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Shading and litter mediate the effects of soil fertility on the performance of an understorey herb

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- **Background and Aims** Soil fertility and topographic microclimate are common determinants of plant species distributions. However, biotic conditions also vary along these abiotic gradients, and may mediate their effects on plants. In this study, we investigated whether soils and topographic microclimate acted directly on the performance of a focal understorey plant, or indirectly via changing biotic conditions.
- **Methods** We examined direct and indirect relationships between abiotic variables (soil fertility and topographic microclimate) and biotic factors (overstorey and understorey cover, litter depth and mycorrhizal colonization) and the occurrence, density and flowering of a common understorey herb, *Trientalis latifolia*, in the Klamath-Siskiyou Mountains, Oregon, USA.
- **Results** We found that the positive effects of soil fertility on *Trientalis* occurrence were mediated by greater overstorey shading and deeper litter. However, we did not find any effects of topographic microclimate on *Trientalis* distribution that were mediated by the biotic variables we measured. The predictive success of *Trientalis* species distribution models with soils and topographic microclimate increased by 12 % with the addition of the biotic variables.
- **Conclusions** Our results reinforce the idea that species distributions are the outcome of interrelated abiotic gradients and biotic interactions, and suggest that biotic conditions, such as overstorey density, should be included in species distribution models if data are available.

Key words: Abiotic factors, biotic conditions, distribution, mycorrhizae, overstorey shading, soil fertility, topographic microclimate, *Trientalis latifolia*.

INTRODUCTION

The performance and distribution of plant species with respect to climate (Araújo and Luoto, 2007; Meier *et al.*, 2010) and soil fertility (Elmendorf and Moore, 2008) can also be strongly affected by biotic conditions such as the degree of mycorrhizal symbiosis (Ruotsalainen *et al.*, 2004), competition or facilitation by neighbours (Choler *et al.*, 2001; Freestone, 2006) and overstorey cover (Meier *et al.*, 2010). However, biotic conditions are often omitted in species distribution models (Elith and Leathwick, 2009) due to scarcity of relevant data, close correlations between biotic and abiotic variables, and uncertainty regarding the relative importance of biotic conditions at the larger spatial scales typically considered in distribution models (Wiszbach *et al.*, 2013). To assess whether this absence of biotic variables is a significant problem, the relative importance of, and correlations between, abiotic and biotic variables need to be better understood. Here we investigated how four biotic variables (overstorey and understorey cover, litter, and mycorrhizae) varied along two abiotic gradients (topographic microclimate and soil fertility), and whether the biotic variables mediated the effects of the abiotic variables on the distribution and performance of a focal forest understorey plant.

Biotic factors such as overstorey canopy density, neighbouring plant abundance and mycorrhizae can strongly influence the amount of abiotic stress experienced by understorey plant species in woodlands and forests. Overstorey vegetation provides

shade and abundant litter, which can reduce extreme high or low temperatures, decreasing moisture stress for understorey plants (Pugnaire and Luque, 2001; Albrecht and McCarthy, 2009; Suggitt *et al.*, 2011). Negative effects of overstorey vegetation are also possible; a dense overstorey can compete with understorey species by taking up water and nutrients (Coomes and Grubb, 2000) and shading from dense canopies may limit understorey growth. Neighbouring understorey plants can reduce soil moisture loss through evaporation (Armas *et al.*, 2011) or buffer neighbours from freezing temperatures (Callaway *et al.*, 2002), but can also compete with neighbours for water (Liancourt *et al.*, 2012), nutrients (Casper and Jackson, 1997) and space.

Mycorrhizal symbiosis can alleviate plant water and nutrient stress (Augé, 2001) and mycorrhizal associations are found in 80 % of terrestrial plant species (Wang and Qiu, 2006), yet the symbiotic fungi also require carbon from their plant hosts, which could lead to neutral or negative effects of this interaction in environments with abundant soil resources (Johnson *et al.*, 1997). While mycorrhizal associations are widespread among terrestrial plant communities, the degree of colonization and the benefit of mycorrhizal symbiosis vary with plant and fungal identity (e.g. Bennett and Bever, 2007; Scheublin *et al.*, 2007) and the effects of the environmental conditions on the symbiosis (Schechter and Bruns, 2008; Eschen *et al.*, 2009; Doubkova *et al.*, 2012).

Biotic factors that influence abiotic stress of understorey plants are also in turn affected by abiotic conditions such as

topographic microclimate or soil fertility, leading to indirect effects of these abiotic factors on understorey plant species via their influence on biotic conditions. For example, in mild climates and on nutrient-rich soils both understorey and overstorey plant biomass is likely to increase, leading to greater overstorey cover and competition between herbaceous understorey neighbours. The abundance and composition of mycorrhizal communities are also affected by soil fertility (Branco, 2010; Ji *et al.*, 2010) and climate (Fisher and Fule, 2004; Hawkes *et al.*, 2011), which could alter mycorrhizal colonization rates and the degree of benefit conferred by mycorrhizal symbiosis.

If abiotic conditions strongly affect understorey plant performance via their effects on biotic variables, such as overstorey cover, then biotic factors may be important mechanistic links between abiotic variables and plant distribution patterns, and should be included in species distribution models and experiments that address the effects of the abiotic environment. However, abiotic factors may have strong direct effects on plant performance independent of their relationships with biotic variables.

Our overarching hypothesis was that the effects of abiotic gradients (soil fertility and topographic microclimate) on plant performance would be largely or fully explained by their indirect effects acting through biotic conditions (shading, understorey cover, mycorrhizae). As plant performance indicators, we used (1) distribution (presence/absence), (2) abundance and (3) flowering. To test this hypothesis, we used structural equation modelling, followed by mediation tests to select the combination of biotic conditions that explained a significant proportion of the effect of the abiotic environment on plant performance. We also tested the ancillary hypothesis that our focal biotic conditions serve to ameliorate plant stress, which we measured using foliar traits (specific leaf area, carbon/nitrogen and carbon isotope ratio) as indicators. Finally, we assessed the potential contribution of our biotic variables to the predictive power of abiotically based species distribution models.

Our focal species was a common understorey herb, *Trientalis latifolia* (Myrsinaceae), which is found across major abiotic gradients, elevation, slope and aspect, and soil fertility, in the topographically and geographically complex Klamath-Siskiyou Mountains. We also focused on the soil type contrast represented between serpentine and adjacent non-serpentine soils in the region. Serpentine soils are characterized by low macronutrients, high heavy metal content and low water-holding capacity (Whittaker, 1954; Kruckeberg, 1984; Brooks, 1987; Brady *et al.*, 2005) and are known to strongly affect distributions of herbaceous species (Whittaker, 1960). Classic observational work noted the apparently high sensitivity of *Trientalis* to soils, topographic microclimate and shading in this region (Whittaker, 1960).

MATERIALS AND METHODS

Study system: Klamath-Siskiyou Mountains

The flora of the Klamath-Siskiyou Mountains is diverse (1859 vascular plant species according to DellaSala *et al.*, 1999) and floristic composition responds strongly to variation in parent material, elevation, topographic relief and distance from the

coast (Whittaker, 1960, 1961; Damschen *et al.*, 2010). The geological history of the region is complex with a wide variety of parent materials and derived soil types occurring in close proximity (Whittaker, 1960). A large proportion of the region's diversity is due to 'serpentine' soils derived from ultramafic bedrock characterized by low levels of macronutrients such as phosphorus and nitrogen and high levels of toxic minerals such as nickel and chromium (Whittaker, 1954). Among soil properties, the calcium/magnesium ratio has a particularly strong influence on vegetation composition associated with serpentine soils (Grace *et al.*, 2007). In the Klamath Mountains, serpentine soils also vary in texture and mineral properties based on metamorphism of the parent ultramafic rock and soil development related to slope position (Alexander *et al.*, 2007; Alexander, 2009). In addition to serpentine soils, the region includes large areas of soil types derived from intrusive igneous rocks, from mafic gabbro to less mafic diorite and felsic granite, and smaller areas of sedimentary and non-serpentine metamorphic rock, such as limestone (Whittaker, 1960).

Study species

Trientalis latifolia (starflower) is a common annual herb of Western North America that primarily reproduces asexually via tuber formation at distances varying from <1 to 50 cm (our pers. obs., consistent with the study of *T. europea* by Piqueras and Klimeš, 1998). Occasional sexual reproduction occurs via flowering and production of outcrossed seed (Anderson and Loucks, 1973). *Trientalis* occurs across soil fertility gradients in the Klamath-Siskiyou Mountains but is more abundant with a greater altitudinal range on nutrient-rich diorite soils than on nutrient-poor serpentine or gabbro soils (Whittaker, 1960). *Trientalis* is tolerant of fire and logging disturbance, perhaps due to survival of underground tubers, but requires several years to reach peak abundance after disturbance (Halpern, 1989). Environmental characteristics from a database of forest plots (present in 273 plots, ECOSHARE, 2011) suggest that *Trientalis* is most common on south-west aspects (median of occurrences at 198°), elevations of ~ 1000 m (median) and moderate slopes (median: 45 %). *Trientalis* occurs in greater abundance in shaded microclimates than on open slopes, and occurs in cooler topographic microclimates on nutrient-poor serpentine soils than on diorite soils (Whittaker, 1960).

Plot sampling

Serpentine versus non-serpentine soils were identified by combining GIS layers for soil type (SSURGO, 2011) and geological parent material (DOGAMI, 2009). Plot locations were randomly selected by stratifying into four elevation bands for each soil type based on the distribution of elevations across the region (equal quantiles for the elevation distribution of the soil type, higher fertility non-serpentine: 381–595, 596–973, 974–1290, 1291–1855 m, low-fertility serpentine: 401–533, 534–745, 746–1051, 1052–1587 m) in ArcGIS 10 (ESRI, 2011). Plots were chosen to span the full range of aspects (NE–SW) with even numbers of plots within the following four aspect categories: 0–89° (NE), 90–179° (SE), 180–269° (SW) and 270–359° (NW) for each elevation band and soil type. Plot locations

were also restricted to late-seral vegetation types with minimal disturbance classified as forests or woodlands (Atzet *et al.*, 1996). High-severity burned areas and areas with evidence of recent thinning (e.g. stumps and slash piles) were avoided because these disturbances have the potential to alter relationships between abiotic and biotic conditions and plant response. The plots included the common vegetation types of the vast majority of the regions' federal lands; however, some distinct, regionally uncommon, vegetation types were not represented, such as low-elevation wetlands and alpine zones.

Plot sampling occurred over three growing seasons (March–August, 2010–2012). Sites were visited twice if they had a high percentage of annual understorey species (i.e. low-elevation serpentine plots) or once during peak biomass if the understorey was primarily perennial species (i.e. high-elevation non-serpentine plots) to estimate plant community cover. The final dataset included 54 serpentine plots and 59 non-serpentine plots across ~ 1500 km² and spanning the elevation range of the study area (Fig. 1). Plots were 5 × 5 m with four randomly located 1 × 1-m subplots sampled for understorey community abundance and *Trientalis* density. Topographic variables related to microclimate, slope, aspect and elevation were recorded at the whole plot level. Slope per cent was determined with a clinometer (Suunto PM-5, Vantaa, Finland) and aspect was measured with

a high-precision compass (Suunto Vista KB-20). Measured aspect was used to calculate Beers' aspect (Beers *et al.*, 1966), a linear transformation of aspect that ranges from 0 to 2. Low Beers' aspect (0) represents slopes with SW orientations which receive high amounts of solar radiation and are therefore relatively warm, whereas high Beers' aspect slopes (2) are NE-facing and tend to be cool due to low solar radiation. Plots spanned almost the entire elevation range of the region (plot range: 380–1850 m, region range: 380–1900 m), slopes ranged from level to steep (3–145 %) and the complete range of aspects (0–359°, 0–2 Beers aspect) was represented. Mineral soil samples were collected from each of the four subplots to 10 cm depth and homogenized to one sample per plot, air-dried and sieved to 2 mm. Soil samples were air-dried, sieved at 2 mm, and analysed for calcium/magnesium ratio (Ca:Mg, a key attribute of serpentine soils affecting vegetation, Grace *et al.*, 2007), phosphorus (P, weak Bray method), and organic matter (A & L Western Laboratories, Modesto, CA, USA; for methods see Gavlak *et al.*, 2005). A key characteristic of soil fertility on serpentine soils is the low Ca:Mg ratio, which tends to inhibit plant absorption of calcium, a required nutrient. Our study also included sites that were non-serpentine, with higher Ca:Mg, but relatively infertile due to other factors related to soil development such as parent material, age and topographic position. We

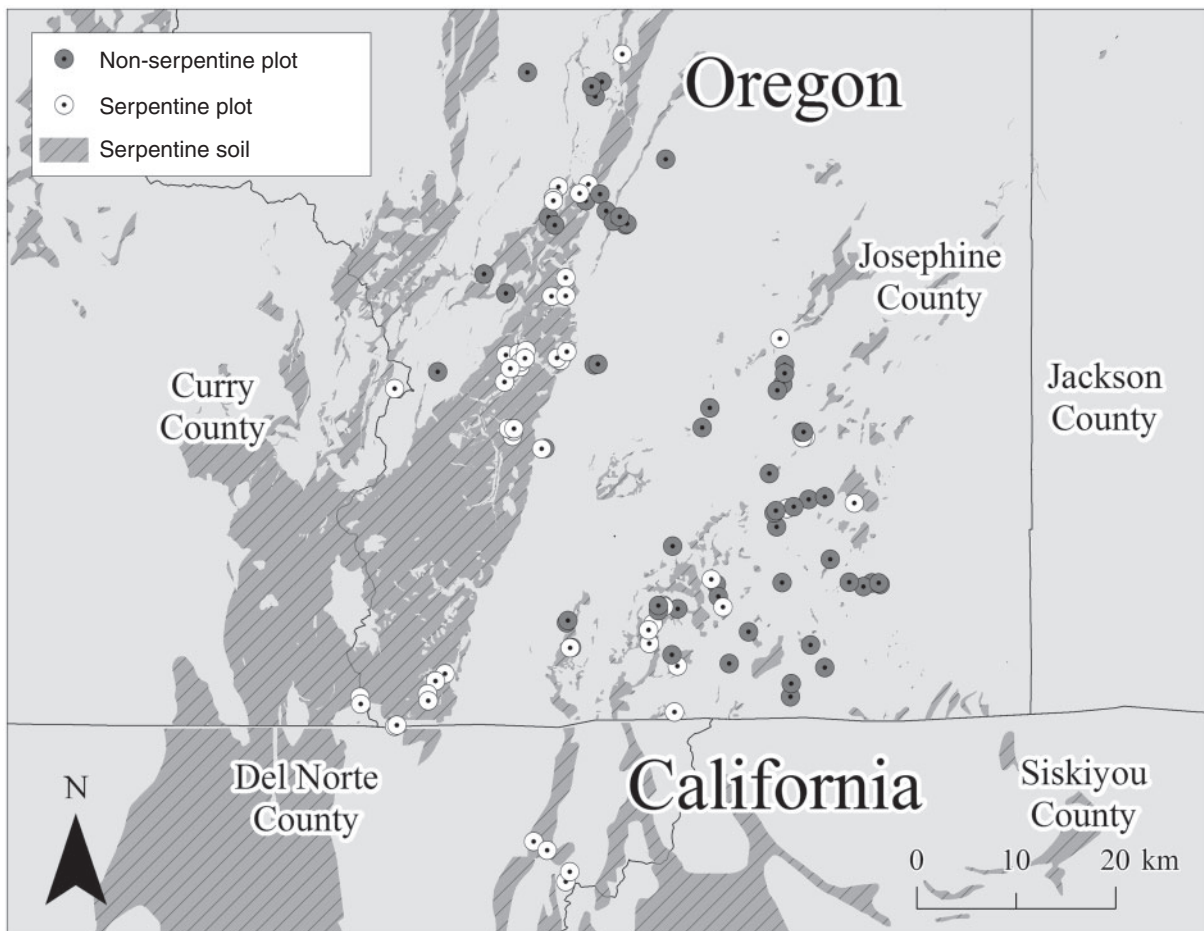


Fig. 1. Map of plot locations in the Klamath-Siskiyou Mountains by soil type illustrating the distribution of serpentine soils.

chose soil phosphorus and organic material as general indicators of soil fertility because soil phosphorus is less likely to change seasonally or due to atmospheric inputs (as in the case with nitrogen), and is tied to geological substrate and soil development (Vitousek *et al.*, 2010), while organic material reflects plant productivity and decomposition rates at a site, which are tied to factors such as temperature and moisture in addition to soil nutrients.

Litter depth (leaf litter and duff) was measured with a ruler from the soil surface at four randomly selected locations within each subplot and averaged. Percent cover was visually estimated for all understorey species (defined as species with heights < 1.3 m), allowing for overlapping cover, for each of the four 1 × 1 subplots and averaged. Light availability, determined by overstorey shading by trees and tall shrubs, was estimated as annual solar radiation with a hemispherical device that accounts for the effects of canopy and slope shading given the sunpath for that latitude (average of four measurements, one from each 1 × 1 subplot, Solar PathFinder & Assistant, Solar PathFinder, Linden, TN, USA).

Trientalis performance and leaf traits

The occurrence, number and flowering status of *Trientalis* individuals were recorded by subplot. Ten or more individuals were collected per plot for mycorrhizal colonization and traits associated with low soil nutrients and climate (Diaz *et al.*, 1998; Dawson *et al.*, 2002; Wright *et al.*, 2004; Ordonez *et al.*, 2009). The traits measured, specific leaf area (SLA), leaf C:N and carbon isotope ratio ($\delta^{13}\text{C}$), were chosen because they indicate a resource conservation strategy with high leaf C:N and low SLA, and high water use efficiency as measured by $\delta^{13}\text{C}$ (Dawson *et al.*, 2002; Lavorel and Garnier, 2002; Perez-Harguindeguy *et al.*, 2013). Leaves were collected and maintained in cool, moist conditions, either in a cooler or refrigerator, and scanned within 24 h of collection. Fresh leaf area was calculated from scanned images with ImageJ (Rasband, 1997–2012). Dry biomass was calculated from samples dried at 60 °C for 48 h. Fresh leaf area and dry biomass were used to compute SLA (g cm^{-2}). Samples were ground and analysed for natural $\delta^{13}\text{C}$, C and N percentage (UC Stable Isotope Facility, Davis, CA, USA), and foliar P (A & L Western Laboratories, Modesto, CA, USA; for methods see Gavlak *et al.*, 2005).

Symbiotic fungal colonization

Fresh roots from ten or more individuals collected per plot were washed and placed in ethanol for storage within 24 h. Roots were stained with ink and vinegar (Vierheilig *et al.*, 1998) and scored with the intersection method (McGonigle *et al.*, 1990). Percentages of arbuscular mycorrhizae (phylum Glomeromycota) and endophyte septate fungi (phylum Ascomycota) were tallied separately. Endophytic septate fungi are a group of diverse taxonomic origin (Jumpponen and Trappe, 1998) that are found in roots of healthy plant species worldwide, including a variety of species in temperate forests and grasslands (Mandyam and Jumpponen, 2005) and in a related herbaceous species, *Trientalis europaea* (Tejesvi *et al.*, 2013). Although they have been less well studied than arbuscular mycorrhizae, endophytic septate fungi can

have similar positive effects on plant growth and nutrient status (Newsham, 2011).

Statistical analysis

Biotically mediated effects of abiotic gradients on plant performance. We tested the hypothesis that abiotic conditions affected *Trientalis* performance via their relationships with biotic conditions using structural equation models (Grace, 2006) and mediation tests (d-separation tests, Shipley, 2009; Clough, 2012). With the structural equation models we were able to test for potential direct and indirect associations between broad categories of abiotic conditions (soil and topographic microclimate) and plant performance, while with the mediation tests we were able to select the combination of biotic conditions that explained a significant proportion of the effect of abiotic variables on plant performance.

Our structural equation models (Fig. 2) included pathways between abiotic conditions (soil fertility and topographic microclimate) and biotic conditions (overstorey shading, litter, understorey cover and symbiotic fungal colonization) built with the R package lavaan (sem function, Rosseel, 2012) with composite variables for soil fertility and topographic microclimate and response variables for plant occurrence (presence/absence, ordered option in lavaan syntax), abundance (number of individuals, logged) and flowering proportion (Fig. 2, see details in Supplementary Data Appendix S1). We constructed independent structural equation models for each biotic variable, to avoid the effects of high correlations between some biotic variables (i.e. overstorey cover and litter depth). Composite variables describe the joint effects of multiple measured variables which relate to a conceptual factor, either soil fertility or topographic microclimate in this study (Grace and Bollen, 2008). The soil fertility composite variable included soil Ca:Mg, phosphorus and organic matter. The topographic microclimate composite variable included slope, Beers' aspect and elevation. The biotic conditions considered were overstorey variables (understorey light availability through the canopy and litter depth), understorey cover and colonization by arbuscular mycorrhizae or septate fungi.

Significant indirect effects, i.e. 'mediating' effects (defined in Grace *et al.*, 2012), were examined with mediation tests (d-separation tests, Shipley, 2009; Clough, 2012). We first considered which abiotic variable (serpentine soils or elevation) was significantly related to each biotic condition (overstorey shading, litter, understorey cover, mycorrhizal or septate fungal colonization) and whether these biotic conditions were significantly associated with plant variables (presence, abundance or reproduction). We used the mediation test to confirm the significance of the hypothesized indirect effect of the abiotic variable. For cases where multiple biotic variables might mediate the effects of abiotic variables, we used individual d-separation tests to evaluate inclusion of each possible indirect pathway.

The effects of elevation and serpentine on biotic variables were modelled individually with linear models. The effects of variables on plant performance were modelled with generalized linear models with the distribution varying with the variable. Presence/absence was modelled with the binomial distribution, abundance (numbers of individuals found in the plot) with the negative binomial distribution in package MASS (Venables and Ripley, 2002)

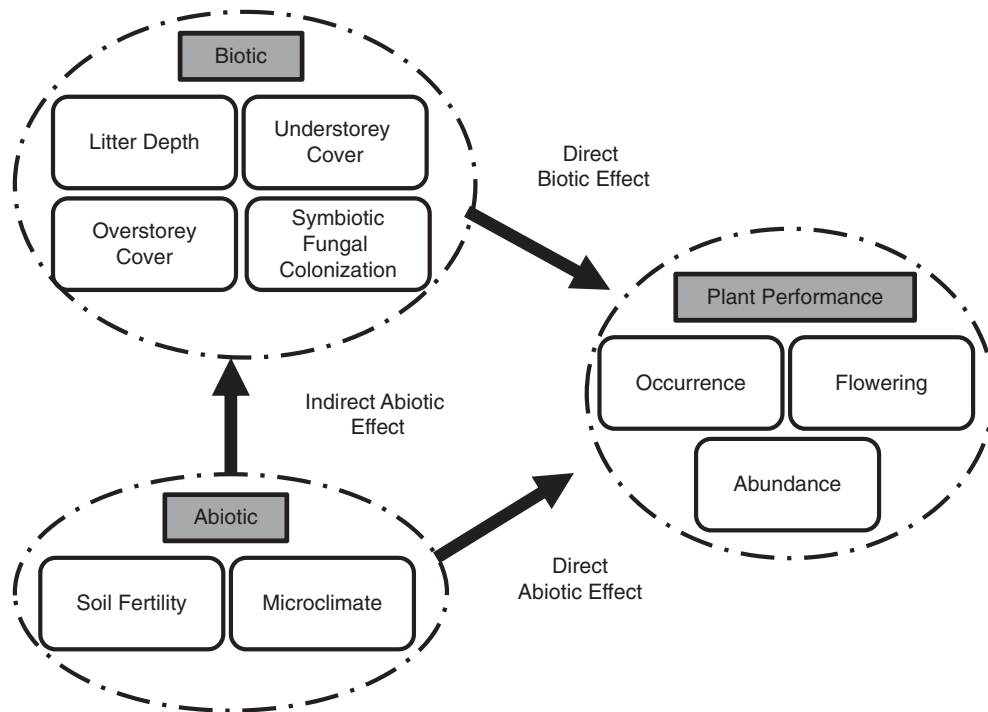


Fig. 2. Conceptual model of direct abiotic and biotic and indirect abiotic effects on *Treintalis* performance.

and proportion of flowering individuals with a binomial model corrected for overdispersion (quasi-binomial model).

Effects of biotic conditions on stress-related plant traits

We tested our ancillary hypothesis that biotic conditions affected plant performance via their effects on water and nutrient stress by using linear models for the effects of biotic conditions (shading and mycorrhizae) on leaf traits related to these stresses (SLA, C:N and carbon isotope ratio).

Improvement of species distribution models using biotic variables

We analysed the potential for biotic variables to improve species distribution models by comparing the performance of models with abiotic variables, biotic variables or both (presence/absence, binomial distribution, generalized linear models). We quantified the predictive power of each model by comparing the rate of true positives versus false positives with Wilcoxon signed-rank tests (e.g. Araújo and Luoto, 2007). This test indicates whether model predictions for true and false positives are significantly different, indicating that models are able to distinguish conditions for presences and absences. We compared models with combinations of variable groups representing topographic microclimate conditions (elevation, slope, Beers' aspect), soil fertility (serpentine, phosphorus, organic matter), and biotic conditions (litter depth, understorey cover, overstorey shading). We omitted fungal colonization, as this variable could not be evaluated in locations where the species was absent. We also used the caret package to calculate variable importance for each model (varImp function, Kuhn *et al.*, 2015).

Analyses were conducted in R 3.1.3 (R Core Team, 2015).

RESULTS

Biotically mediated effects of abiotic gradients on plant performance

Overstorey cover and litter. In support of our hypothesis of biotically mediated indirect effects, both structural equation models and mediation tests indicated that soil fertility positively affected *Trientalis* occurrence via positive effects on overstorey density, leading to higher shading and increased litter depth (Table 1). Structural equation models showed that the composite variable for soil fertility was associated with lower light availability in the understorey (due to higher canopy density, standardized coefficient, -0.58 , $P < 0.01$) and increased litter depth (standardized coefficient: 0.42 , $P < 0.01$). Lower light availability (higher canopy density) and increasing litter depth were both associated with greater probability of *Trientalis* occurrence in structural equation models including light availability or litter depth (light through canopy, standardized coefficient, -0.39 , $P = 0.04$, model fit: occurrence, $\chi^2 = 2.35$, d.f. = 2, $P = 0.31$, Supplementary Data Fig. S1a, litter depth, standardized coefficient, 0.34 , $P < 0.01$, model fit: occurrence, $\chi^2 = 2.33$, d.f. = 2, $P = 0.31$, Fig. S1b). The associated mediation tests showed that decreased overstorey shading mediated the negative effect of infertile serpentine soils on *Trientalis* occurrence, with final models including both litter and overstorey cover (final model fit: d.f. = 4, $C = 4.45$, $P = 0.35$, Table 2, Fig. 3, intermediate steps in Appendix S1). As in structural equation models, soil fertility was associated with overstorey shading, with lower overstorey cover (and greater light

TABLE 1. Summary of significant results for direct effects of biotic conditions [overstorey cover, litter depth, understorey cover, arbuscular mycorrhizae (AMF), or septate colonization] and indirect effects of abiotic conditions (topographic microclimate and soil fertility or serpentine soils) by analysis approach (generalized linear models: GLM, structural equation models: SEM, and mediation tests: MT) and *Trientalis* response variable (occurrence, abundance, or flowering); there were no significant direct effects of abiotic conditions independent of biotic conditions in SEM or MT models

<i>Trientalis</i> variable	Direct effects of biotic conditions	Indirect effects of abiotic via biotic conditions
Occurrence	Overstorey cover (GLM, SEM)	Soil fertility/serpentine → overstorey cover (SEM, MT)
	Litter depth (GLM, SEM)	Soil fertility/serpentine → litter depth (SEM, MT)
	Understorey cover (GLM, SEM)	Serpentine → understorey cover (MT)
Abundance	Overstorey cover (GLM)	
	Litter depth (GLM)	
	AMF colonization (GLM, SEM)	
Flowering	Overstorey cover (GLM, SEM)	Serpentine → overstorey cover (MT)
	Understorey cover (GLM)	Serpentine → understorey cover (MT)

availability) and litter depth on serpentine soils (Fig. 4, overstorey: F -test = 131.0, $P < 0.01$, litter: F -test = 40.5, $P < 0.01$). Greater overstorey cover (lower light availability) and increased litter depth were also associated with increased probability of occurrence (Fig. 5, $\chi^2 = 7.8$, $P < 0.1$, $\chi^2 = 9.9$, $P < 0.01$).

When *Trientalis* flowering instead of occurrence was considered, the presence of indirect effects was also supported by mediation tests, but not by structural equation models (Supplementary Data Fig. S1c). Mediation tests showed that infertile serpentine soils had a significant positive effect on *Trientalis* flowering via lower canopy density and associated higher light availability (final model fit: d.f. = 4, $C = 3.92$, $P = 0.42$, Table 2, Fig. 6, intermediate steps in Appendix S1, light availability: F -test = 13.2, $P < 0.01$, Fig. 7). Litter depth did not have significant direct effects on flowering (Supplementary Data Fig. S2).

When *Trientalis* abundance was considered, overstorey variables were not significant in structural equation models

TABLE 2. Mediation (d -separation) test statistics for biotic conditions mediating the effect of serpentine soils on plant responses (occurrence: presence/absence, abundance: number of individuals per plot, flowering: ratio of flowering to non-flowering)

Biotic variable	Plant response					
	Occurrence		Abundance		Flowering	
Mediation of serpentine effect	C	P	C	P	C	P
Overstorey cover	2.6	0.28	13.6	<0.05	1.2	0.54
Litter depth	0.3	0.85	10.3	<0.05	9.8	<0.05
Understorey cover	5.5	0.07	9.2	<0.05	2.1	0.35

P -values > 0.05 indicate support for a mediation effect (bold type).

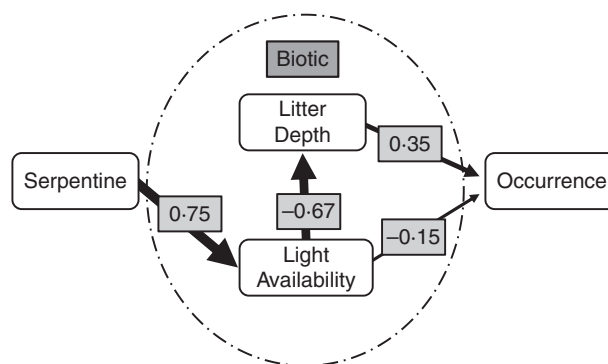


Fig. 3. Diagram of supported mediation effects of litter depth and understorey cover on *Trientalis* occurrence (d -separation test, $C = 4.5$, $P = 0.35$).

(standardized coefficients, $P > 0.10$) nor did they have significant mediating effects on the effect of serpentine soils (Table 2), contrary to our expectations of significant indirect effects. However, litter depth was associated with higher abundance when modelled independent of soil fertility (Fig. 8, Supplementary Data Fig. S2c).

In contrast to soil fertility, topographic microclimate did not significantly affect plant occurrence, abundance, or flowering via its effects on overstorey cover or litter, even though there were some significant direct pathways between topographic microclimate and overstorey variables and overstorey variables and performance (Supplementary Data Fig. S2a–d). We also did not find direct effects of topographic microclimate on plant performance variables in structural equation models. Because elevation did not significantly affect overstorey biotic conditions (Supplementary Data Table S1, Fig. 9), no mediation tests were performed for this variable.

Understorey cover. In partial support of our hypothesis of indirect effects, understorey cover mediated the effects of serpentine soils on occurrence and flowering, although not on abundance (Table 2, Fig. 6, Tables S1 and S2). Serpentine soils were associated with higher understorey cover (Fig. 4), while increasing understorey cover was associated with a higher probability of occurrence and flowering percentage according to mediation tests (Table 2, Figs 5 and 7, Supplementary Data Tables S1 and S2). Understorey cover did have a direct positive effect on occurrence in structural equation models, but no significant indirect effects were observed (standardized coefficients, with soil: 0.29, $P < 0.01$, with topographic microclimate: 0.24, $P = 0.02$, soil model fit: $\chi^2 = 1.90$, d.f. = 2, $P = 0.39$, topographic microclimate model fit: $\chi^2 = 2.53$, d.f. = 2, $P = 0.28$, Supplementary Data Fig. S3a, b).

Mycorrhizal colonization. Structural equation models and mediation tests did not support indirect effects of soil or topographic microclimate on plant flowering or abundance via either category of mycorrhizae (Table S1). However, arbuscular mycorrhizae colonization was negatively associated with abundance in structural equation models with soil fertility (abundance, standardized coefficient: -0.57 , $P < 0.01$, model fit: $\chi^2 = 1.44$, d.f. = 2, $P = 0.49$, Supplementary Data Fig. S4). Soil fertility and topographic microclimate did not have direct effects on

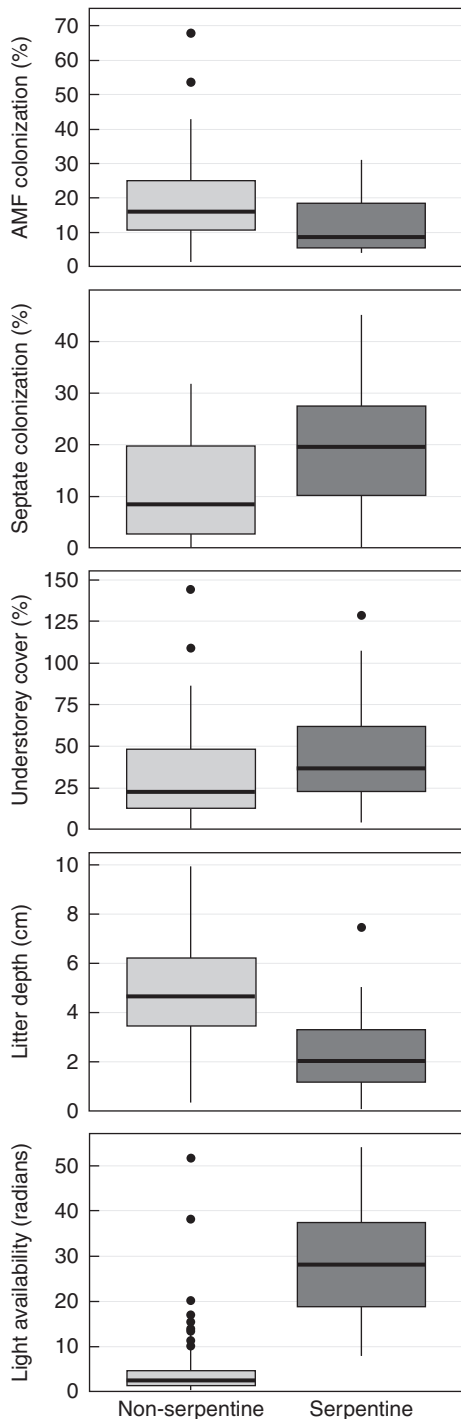


FIG. 4. Boxplots of serpentine soil type and biotic variables (whiskers represent $1.5 \times$ the interquartile range).

plant flowering or abundance in structural equation models with mycorrhizae.

Effects of biotic conditions on stress-related plant traits

In agreement with our hypothesis about biotic mediation of abiotic stress, greater overstorey shading was associated with

plant traits indicative of lower tolerance for water scarcity (lower $\delta^{13}\text{C}$; $F = 49.2$, $P < 0.01$), higher SLA ($F = 14.1$, $P < 0.01$) and marginally higher foliar P ($F = 3.9$, $P = 0.06$). Likewise, increasing litter depth was associated with more drought-intolerant foliar trait values (lower $\delta^{13}\text{C}$; $F = 6.3$, $P = 0.02$). In contrast, higher understorey cover was associated with traits indicating higher drought tolerance (higher $\delta^{13}\text{C}$, $\delta = 6.7$, $P = 0.01$), lower foliar P ($F = 4.5$, $P = 0.04$), lower SLA ($F = 7.1$, $P < 0.01$) and marginally higher foliar C:N ($F = 3.2$, $P = 0.09$). Septate fungi colonization was associated with lower foliar P ($F = 5.1$, $P = 0.04$) and higher C:N ($F = 10.1$, $P < 0.01$) while arbuscular mycorrhizal colonization was not significantly associated with these plant traits.

Improvement of species distribution models using biotic variables

Models for *Trientalis* occurrence built with the significant biotic variables (overstorey shading, litter depth and understorey cover) were able to correctly predict 70 % more occurrences than models with abiotic variables alone (elevation, aspect and slope, 10 % correct for the abiotic variable model, 17 % for the biotic variable model). Models with combined biotic and abiotic conditions correctly identified occupancy for more than twice as many occurrences as the abiotic-only model (22 % for models with combined abiotic and biotic variables). All models with different combinations of abiotic and biotic variables distinguished between conditions for presences and absences (significant difference between models for presence and absence), including models with biotic variables alone (Table 3). Biotic variables had consistently higher importance than abiotic variables when combined in models, with understorey cover, light availability and litter depth ranking as the top three variables in all models (Table 3).

DISCUSSION

The effects on plant performance of abiotic conditions, particularly soil fertility, were largely mediated by the effects of these variables on biotic conditions. Biotic conditions were associated with the abundance, presence and flowering of our focal species, while our two categories of abiotic conditions, soil fertility and topographic microclimate, were not significant predictors of plant response when biotic conditions were included in models. Of biotic conditions, overstorey cover had the most consistent effects on plant responses, while symbiotic fungal colonization had weaker or no significant effects on our focal species. These results suggest that the effects of soil fertility on biotic conditions may be important mechanistic links between this type of abiotic variable and plant performance (Pugnaire *et al.*, 2004; Kunstler *et al.*, 2011; Fernandez-Going *et al.*, 2012).

We also found that the predictive performance of distribution (occurrence) models for *Trientalis* was markedly improved by the inclusion of biotic conditions, reflecting the strong associations between biotic conditions and plant responses in the interaction models. Models with biotic conditions alone were able to significantly distinguish presence from absence points, while models with topographic microclimate and/or soil fertility alone only weakly differentiated them (P -values close to 0.05,

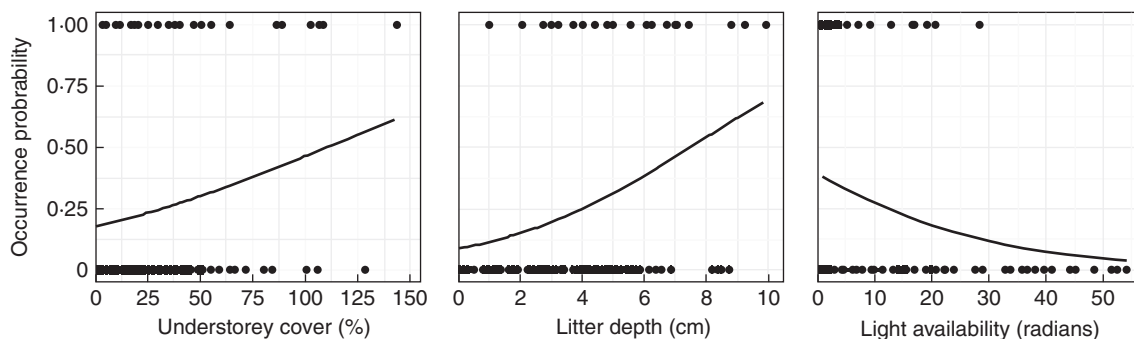


Fig. 5. Plots of significant relationships between biotic variables (understorey cover, litter depth, and light availability) and *Trientalis* occurrence.

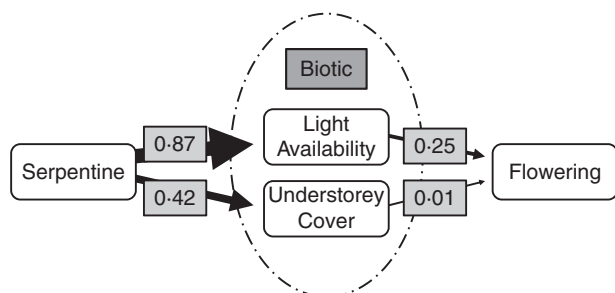


Fig. 6. Diagram of supported mediation effects of light availability, due to overstorey shading, and understorey cover on *Trientalis* flowering (d-separation test, $C = 3.9$, $P = 0.42$).

Table 3). These results suggest that inclusion of biotic conditions may significantly improve distribution model predictions in space and time (Wisz *et al.*, 2013), although the relative contribution of biotic conditions to distribution is likely to vary with species tolerance to disturbance and environmental stress (Meier *et al.*, 2010).

The strength of biotic conditions compared to abiotic factors in our models suggests that changes in biotic factors could significantly alter distribution patterns with respect to abiotic factors. Understorey species such as *Trientalis*, which make up a diverse and abundant component of the vegetation of the Klamath-Siskiyou Mountains (Whittaker, 1960), may be especially sensitive to overstorey conditions. For example, we found that *Trientalis* occurrence is highly related to overstorey cover rather than topographic microclimate, suggesting that small shifts in climate may have little effect on distribution if overstorey cover does not significantly change, whereas loss of overstorey due to increasingly severe or frequent fires could have much more drastic consequences. Facilitative effects of canopy cover may also explain patterns such as persistence of species with ‘cool-adapted’ traits through long-term drying trends (Valiente-Banuet *et al.*, 2006) and the positive effect of forest density on tree regeneration niche (Dobrowski *et al.*, 2015). These results also imply that changes in biotic conditions independent of climate could lead to shifts in distribution and abundance that were not predicted by climate-based models. While information on the prevalence of some biotic variables may be lacking or difficult to obtain, overstorey shading and composition can be mapped with combinations of remote

sensing and surveys (Ohmann and Gregory, 2002), and the resulting data could be used to test for the importance of these biotic conditions in distribution models for understorey species (Joshi *et al.*, 2006).

We found that understorey neighbouring plant cover was higher in low-fertility soils, perhaps due to the greater light availability on serpentine soils, due to lower overstorey cover, and this was associated with positive effects on plant performance. These results are in contrast to the potential for higher competition in milder abiotic conditions (Bruno *et al.*, 2003), such as on higher fertility soils. The positive effects of cover on serpentine soils could also be related to facilitative effects of neighbours in this stressful abiotic environment (Freestone, 2006; Spasojevic *et al.*, 2014); for instance, higher neighbour cover may be associated with increased soil moisture retention due to higher soil organic matter.

Trientalis abundance and occurrence were strongly positively linked to overstorey variables, litter depth and shading by trees. These results suggest that our focal species is shade tolerant, as negative effects of increased overstorey shading were not observed, at least at the levels examined in this study. The positive effects of overstorey vegetation we observed could also be related to the capacity for canopy cover to reduce extremes in microclimate temperature and humidity (Ashcroft and Gollan, 2012) and consistent with our results for leaf traits, which suggested that overstorey shading ameliorated water stress.

We did not observe strong positive effects of symbiotic fungi on plant performance as expected, even on infertile soils. Associations between fungal colonization and plant performance variables, when present, were somewhat negative (arbuscular mycorrhizae and abundance). These results could be due to the symbiotic nature of this biotic interaction – with plants allocating more carbon resources to fungi as plant nutrient or water stress increases (Ruotsalainen and Eskelinen, 2011), and reducing investment in symbiotic fungi under favourable abiotic conditions, leading to a weak relationship between colonization and abundance.

In addition, in contrast to the other biotic conditions we examined, our observations for fungal colonization were limited to the locations where plants occurred and the range of abiotic stress for these presence locations. Despite this limitation, we did find significant relationships between septate fungal colonization and indicators of increased plant nutrient stress (lower foliar P and higher C:N) and a weak tendency for higher septate colonization on serpentine soils. This supports research which shows that dark

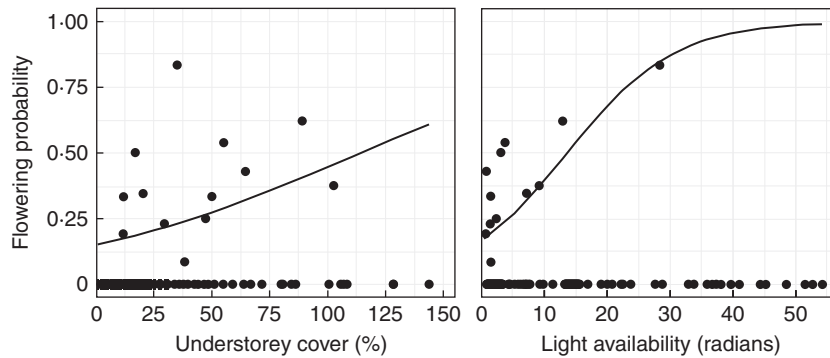


FIG. 7. Plots of significant relationships between biotic variables (understorey cover and light availability) and flowering probability.

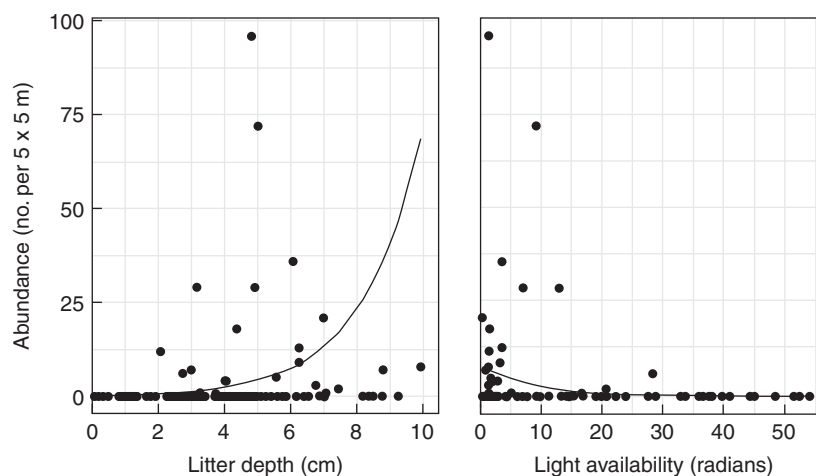


FIG. 8. Plots of significant relationships between biotic variables (litter depth and light availability) and abundance.

septate endophytes may play mycorrhizal (facilitative) roles in environments with high soil toxicity (Postma *et al.*, 2007; Ban *et al.*, 2012) and supports evidence for distinct mycorrhizal communities on low-fertility soils such as serpentine soils (Ji *et al.*, 2010; Doubkova *et al.*, 2012; Schechter and Bruns, 2013).

We found distinct differences in the optimum conditions for abundance of clonal tubers, related to asexual reproduction, and flowering, indicative of plant investment in sexual reproduction. *Trientalis* tended to flower at higher rates in open environments, such as on low-fertility serpentine soils, which could increase the potential for gene flow between populations and formation of distinct genotypes in these conditions (Cosendai *et al.*, 2013). Higher fruit set due to increased pollinator activity has been observed in open environments for a closely related species, *Trientalis borealis* (Anderson and Beare, 1983); a similar effect with *T. latifolia* would tend to further amplify the positive effect of open environments on sexual reproduction. Many other understorey herbaceous species reproduce via both asexual and sexual modes (i.e. stoloniferous plants, Harper, 1977). The relative contributions of sexual and asexual reproduction to recruitment can strongly affect population dynamics and genetic diversity of understorey herbaceous species (Bierzychudek, 1982; Eriksson, 1989). This suggests that differences between optimum

abiotic and biotic conditions for these two reproductive modes could affect distribution patterns and demographic response to changing environmental conditions.

Indicators of plant nutrient status and water use efficiency as indicated by functional traits generally supported the relative importance of biotic conditions. Leaf traits, such as SLA, appeared to provide a mechanistic basis for the relationships between environmental variables and plant performance, and could be more widely sampled to create explicitly mechanistic models (Kearney and Porter, 2009) of plant distribution patterns with respect to biotic and abiotic factors. For example, in this study leaf traits indicated higher resource availability with higher overstorey shading and increased litter depth, suggesting a mechanism for the effects of these variables on plant abundance and occurrence.

Our results are limited by the observational nature of the study and our focus on one model species. However, this focus allows us to include a broad range of abiotic and biotic conditions, from overstorey cover to mycorrhizal colonization, likely to influence our study species and other understorey herbs in this region. Correlations between biotic conditions may also have affected our results, potentially decreasing the power of our statistical tests (Grewal *et al.*, 2004), meaning our results may be relatively conservative. For example, overstorey density directly affects both litter depth and shading, and we cannot

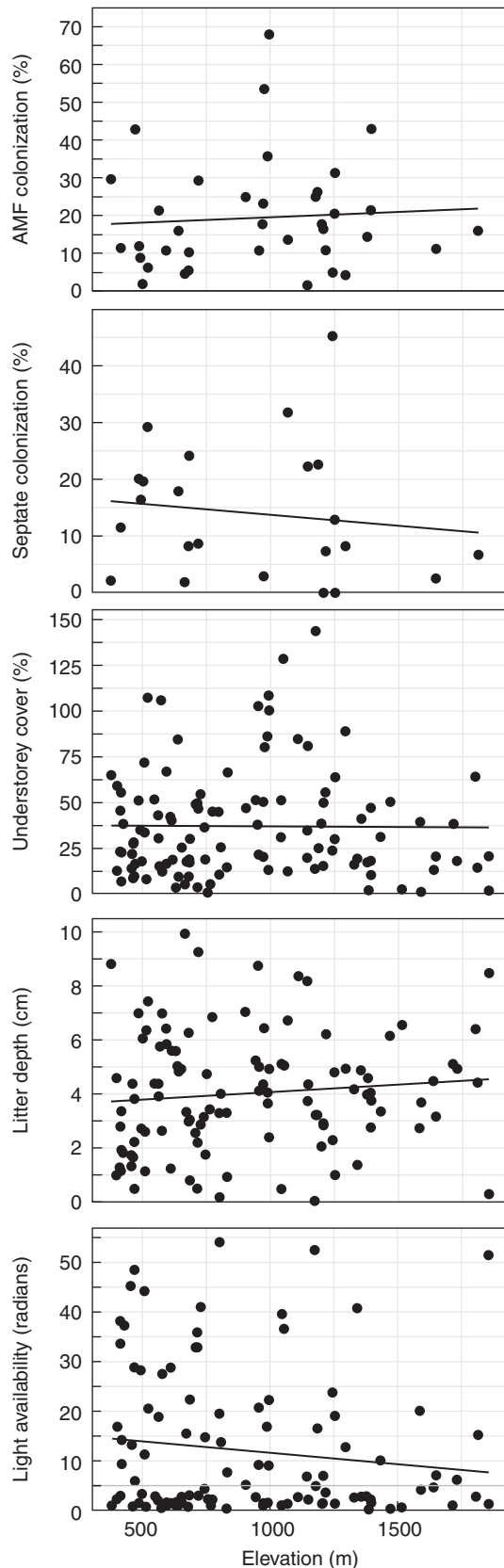


FIG. 9. Plots of elevation and biotic variables.

TABLE 3. Importance values for variables in presence/absence models (generalized linear models, binomial distribution) with and without topographic microclimate, soil and biotic variables

Model	Wilcoxon signed rank test	Variable	Importance
Topographic microclimate only	$W = 1593$ $P = 0.04$	Slope	1.66
		Elevation	0.99
		Beers' aspect	0.07
Soil only	$W = 1610$ $P = 0.01$	Organic matter	2.08
		Phosphorus	0.99
		Serpentine	0.43
Abiotic only: soil & topographic microclimate	$W = 1628$ $P < 0.01$	Organic matter	1.91
		Slope	1.42
		Phosphorus	1.21
		Serpentine	0.37
		Beers' aspect	0.30
		Elevation	0.02
Biotic conditions only	$W = 1761$ $P < 0.01$	Understorey cover	2.61
		Light availability	1.65
		Litter depth	1.34
Topographic microclimate & biotic conditions	$W = 1760$ $P < 0.01$	Understorey cover	2.56
		Light availability	1.51
		Litter depth	1.32
		Slope	0.99
		Beers' aspect	0.51
		Elevation	0.49
Soil & biotic conditions	$W = 1835$ $P < 0.01$	Understorey cover	2.29
		Light availability	1.85
		Litter depth	1.57
		Organic matter	1.44
		Phosphorus	1.38
		Serpentine	0.43
Abiotic & biotic: soil, topographic microclimate & biotic conditions	$W = 1845$ $P < 0.01$	Understorey cover	2.31
		Light availability	1.95
		Litter depth	1.59
		Organic matter	1.57
		Phosphorus	1.57
		Serpentine	0.43

readily separate their effects on plant performance. Despite these limitations, the multiple analysis approaches we employed suggested that several biotic variables have significant direct and indirect effects, which supports the growing evidence that biotic interactions can strongly affect plant distributions across abiotic gradients (Wiszczyńska *et al.*, 2013).

Overall, our results highlight how biotic conditions and soil fertility are strongly associated with regional distribution patterns and may interact with climate-related variables (e.g. Grace *et al.*, 2011). Where biotic conditions significantly interact with and mediate the effects of abiotic variables, models constructed with abiotic variables alone may lack the mechanism for the observed distribution pattern and may overestimate the capacity of changing climates to affect future distributions (Araújo and Luoto, 2007). Models built without biotic conditions could lead to erroneous predictions if the existing correlations between abiotic and biotic conditions (i.e. climate and overstorey cover) shift in response to changing climate.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Table S1: Meta-model used to select combinations of abiotic and biotic variables to

include in mediation tests. Table S2: Meta-models used to select combinations of biotic and plant performance variables to include in mediation tests. Figure S1: structural equation models with significant direct or indirect pathways between soil fertility, overstorey variables (light availability and litter depth) and plant response variables. Figure S2: structural equation models with significant direct or indirect pathways between soil fertility, overstorey variables (light availability and litter depth) and plant response variables. Figure S3: structural equation models with significant direct or indirect pathways between soil fertility, understorey cover and plant response variables. Figure S4: relationships between soil fertility, arbuscular mycorrhizae colonization and abundance with standardized coefficients. Appendix S1: structural equation models, d-separation tests.

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