDA Forest Service.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Appendix S1 Joint species distribution modelling details and accuracy assessment results
Appendix S2 Supplementary figures
Appendix S3 Fitted parameter estimates and convergence diagnostics

How to cite this article: Copenhaver-Parry PE, Bell DM. Species interactions weakly modify climate-induced tree co-occurrence patterns. *J Veg Sci*. 2018;29:52–61. https://doi.org/10.1111/jvs.12597