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Incorporating biotic factors in species distribution modeling: are interactions with soil microbes important?

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It is increasingly recognized that species distributions are driven by both abiotic factors and biotic interactions. Despite much recent work incorporating competition, predation, and mutualism into species distribution models (SDMs), the focus has been confined to aboveground macroscopic interactions. Biotic interactions between plants and soil microbial communities are understudied as potentially important drivers of plant distributions. Some soil bacteria promote plant growth by cycling nutrients, while others are pathogenic; thus they have a high potential for influencing plant occurrence. We investigated the influence of soil bacterial clades on the distributions of bryophytes and 12 vascular plant species in a high elevation talus-field ecosystem in the Rocky Mountain Front Range, Colorado, USA. We used an information-theoretic criterion (AICc) modeling approach to compare SDMs with the following different sets of predictors: abiotic variables, abiotic variables and other plant abundances, abiotic variables and soil bacteria clade relative abundances, and a full model with abiotic factors, plant abundances, and bacteria relative abundances. We predicted that bacteria would influence plant distributions both positively and negatively, and that these interactions would improve prediction of plant species distributions. We found that inclusion of either plant or bacteria biotic predictors generally improved the fit, deviance explained, and predictive power of the SDMs, and for the majority of the species, adding information on both other plants and bacteria yielded the best model. Interactions between the modeled species and biotic predictors were both positive and negative, suggesting the presence of competition, parasitism, and facilitation. While our results indicate that plant–plant co-occurrences are a stronger driver of plant distributions than plant–bacteria co-occurrences, they also show that bacteria can explain parts of plant distributions that remain unexplained by abiotic and plant predictors. Our results provide further support for including biotic factors in SDMs, and suggest that belowground factors be considered as well.

Understanding the drivers of species distributions is a central topic in ecology, and species distribution modeling today is more important than ever for predicting the impacts of climate change on plant and animal populations (Hutchinson 1957, Araújo and Luoto 2007, HilleRisLambers et al. 2013). Recent work has demonstrated that biotic interactions may be essential to incorporate in species distribution modeling, in essence modeling a species' realized niche rather than fundamental niche (Hutchinson 1957, MacArthur 1972, Pulliam 2000, Bruno et al. 2003). A growing number of studies show that adding biotic variables, such as the abundance of competitors or host plants, improves the fit and predictive power of topo-climatic models for both animals (Davis et al. 1998, Araújo and Luoto 2007, Heikkinen et al. 2007, Preston et al. 2008, Hof et al. 2012) and plants (Leathwick et al. 1996, Meier et al. 2010, 2012, Pellissier et al. 2010, Meineri et al. 2012, Giannini et al. 2013, HilleRisLambers et al. 2013). However, these studies have all focused on aboveground interactions among macroorganisms. Given that plant interactions with soil microbes are ubiquitous and often critical for plant survivorship (Wardle et al. 2004, Van der Heijden et al. 2008), vegetation models should incorporate interactions with belowground organisms.

Soil microbes are important drivers of aboveground patterns of vegetation productivity, diversity, community assembly, and community structure (Klironomos 2002, Wardle et al. 2004, Van der Heijden et al. 2008). Thousands of plant species are dependent on microbial symbionts for growth and survival (Van der Heijden et al. 2008), and many plants are also harmed by soil borne microbial pathogens (Jackson 2009). Furthermore, these organisms are not everywhere – fungi and bacteria show

biogeographic patterns based on environmental and biotic variables (Fierer et al. 2009, Lauber et al. 2009, Tedersoo et al. 2014). Thus, in addition to abiotic factors, the distributions of microorganisms could be important drivers of plant distributions. In the only example to date, Pellissier et al. (2013) found that including fungal diversity as a predictor variable improved species distribution models (SDMs) of alpine plants.

Soil bacteria may play a particularly important role in mediating plant species distributions in high elevation alpine habitats, where plants are at the limits of their physical tolerances (Sheng et al. 2011, King et al. 2012). In these habitats, soil is shallow, undeveloped, and low in nitrogen and phosphorus (Aide and Cwick 1998, Seastedt 2001). Bacterial taxa that perform nitrogen fixation, mineralization, immobilization, and nitrification are important in governing plant nutrient availability and may be important facilitators of plant growth (Schmidt et al. 2008). Furthermore, several genera of bacteria can solubilize phosphorus (Rodríguez and Fraga 1999), which may also limit plant growth in these landscapes. Conversely, plants may be especially susceptible to negative interactions when at their distributional limits. Many groups of bacteria are pathogens, parasites, or root herbivores that could hinder plant establishment (Wardle et al. 2004, Sinclair and Lyon 2005, Jackson 2009). Bacteria may also compete with plants for resources, which can be detrimental to plants in nutrient limited systems (Van der Heijden et al. 2008). Overall, bacteria, through these positive and negative relationships with plants, could play a role in determining a plant's realized niche.

Here we incorporate species co-occurrences into species distribution modeling by adding abundances of co-occurring plants and relative abundances of co-occurring bacteria to abiotic distribution models of 12 vascular alpine plants and bryophytes. To our knowledge, no other study has included bacterial clade relative abundances in plant distribution modeling. Our work takes advantage of a rich dataset across an elevation gradient, which previously showed that pH, plant abundance, and snowpack are the primary drivers of the soil bacteria community (King et al. 2010), and demonstrated the presence of species-specific plant–bacteria associations (King et al. 2012). To examine the potential importance of soil bacteria in plant species distribution modeling, we asked two main questions: 1) are bacteria–plant co-occurrences more important than plant–plant co-occurrences in predicting plant species distributions? 2) Does including a combination of three predictor sets – abiotic, plant, and bacteria factors – yield the best distribution model? To address these questions, we used an information-theoretic approach to compare models with various sets of predictor variables.

Methods

Study area and data collection

The study site was the upper Green Lakes Valley (GLV), located in the Colorado Front Range on the south side of the Niwot Ridge Long Term Ecological Research site. The site is a matrix of block slope, late-melting snowbanks overlaying unvegetated gravel soils, fellfields, and small patches of vegetation (King et al. 2010). Soil texture is high in sand content and soil depth is shallow. Precipitation averages 930 mm yr^{-1}, 80% of which falls as snow (Nemergut et al. 2005). Sampling was done in September 2007 and August–September 2008, at locations spanning an elevation gradient of 3635–3935 m. Locations were spaced every 50 m across the landscape (50 plots) except in three targeted 30×30 m areas where they were spaced every 5 m (16 plots) (see King et al. 2010 for more detailed sampling information).

The abiotic factors measured were altitude, pH, soil moisture, snowpack, total phosphorus, inorganic phosphorus, total dissolved nitrogen (TDN), dissolved organic carbon (DOC), and percent sand. Soil samples were collected on 4–8 September, 2007, by homogenizing in situ ~ 100 g of soil at that location to a depth of 5 cm and then scooping 50 g of soil into a new sealable plastic bag. Soils were stored at 4°C for a maximum of 1 week while TDN and DOC measurements were taken, and then stored at –20°C. Altitude measurements are from a Garmin eTrex Vista gps (Garmin International). Soil pH was measured from a slurry of 2 ml water and 2 g soil, shaken for 1 h. Soil moisture was measured gravimetrically. Snow depth values at each point are from kriging interpolations of snow surveys in the GLV from 1997 to 2003 (Niwot Ridge LTER, <http://culter.colorado.edu/exec/Database/gis_layer_query.cgi>). Soil texture analysis was done for samples collected in September 2008 in the South Dakota Soil Laboratory (South Dakota State Univ., Brookings, SD, USA). Plants were identified based on Webber and Whittmann (2001) and abundances were based on exhaustive stem counts of 1 m radius plots established in August 2008 around the location where soil was sampled (King et al. 2012). Although the plant and soil texture surveys were done a year later than the original bacterial sampling, we expect little year-to-year variation in these measures. To focus on locations recently colonized by plants and to limit circularity in our models by avoiding plots where the microbial community is more strongly influenced by plants, only plots with < 100 stems were included in the analysis ($n = 66$; Supplementary material Appendix 1, Fig. A1), a subset of previously studied sites (King et al. 2012, $n = 76$). The majority of plots had fewer than 100 stems, while several plots from our previous work (King et al. 2012) that had well over 100 stems were removed.

For the bacterial community assessment, DNA was extracted from 1 g of soil using a MO BIO PowerSoil DNA Isolation Kit (MO BIO Laboratories) and PCR was used to amplify the V1–V2 hypervariable region of the bacterial 16S SSU ribosome gene using 27F and 338R primers following the methods of Fierer et al. (2008). Sequencing was performed on the Roche 454 platform using FLX chemistry. Raw sequence data were processed using the methods of Hamady et al. (2010), resulting in 6151 representative Operational Taxonomic Units (OTUs) at 3% similarity with 10 000 total reads and an average of 200 (ranging from 50 to 1073) reads per sample (King et al. 2012). Data were not rarefied and the Good's coverage was 0.65. While this coverage is sparse, we focused on the relative abundance of family to phylum level clades (Supplementary material Appendix 2, Table A2), and did not do any analyses of diversity or rare OTUs. Clades were defined by selecting all nodes on the full community tree that aggregated at least 100 sequences,

which resulted in 22 clades. To further minimize the inclusion of bacteria that are influenced by plant abundance in the SDMs, we removed the seven clades that were significantly correlated (Kendall's tau, $p < 0.05$) with total stem count, leaving 15 clades to be included in the modeling analyses. Relative abundances (Supplementary material Appendix 2, Table A2) were calculated by dividing the number of each OTU's sequence reads by the total number of sequences in a sample. More details about the bacterial community analysis can be found in King et al. (2010, 2012).

Modeling

Models of plant presence/absence were constructed in the generalized linear model (GLM) framework with a logit link and binomial distribution. We modeled presence/absence to focus on plant colonization and establishment in the subnival talus. The plants selected for the modeling analysis ($n = 13$) were present in at least 9 of the 66 plots we analyzed; those that were found in fewer than 9 plots were not modeled but were included as predictors for the modeled species. A SDM built on data from less than 9 sites likely would not accurately reflect a plant's niche, and a cutoff greater than 9 would have limited the number of modeled species. Previous work used 10 occurrences as a cutoff for their modeled species (Pellissier et al. 2013). On average, our modeled species were present in 21 of 66 sites. Abiotic factors were included as the baseline model for all models and biotic factors were added in addition to abiotic factors. For each species, four models were constructed: one with abiotic factors (ABIOT), one with abiotic and plant factors (ABIOT + PLANT), one with abiotic and bacteria factors (ABIOT + BACT), and one with all three predictor sets (FULL; Fig. 1). The order of variable input for the FULL model was abiotic factors, then plants, then bacteria. The direction of the association (positive or negative) with a factor was inferred by the sign of the coefficient in the model.

For each species, the best combination of abiotic factors was selected using an exhaustive all subsets method (package bestglm, McLeod and Xu 2014) with the Akaike information criterion (AIC; Akaike 1974) as the selection criterion. We then calculated the corrected Akaike information criterion (AICc, Sugiura 1978, Burnham and Anderson 2002) and performed AICc selection on the AIC selected variables (bestglm does not include AICc as an option). We used the AICc because of the small sample size and relatively large number of parameters ($n/K < 40$; Burnham and Anderson 2002). For the ABIOT + PLANT model, the abundances of neighbor plant species (rare or modeled species) were added as predictors using the forward/backward stepwise method, using AICc as the criterion. The same was done for bacteria clades to yield the best fit ABIOT + BACT model. For the FULL model, bacteria clades were added to the ABIOT + PLANT model using the forward/backward stepwise method and AICc selection.

We evaluated our models with several different metrics. To assess the amount of variance explained by each model, we calculated the adjusted D^2 value (package ModEvA, Barbosa et al. 2014). In likelihood methods, the D^2 value is the amount of variance explained by the model, and the adjusted D^2 value takes into account the number of predictor variables in the model and allows for direct comparison between models (Guisan and Zimmerman 2000, Meier et al. 2010). Nagelkerke's pseudo R^2 value was also calculated, but will not be presented as it yielded the same results as the adjusted D^2 (Nagelkerke 1991, Field et al. 2012). To examine the redundancy of the biotic predictor sets (Meier et al. 2010), the joint D^2, or the amount of overlap in the deviance explained by plants and bacteria (Fig. 1), was calculated by subtracting the D^2 value of the ABIOT model from that of the ABIOT + BACT model, subtracting the D^2 value from the ABIOT + PLANT model from the FULL model, and taking the difference of these two values $((D^2_{\text{ABIOT + BACT}} - D^2_{\text{ABIOT}}) - (D^2_{\text{FULL}} - D^2_{\text{ABIOT + PLANT}}))$. To determine if bacteria improved models for certain types of plants more than others, we compared the D^2 attributed to bacteria ($D^2_{\text{ABIOT + BACT}} - D^2_{\text{ABIOT}}$) by plant elevation average and functional group and whether the plant was a talus specialist or tundra generalist (Supplementary material Appendix 3, Table A3). We considered *Carex nardina*, *Carex phaeocephala*, *Cirsium scopulorum*, *Oxyria digyna*, and *Senecio fremontii* to be talus specialists, whereas the other species are all commonly found in intact tundra locations at Niwot Ridge (Spasojevic and Suding 2012) or are known to have broad ranges in many habitats (Harberd 1961, Berg et al. 1997). We evaluated model accuracy internally by 10-fold cross-validation. There was no external data set for an external validation of the models. For some of the more rare species, some (no more than 4) of the runs resulted in errors because of no presence. Model predictive power was assessed with the area under the receiver operating characteristic curve (area under the curve, AUC). The AUC value is a description of the predictive power of the logistic regression model in that it is a measure of the rate of false positives and negatives and rate of true positives and negatives, while the adjusted D^2 is a measure of the amount of variance the model explains. Lastly, for each modeled plant, the four models were compared with Akaike weights, which are the probabilities that each model

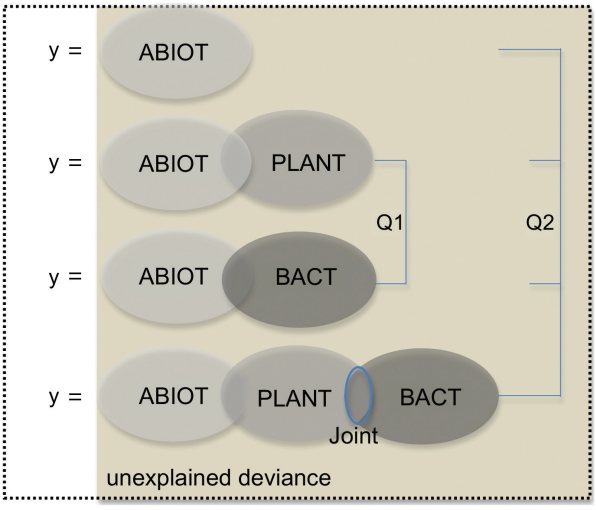

Figure 1. Conceptual diagram of the modeling approach and questions asked. Circles represent the deviance explained by the predictor set and joint is the overlap in deviance explained by plants and bacteria. Adapted from Legendre (1993) and Meier et al. (2010).

was the best predictor of the data. The highest Akaike weight is the most probable best model (Burnham and Anderson 2002).

The models were tested for independent errors using the Durbin–Watson test and for multicollinearity using VIF statistics (Supplementary material Appendix 4, Table A4, Field et al. 2012). All statistical analyses were performed with the software R (ver. 3.1.2, R Core team).

Results

According to all four of our criteria for assessing alternative models, incorporating biotic interactions was important to understand plant species occurrences; biotic interactions increased model fit (AICc, Akaike weights), deviance explained (adjusted D^2), and predictive power (AUC). For all 13 plants, the best fit model included abiotic predictors plus plant predictors, bacterial predictors, or both (AICc, Akaike weights, Table 1). The best fit model substantially increased both the explained deviance (mean increase in adj. $D^2 = 0.19$, Fig. 2), and predictive power (mean increase in AUC = 0.09) compared to the ABIOT model, demonstrating the increased explanatory power and accuracy of models including biotic factors.

Including abiotic, plant, and bacteria variables (the FULL model) outperformed the other models for the majority of plants (Table 1). The FULL model had the highest predictive power (AUC) for all plants we analyzed, and it generally explained the most variance in the dataset (adjusted D^2, 12 of 13 plants) and was the best fit (AICc) and most likely the best prediction of the data (Akaike weights, 9 of 13 plants). Inclusion of bacteria abundances did not improve our ability to describe the occurrences of two plants (*Carex nardina* and *Festuca rubra*): the ABIOT + PLANT model was the best fit model. For two other plants, (*Kobresia myosuroides* and *Senecio fremontii*), inclusion of plant variables was not important: the ABIOT + BACT model was the best fit model. Considering abiotic factors alone (the ABIOT model) was never superior to the inclusion of biotic factors.

Some of the focal plant species more strongly associated with other plant species while other focal plant species more strongly associated with bacteria (ABIOT + PLANT versus ABIOT + BACT model comparisons, Table 1). Overall, plant–plant co-occurrences appeared to be somewhat more important than plant–bacteria co-occurrences: for over 60% of the plant species, the ABIOT + PLANT models were better fit (9 of 13 plants) and explained more deviance (8 of 13 plants) than the ABIOT + BACT model. However, there were several cases where metrics of model performance gave differing indications of the superior model (*Carex phaeocephala*, *Trisetum spicatum* and bryophytes), indicating that there were only subtle differences between the importance of the plant and bacteria variables. Growth form did not help clarify the patterns across species; the ABIOT + PLANT model had a better fit in 5 of 7 graminoids and 3 of 5 forbs.

Plant species exhibited strong associations with abiotic variables, indicating filtering along elevation, growing season, moisture, and nutrient gradients (Supplementary material Appendix 5, Table A5). For many of the plant species we analyzed, variation in snowpack and elevation were important factors. A distinct group of species was more likely to occur at high elevation (*Carex nardina*, *Festuca rubra*, *Silene acaulis*, bryophytes), while others were more likely to occur at lower elevations (*Kobresia myosuroides*, *Cirsium scopulorum*). Similarly, some plants occurred more frequently in high snowpack areas (*C. nardina*, *Oxyria digyna*, bryophytes), while others preferred less snowpack (*Elymus scriberneri*, *Trisetum spicatum*, *C. scopulorum*, *S. acaulis*). The distribution of some species was also influenced by soil moisture, DOC, total phosphorus and inorganic phosphorus, pH, total dissolved nitrogen, and percent sand. For instance, some plant species tended to occur in areas with high DOC (*C. nardina*, *Geum rossii*, *S. acaulis*) or high pH (*Deschampsia cespitosa*, *O. digyna*, *Senecio fremontii*), two variables that had consistently positive relationships with the modeled plants (Supplementary material Appendix 5, Table A5).

Neighboring plant species both positively and negatively co-occurred with the focal plant species. Of the 31 co-occurrences we identified, a little over half (58%) were positive (Supplementary material Appendix 6, Table A6). Several focal species (sedges *Carex nardina* and *Carex phaeocephala*, forb *Geum rossii*) were more likely to occur with other plant species. On the other hand, two of the talus specialists (*Oxyria digyna*, *Senecio fremontii*), as well as moss, were less likely to occur in association with other plant species. A group of forb species (*Angelica grayi*, *Geum rossii*, *Hymenoxis grandiflora*) most frequently had positive co-occurrence patterns with the modeled plants. In contrast, several graminoid species (*Carex phaeocephala*, *Festuca rubra*, *Kobresia myosuroides*) had the most negative associations with the modeled plants, although each of these species was also positively associated with some focal plant species as well.

Bacteria also both positively and negatively co-occurred with the focal plant species. Of the 28 co-occurrences we identified, slightly over half (53%) were positive (Table 2). Five bacterial clades had positive relationships with some plant species and negative relationships with other plant species, indicating diverse and species-specific co-occurrence patterns. However, several clades (the three Acidobacteria groups and Deltaproteobacteria) frequently and consistently exhibited positive associations with plants. These clades include some of the more abundant clades (Deltaproteobacteria) as well as some of the more rare clades (Acidobacteria Gp3) that were analyzed (Supplementary material Appendix 2, Table A2). We also identified several clades (Burkholderiales, Oxalobacteraceae, Rhodospirillales) that most frequently had negative associations with plants.

The majority of the clades tested in the analysis (13 of 15), including both the most abundant and most rare clades improved the SDM for at least one plant; only Clostridiales and Rubrobacteraceae did not improve any of the SDMs. Clostridiales and Rubrobacteraceae were two of the more rare clades included in the analyses. TM7, however, was the rarest clade included in the analysis, and improved the SDMs of two plants. The relative abundances of the most important clade for each plant (clade that most improved AICc, Fig. 3) were significantly correlated with the predicted probability of occurrence of the plant for 8 of 12 vascular plants (Kendall's tau, $p < 0.05$, Fig. 3).

The amount of deviance explained shared by plants and bacteria in the FULL model was only 0.017. This

Table 1. Comparison of model fit (AICc, Akaike weights), deviance explained (D^2, adjusted for the number of predictor variables), and predictive power (AUC) for the four models. Bolded values are the lowest AICc, and highest Akaike weight (multiplied by 100), D^2, and AUC values.

Plant	Model	AICc	Akaike weight	Adjusted D^2	AUC
Carex nardina	ABIOT + PLANT	**69.1591**	**53.93**	0.401	0.9190
	FULL	69.5050	45.36	**0.425**	**0.9259**
	ABIOT + BACT	78.4370	0.52	0.233	0.8507
	ABIOT	80.4296	0.19	0.171	0.8293
Carex phaeocephala	FULL	**48.5399**	**41.69**	**0.287**	**0.8804**
	ABIOT + PLANT	49.2826	28.76	0.241	0.8446
	ABIOT + BACT	49.9701	20.39	0.199	0.8482
	ABIOT	51.5697	9.16	0.143	0.7821
Deschampsia cespitosa	FULL	**69.0363**	**92.82**	**0.304**	**0.8812**
	ABIOT + PLANT	74.6818	5.52	0.192	0.8223
	ABIOT + BACT	77.3984	1.42	0.175	0.8037
	ABIOT	80.8759	0.25	0.099	0.7407
Elymus scriberneri	FULL	**44.7362**	**38.87**	**0.316**	**0.8928**
	ABIOT + BACT	45.2885	29.49	0.237	0.8499
	ABIOT + PLANT	46.3103	17.69	0.217	0.8265
	ABIOT	46.7872	0.25	0.177	0.8051
Festuca rubra	ABIOT + PLANT	**74.9179**	**63.09**	0.307	0.8765
	FULL	76.4520	29.30	**0.310**	**0.8728**
	ABIOT	80.2030	4.49	0.165	0.7677
	ABIOT + BACT	80.9339	3.12	0.170	0.7696
Kobresia myosuroides	ABIOT + BACT	**69.3965**	**38.80**	0.111	0.7425
	FULL	69.5209	36.46	**0.147**	**0.7875**
	ABIOT	71.6094	12.83	0.063	0.7038
	ABIOT + PLANT	71.7590	11.91	0.077	0.7263
Trisetum spicatum	FULL	**78.3555**	**47.31**	**0.240**	**0.8546**
	ABIOT + PLANT	79.7835	23.17	0.190	0.8299
	ABIOT + BACT	79.8116	22.84	0.190	0.8285
	ABIOT	82.2695	6.68	0.135	0.7796
Cirsium scopulorum	FULL	**43.3514**	**89.34**	**0.656**	**0.9728**
	ABIOT + PLANT	48.6046	6.46	0.555	0.9543
	ABIOT + BACT	49.9694	3.27	0.511	0.9467
	ABIOT	52.4776	0.93	0.433	0.9152
Geum rossii	FULL	**50.1202**	**61.81**	**0.405**	**0.9256**
	ABIOT + PLANT	51.1933	36.15	0.312	0.8678
	ABIOT + BACT	58.2956	1.04	0.153	0.8281
	ABIOT	58.3605	1.00	0.124	0.7818
Oxyria digyna	FULL	**41.9309**	**53.06**	**0.654**	**0.9753**
	ABIOT + BACT	43.3568	26.01	0.592	0.9643
	ABIOT + PLANT	44.2358	16.76	0.543	0.9451
	ABIOT	47.0146	4.18	0.437	0.9121
Senecio fremontii	ABIOT + BACT	**66.1767**	**70.46**	**0.320**	0.8760
	FULL	68.0320	27.87	0.316	**0.8810**
	ABIOT + PLANT	74.4281	1.14	0.189	0.8016
	ABIOT	75.9411	0.53	0.158	0.7798
Silene acaulis	FULL	**36.5904**	**91.29**	**0.732**	**0.9840**
	ABIOT + PLANT	41.5426	7.67	0.606	0.9681
	ABIOT + BACT	45.6006	1.01	0.467	0.9260
	ABIOT	52.8054	0.03	0.293	0.8824
Bryophytes	FULL	**81.5441**	**41.87**	**0.191**	**0.8074**
	ABIOT + PLANT	82.4269	26.93	0.165	0.7825
	ABIOT + BACT	82.6510	24.07	0.163	0.7935
	ABIOT	85.0860	7.13	0.110	0.7336

corresponds to only a 20% overlap between plant and bacteria contributions to the variance explained. There was no significant relationship between the deviance explained attributed to bacteria and the elevation average of the plant (Spearman's rho = –0.09, $p > 0.05$). There were marginally significant trends of higher deviance explained attributed to bacteria in forbs (mean = 0.12) than in graminoids (mean = 0.06, T-test, $t = 2.30$, $p = 0.07$) and in talus specialists (mean = 0.10) than in tundra generalists (mean = 0.06, Wilcoxon signed rank test, $W = 26$, $p = 0.09$).

Discussion

Consistent with many recent studies across a range of systems and interaction types, we find strong evidence for the

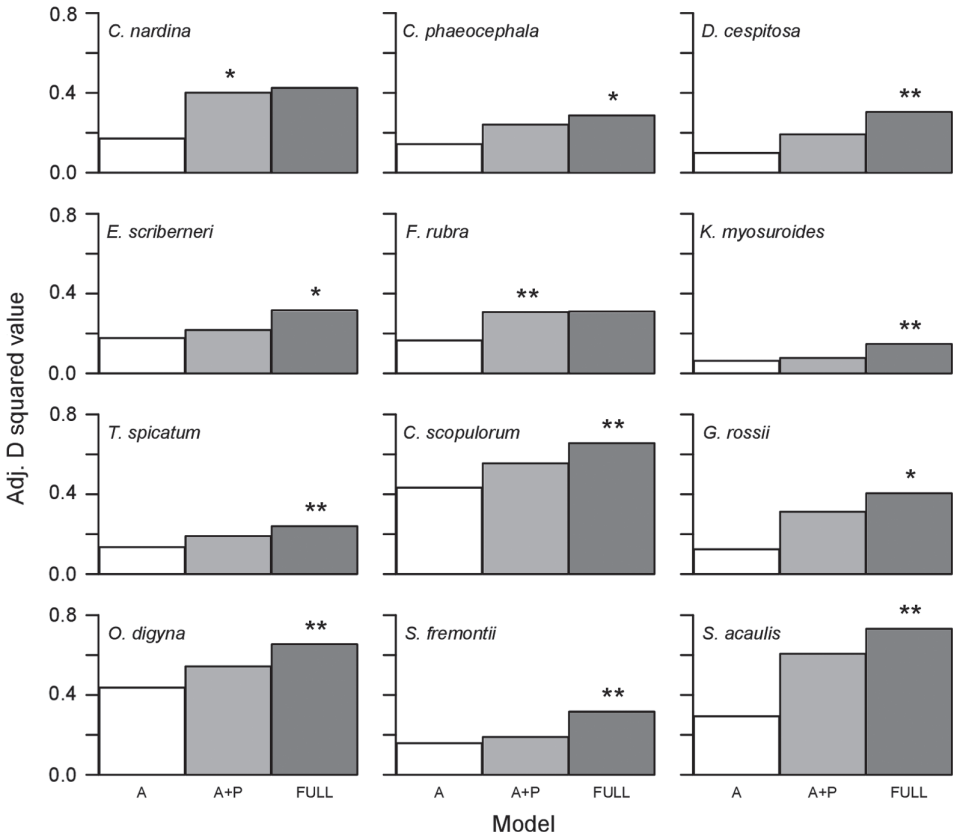

Figure 2. Deviance explained (D^2 values, adjusted for the number of predictor variables) by the model for the 12 modeled vascular plant species with three different sets of predictor variables (A = abiotic factors, A + P = abiotic and plant factors, FULL = abiotic, plant, and bacteria factors). Asterisks indicate the model with the highest Akaike weight (2 asterisks indicate weights > 2 times higher than the next best model; note that for *K. myosuroides* and *S. fremontii*, ABIOT + BACT was even better than FULL). For bryophytes (not included) the FULL model had the highest adj. D^2 and Akaike weight.

importance of biotic factors in species distribution modeling. Including neighbor plants or bacteria as predictors improved the models for all focal plant species. Furthermore, incorporating both plant–plant and plant–bacteria associations (the FULL model), generally had the best fit, most deviance explained, and greatest predictive power of all the models.

Comparing models including plant–plant associations versus models including plant–microbe associations, we found that neighbor plant species were more predictive of plant species distributions than bacterial associations: however, this was not the case for all species, and for several species the inclusion of bacterial associations was as predictive as neighbor plant species. The superior performance of the model with both plant and bacteria variables shows that even after accounting for abiotic factors and other plants, bacteria still explained a substantial part of the remaining variance and improved the model's ability to accurately predict presence or absence. Furthermore, the overlap in the plant and bacteria contributions to the variance explained was small (20%), suggesting that bacteria explain a substantial and distinct part of plant distributions that neighboring plants do not.

Thirteen different bacteria clades improved distribution models for at least one plant. The almost equal prevalence of both positive and negative associations, illustrates the various ways in which bacteria can interact with plants (Table 2), and confirms previous work showing the presence of positive plant–microbe interactions in alpine and subnival systems (Sheng et al. 2011, King et al. 2012). Positive associations may be due to either mutualistic relationships, microbes facilitating plants, plants facilitating microbes, or shared responses to an unmeasured environmental variable (Pellissier et al. 2013). Because our focus was on the influence of microbes on plant distributions, we removed bacterial clades significantly correlated with total plant abundance and did not include occurrences for plots with high plant density. Negative associations may represent antagonistic interactions initiated by either the plant or the microbe, or different responses to an unmeasured environmental gradient (Pellissier et al. 2013).

Information on bacteria function can guide the interpretation of why bacteria improved vegetation SDMs, although for many clades function remains unknown. Groups from the Acidobacteria were some of the most common bacteria that improved plant SDMs. Acidobacteria are an abundant and functionally diverse group of bacteria (Bryant et al. 2007), so it is not surprising that there were positive and negative associations with plants, but it remains unknown exactly how these bacteria interact with plants. Previous work in high elevation unvegetated soils has described an active and diverse microbial community with clades capable of N-fixation and P-mobilization (Nemergut et al. 2007, King et al. 2008, Schmidt et al. 2008). There were several

Table 2. Bacteria clades that improved plant distribution models, with the number and type of associations with the modeled plants, and information on plant symbioses and metabolism. Note that information is for some taxa in the clade, but does not reflect the entire diversity of functions that could be present in a clade. carpha = *Carex phaeocephala*, desces = *Deschampsia cespitosa*, elyscr = *Elymus scriberneri*, silaca = *Silene acaulis*, carnar = *Carex nardina*, fesrub = *Festuca rubra*, kobmyo = *Kobresia myosuroides*, oxydig = *Oxyria digyna*, senfre = *Senecio fremontii*, geuros = *Geum rossii*, circso = *Cirsium scopulorum*, trispi = *Trisetum spicatum*.

Clade	+	Plant	–	Plant	Plant symbiosis	Symbiosis location	Metabolism	References
Acidobacteria Gp1	3	carpha, desces, elyscr	1	silaca	Unknown		Unknown	Lee et al. (2006)
Acidobacteria Gp3	3	carnar, fesrub, kobmyo	0		Unknown		Unknown	Lee et al. (2006)
Acidobacteria Gp7	2	desces, oxydig	0		Unknown		Unknown	Lee et al. (2006)
Actinomycetales	1	silaca	0		N-fixation	Endophytic, roots	N-fixation, heterotrophy	Benson and Sylvester (1993)
Burkholderiales	0		2	senfre, silaca	N-fixation, P-mobilization, pathogenic	Intra/extracellular, roots, stems	Heterotrophy, endosymbiont	Compant et al. (2008), Rodríguez-Díaz et al. (2008)
Cyanobacteria	0		1	geuros	Growth promoting, N and C	Extracellular, roots, stems, leaves	Phototrophy, N-fixation, heterotrophy	Meeks (1998), Adams et al. (2013)
Deltaproteobacteria	3	circso, geuros, oxydig	1	elyscr	Unknown		Heterotrophy, S-reduction, Fe reduction	Brenner et al. (2005)
Ktedonobacteraceae	0		1	senfre	Unknown		CO-oxidation	Webber and King (2010)
Oxalobacteraceae	1	senfre	2	fesrub, bryophytes	Potential pathogen	Roots, seeds, xylem	Heterotrophy	Green et al. (2007), Monteiro et al. (2008), Ofek et al. (2012)
Pseudonocardiaceae	1	trispi	1	oxydig	N-fixation	Endophytic, roots	Heterotrophy, S-oxidation, N-fixation	Reichert et al. (1998), Chen et al. (2009)
Rhodospirillales	0		2	carnar, bryophytes	N-fixation, P-mobilization	Extracellular, endophytic, leaves, stems, roots	Heterotrophy, phototrophy, N-fixation, S-reduction	Madigan (2005), Rodríguez-Díaz et al. (2008)
Sphingomonadaceae	0		1	kobmyo	Indole-3-acetic acid	Rhizosphere	Heterotrophy, phototrophy	Kosako et al. (2000), Tsavkelova et al. (2007), Kumar et al. (2012)
TM7	1	trispi	1	circso	Unknown		Heterotrophy, unknown	Podar et al. (2007)
	15		**13**					

such clades present at our site, but surprisingly, some of these clades had negative relationships with plants (Table 2). This could be due to plants negatively affecting bacteria that are adapted to plant-free landscapes (Knelman et al. 2012) or possible pathogenic functions in the clade. For example, Rhodospirallales, the most abundant clade at our study site, are negatively correlated with plant abundance likely due to light competition (King et al. 2010). Given some previous work on cyanobacteria–plant symbioses (Meeks 1998, Adams et al. 2013), it is surprising that the cyanobacteria only improved the SDMs for one species – *Geum rossii* – and the effect was negative. Depending on how much nitrogen the cyanobacteria fix, the negative association with *Geum* could be due to the negative impact of higher soil nitrogen levels on *Geum*. Previous work near our site showed that *Geum* declined with nitrogen additions with and without the presence of its co-dominant *Deschampsia cespitosa* (Suding et al. 2008, Farrer et al. 2013). Actinomycetales were positively associated with *Silene acaulis*, likely because some taxa in the Actinomycetales (notably *Frankia*) are N-fixers that can colonize plant roots and form mutualisms with a wide range of host plants (actinorhizal plants), including tundra plants (Benson and Sylvester 1993).

If bacteria taxa abundance influences plant species distributions, it would be useful to determine if they influence certain types of plants more than others. Pellissier et al. (2013) showed that the deviance explained by the fungal diversity in alpine plant SDMs increased as the elevation average (average elevation of where a plant is found at a site) of the plants increased, suggesting that soil microbes may be more important for plant establishment and survivorship in harsher locations. In our analyses, the amount of deviance explained by bacteria (adj. $D^2_{ABIOT + BACT}$ – adj. D^2_{ABIOT}) was not correlated with the average elevation of the plant species (Spearman's rho = –0.09, $p > 0.05$). One potential reason for this lack of correlation is that our plants' elevation averages did not vary much within this dataset – there was only a 95 m difference between the averages in the highest

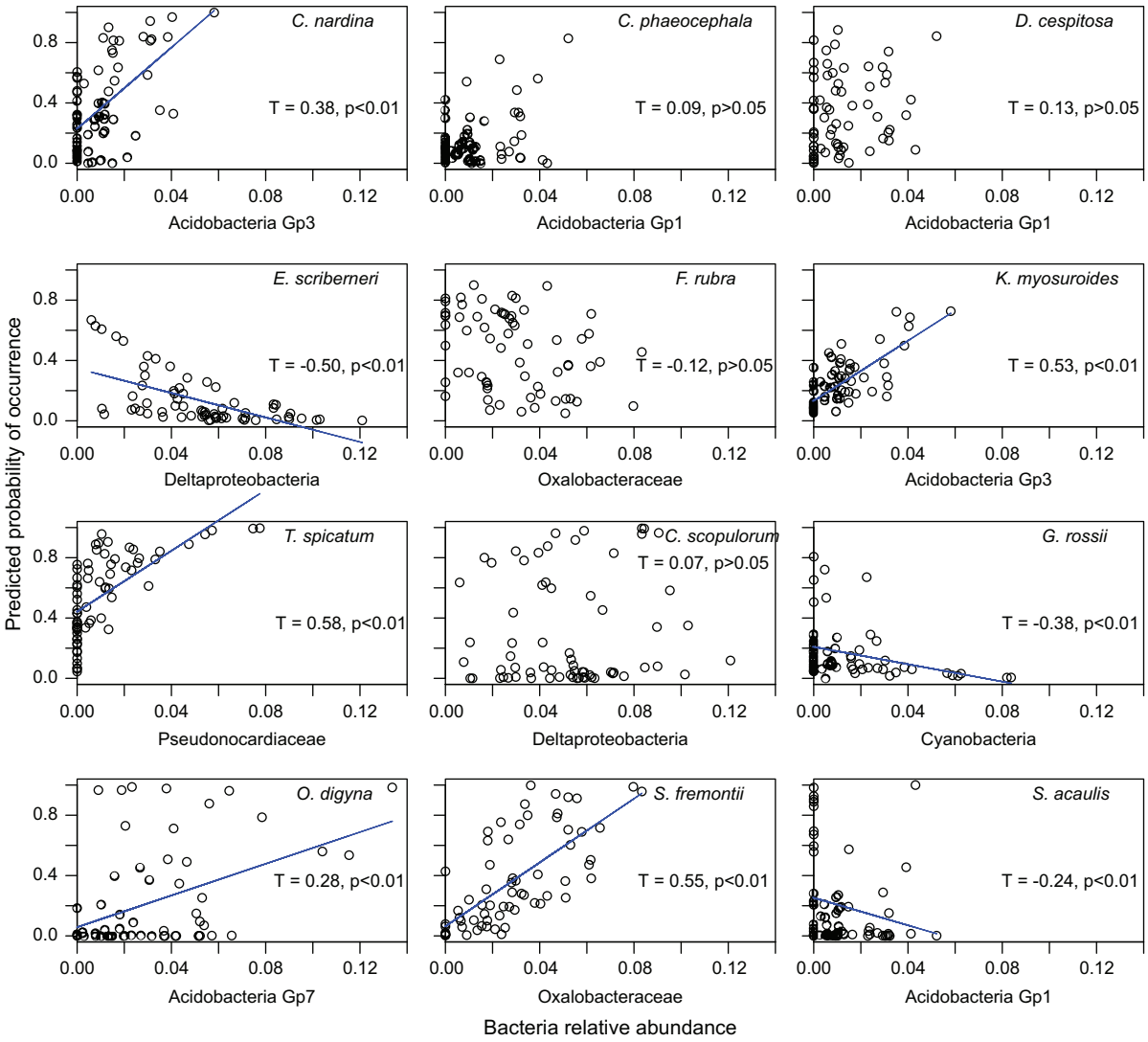

Figure 3. Correlations between the relative abundances of bacteria clades and the plants' predicted probability of occurrence from the ABIOT + BACT model. The clades shown are the clades that most improved the AICc value of the model for each plant. Correlation coefficients and significance levels are from Kendall's tau rank correlation test.

and lowest elevation species. However, many of the plant species in this analysis are abundant at lower elevation sites not included in this survey. The strength of plant–bacterial associations might indeed dissipate if lower elevations were surveyed.

We largely found species-specific, rather than functional group-specific, interactions with bacteria clades (Table 2, Bezemer et al. 2006, King et al. 2012). A trend towards more dependence on bacteria in forbs compared to graminoids may suggest that forbs are more strongly influenced by microbial symbionts or pathogens than are graminoids. In a tallgrass prairie, mycorrhizal colonization in forbs is greater than in cold season C_3 grasses (Wilson and Hartnett 1998) and this pattern may extend to bacterial root symbionts as well. Lastly, talus plant specialists appeared to be more dependent on bacteria than tundra generalists, consistent with our expectation that soil microbes may play a particularly important role in governing where colonizers establish in the largely unvegetated talus (King et al. 2012).

Plant–plant co-occurrences are added to distribution models to account for competitive or facilitative interactions or shared environmental tolerances that affect species occurrence (Leathwick et al. 1996, Meier et al. 2010, Pellissier et al. 2010). We found many positive (18) and some negative (13) relationships among plants in our SDMs. These relationships may be indicative of competitive and facilitative interactions, or they may represent unmeasured abiotic gradients to which the focal species is responding. In the harsh, windswept, sparse habitats of the subnival zone, plant establishment is difficult, so it is likely that some of the positive associations are due to facilitation (Brooker and Callaghan 1998, Dormann and Brooker 2002). For example, *Silene acaulis* and moss positively affected two plant species distributions, and cushion plants and moss are generally known to facilitate establishment in the tundra (Arroyo et al. 2003, Freestone 2006, Cavieres et al. 2007). Cushion plants can ameliorate extreme soil temperatures and improve soil moisture (Arroyo et al. 2003, Cavieres et al. 2007)

and moss can improve seed retention and moisture levels, stabilize sediment, and protect seeds from consumers (Freestone 2006). *Angelica grayi* positively affected three plant distributions, which could be due to a nursing effect. *Angelica grayi* is a large alpine plant, and could facilitate other plants' establishment by providing shelter or contributing to soil development and fertility (Callaway 1995). Some negative associations are probably due to different responses of species to unmeasured abiotic gradients, since competitive exclusion in this habitat is unlikely. Although soil texture and moisture were measured, other factors such as soil depth were not. Furthermore, plants can also represent an integration of abiotic factors throughout the year, while our soil moisture measurement only represents one time point in the year. For example, *Deschampsia cespitosa* prefers moist, wet environments (Walker et al. 2001) while *Senecio fremontii* specializes in rocky, shallow soils (Mooney and Billings 1961), thus a negative correlation between them is likely due to differing environmental preferences that were not well explained by our environmental measures. Other studies incorporating plant–plant interactions for many modeled species found more negative relationships than positive ones (Meier et al. 2010, Pellissier et al. 2010). If our models reflect species interactions, the higher prevalence of positive associations would be consistent with other research that has shown that facilitation is more common than competition in harsh environments (Brooker and Callaghan 1998, Choler et al. 2001, Callaway et al. 2002, King et al. 2012). A next step would be manipulative experiments to determine the nature of positive associations and the role of species interactions.

Limitations

A key limitation to our work is that our approach was correlative and we cannot conclude that co-occurrences are interactions. Experimental manipulations are necessary to understand if species interactions are the mechanism by which SDMs are improved by including abundances of co-occurring species. A combination of field and greenhouse experiments that involve growing plants with different microbial inoculations would be useful to examine the effects of certain microbes on plant growth and survivorship. Additionally, growing plants with different microbes in growth chambers would allow researchers to test specific hypotheses about the role of microbes in enhancing plant tolerance to stressors such as freezing, drought, and low nutrients. Co-occurrence models such as those we have presented here provide strong data for choosing specific plants and bacteria on which to do experiments to test such hypotheses.

One limitation to incorporating soil microbes into plant SDMs is the lack of knowledge of the function of soil bacteria. For some clades we simply lack knowledge of function altogether (Table 2), while for others we are limited by taxonomic resolution (Pellissier et al. 2013). For some clades we infer function based on example taxa in the clade (Table 2), but because of the broadness of the resolution (family to order level) we cannot conclude for certain the function of each of the clades and how their relative abundances influence plant distributions.

A last key caveat in our approach and in other studies where there are positive biotic interactions shaping distributions is the problem of circularity. While the bacteria at our site are primarily structured by soil pH, plant abundances are also an important factor structuring the microbial community (King et al. 2010). Thus, plant–microbe interactions can work in both directions, even for clades not significantly correlated with total stem count. Previous work near our site and elsewhere has shown that the microbial community is active and diverse at the highest elevations above the limit of plant life (King et al. 2008, Schmidt et al. 2008), which suggests that some of the clades included in our modeling were present before plant colonization of our site. Microbes that are present in unvegetated locations may be important for facilitating plant colonization (Schmidt et al. 2008). More work is currently being done at our site to tease apart the temporal relationship between plant and bacteria establishment in new locations, which will help inform us of the direction of plant–microbe interactions in shaping new distribution patterns. Our findings support those of Pellissier et al. (2013) in showing that soil organism data enhance the power of plant SDMs, further highlighting the need for manipulative field experiments to inform the causality behind such models of plant interactions with soil microbes.

Conclusions

Our work provides strong evidence that incorporating biotic factors into SDMs can improve the models. Biotic factors can improve SDMs by explaining unmeasured abiotic gradients or through interactions that actually influence the range of the modeled species. Building on the work of Pellissier et al. (2013), our results suggest that soil microbes can enhance distribution models of vegetation by improving model fit, deviance explained, and predictive power. As sequencing costs continue to decline, more microbial datasets are becoming available that can be of use for plant ecologists. While biotic interactions can be important even at macro scales (Araújo and Luoto 2007), the incorporation of soil microbes into vegetation distribution modeling will be most feasible, and likely most important, at small scales. Our work can be expanded into other systems to discover more about which bacteria have important associations with plants, and which types of plants are more affected by soil microbes than others.

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Supplementary material (Appendix ECOG-01797 at <www.ecography.org/appendix/ecog-01797>). Appendix 1–6.

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