

# Divergent plant–soil feedbacks could alter future elevation ranges and ecosystem dynamics

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**Plant–soil feedbacks (PSF) are important interactions that may influence range dynamics in a changing world. What remains largely unknown is the generality of plant–soil biotic interactions across populations and the potential role of specific soil biota, both of which are key for understanding how PSF might change future communities and ecosystems. We combined landscape-level field observations and experimental soil treatments to test whether a dominant tree alters soil environments to impact its own performance and range shifts towards higher elevations. We show: (1) soil conditioning by trees varies with elevation, (2) soil biota relate to PSF, (3) under simulated conditions, biotic PSF constrain range shifts at lower elevations but allow for expansions at higher elevations, and (4) differences in soil conditioning predict feedback outcomes in specific range-shift scenarios. These results suggest that variable plant–soil biotic interactions may influence the migration and fragmentation of tree species, and that models incorporating soil parameters will more accurately predict future species distributions.**

Climate broadly determines where plants occur on a global scale, but the local influence of soils ultimately affects their distribution on the landscape<sup>1,2</sup>. Understanding how soil variation impacts plant fitness and performance traits is a frontier for predicting how species ranges will respond to climate change<sup>3–6</sup>. As plants move to new soil environments, their performance will vary depending on the net impact of previously conditioned or determined soil communities on plant survival and performance, that is, plant–soil feedbacks (PSF)<sup>4,6,7</sup>. The degree to which plants modify the diversity and activity of soil communities could influence range shifts through such feedback effects. For instance, expansion beyond range limits might be promoted by a release from below-ground enemies when soil pathogens accumulate in the native range and decrease plant fitness relative to plants in the expanded range that have accumulated fewer soil pathogens. Most examples describing how PSF relate to plant range shifts use latitude gradients and make comparisons among species<sup>8–12</sup>, even though plants generally have much shorter distances to travel in elevation (167 m) relative to latitude (145,000 m) to track the same 1 °C temperature change<sup>13</sup>. In addition, within-species variation can have important consequences for understanding the ecological and evolutionary effects of feedbacks in plant–soil systems<sup>5,14,15</sup>. Therefore, the importance of intraspecific PSF in determining range-shift responses to climate warming could be greater and more immediate in populations along elevation gradients than whole species distributions across latitude gradients.

Variation in plant–soil interactions between the interior and edge of plant elevation ranges could determine how PSF affect range shifts. In response to rising global temperatures, plants are widely predicted to move upwards in elevation<sup>13,16</sup>. Interactions between plants and soil communities will probably change along elevation gradients because: (1) patterns of gene flow and adaptation create genetic and phenotypic differences between the interiors and edges of plant ranges<sup>17,18</sup>, and (2) soil microbial diversity is highly variable even at small scales<sup>19</sup>, including along elevation gradients<sup>20</sup>. For example, soil communities across an elevation gradient in the Canadian Rocky Mountains differentially impacted *Pinus contorta* and *Picea*

*glauca* × *engelmannii* growth rates relative to sterile controls<sup>21</sup>, showing how plant–soil biotic interactions can influence plant performance differently across elevation ranges. However, movement towards higher elevations will disrupt these above- and below-ground linkages<sup>5,22</sup>, causing geographic variation in plant–soil interactions that might affect the likelihood of range shifts<sup>3</sup>.

Based on previous work that highlights the importance of plant–soil interactions near geographic limits<sup>21,23</sup>, we examined intraspecific variation in landscape-level patterns of biotic PSF across elevation ranges by comparing patterns from range interiors (lower elevations; henceforth ‘interior’) to range edges (higher elevations; henceforth ‘edge’) and beyond current range limits (henceforth ‘beyond’). We used a combination of field observations (Fig. 1a–c) and experimental soil inoculum treatments from field-collected soils (Fig. 1d,e), obtained from seven populations covering 980–2,900 m in elevation and spanning ~1,500 km of latitude, to measure plant–soil conditioning and feedbacks of a widespread native *Populus* spp. (*Populus angustifolia* James) (Table 1 and Supplementary Table 1). With this approach, we tested the following related hypotheses:

- (1) Plant–soil conditioning across *P. angustifolia* elevation gradients in the field will be greater within the range interior than at the range edge; we did this by comparing soil qualities measured from beneath trees (‘conditioned’) versus random locations in the interspace away from trees (‘unconditioned’).
- (2) Tree growth in the greenhouse will increase with conditioned soil communities from beneath trees versus unconditioned soil communities from random locations away from trees (positive PSF); we did this using paired live and sterile soil inoculum treatments collected from the two soil locations. Moreover, greater plant–soil conditioning (that is, larger differences between conditioned versus unconditioned soil qualities) will positively correspond with PSF, such that trees exerting greater changes to their local soil environment show more positive feedback responses.
- (3) If conditioned soil communities differ across elevation ranges, the performance of *P. angustifolia* trees will depend on whether they are grown with their current soil trees community or a soil community

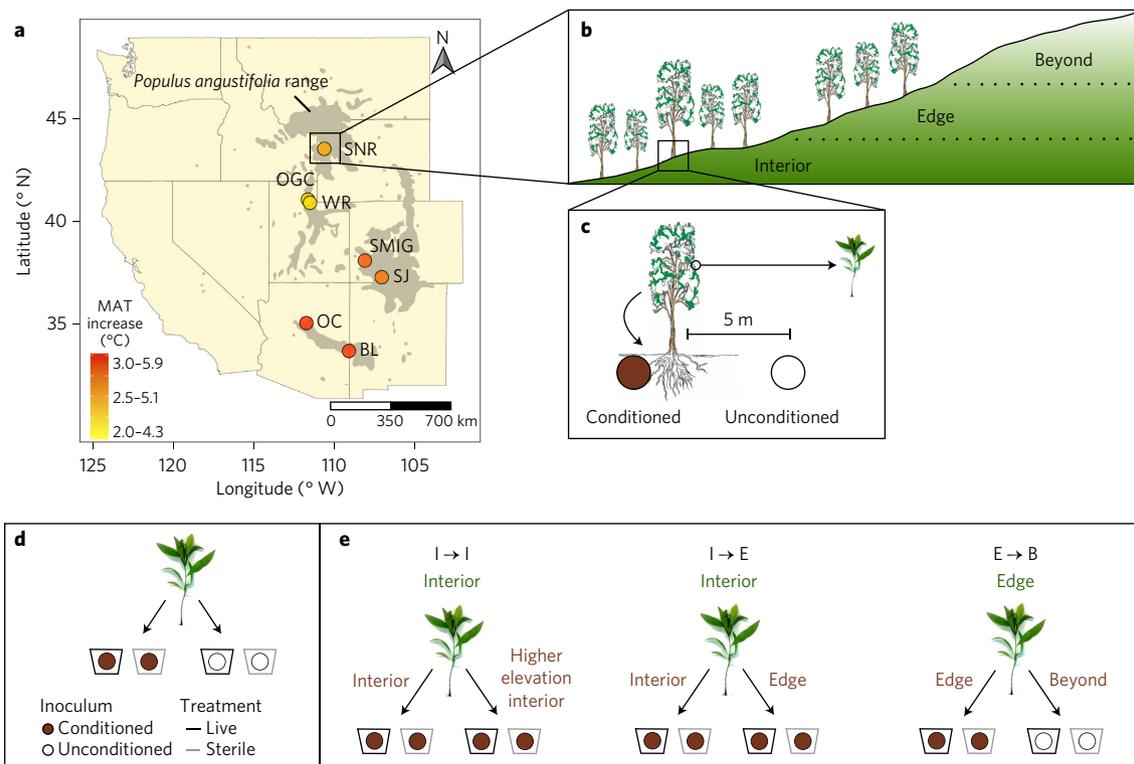
from the next highest elevation. Specifically, feedbacks from simulated upward range shifts ('range-shift PSF') will change with increasing elevation from positive (opposing range shifts) to negative (favouring range shifts).

- (4) Feedbacks will be more positive when plant–soil conditioning improves soil nutrient levels relative to the surrounding environment. Additionally, plant performance under range shifts should be negatively affected when plant–soil conditioning is 'mismatched' between sites. Therefore, greater differences in soil conditioning between elevation sites will correspond to more positive range-shift feedback effects.

## Results

**Soil conditioning and feedbacks.** In support of hypothesis 1, we found the effect of soil conditioning on soil nutrients, pH and possibly soil biota (i.e., *Betaproteobacteria*) by *P. angustifolia* trees in the field (based on the paired comparisons between conditioned versus unconditioned soil locations; Fig. 1c) was greater at range interiors than range edges and may depend on tree age (see 'Soil conditioning effects' in Supplementary Information, Supplementary Table 2 and Supplementary Fig. 1). In support of hypothesis 2, we found in our greenhouse experiment that tree-conditioned soil communities (collected from the field) created significant positive feedback effects for *P. angustifolia* trees. We examined feedback effects by comparing aboveground biomass growth (final – initial biomass)

in the greenhouse in response to experimental soil biotic treatments that were related to conditioned soil communities from the field (initial tree biomass was calculated using an allometric equation that explained >98% variation in biomass; see Supplementary Information and Supplementary Figs 2 and 3). There was no effect of soil location (variance ratio ( $F_{1,359} = 0.6, P = 0.4$ ) or soil treatment (live versus sterile soil inoculum;  $F_{1,391} = 0.2, P = 0.6$ ) on biomass growth, indicating that these factors alone did not affect tree performance in the greenhouse (Supplementary Table 4 and Supplementary Fig. 4). However, there was a significant soil location  $\times$  soil treatment interaction ( $F_{1,368} = 4.0, P = 0.05$ ), whereby trees grew an average of 24% larger with live-conditioned soil relative to live-unconditioned soil (Fig. 2a). Removing field soil biota in sterile inoculum (gamma irradiated) also removed the effect of soil location on *P. angustifolia* growth, suggesting that biotic variation in live soil inoculum from the two soil locations (plant conditioned versus unconditioned soils) led to growth differences. We found no interaction between soil location and soil treatment when interior trees (that is, trees collected from the interior of their population) and edge trees (that is, trees collected from the edge of their population) were analysed individually (Supplementary Table 4). In other words, positive feedbacks were not limited to plant–soil interactions from any particular range location, but instead only appeared as a range-wide phenomenon. This also means that, although there was little evidence that edge trees condition soil nutrient or pH



**Figure 1 | Field sampling and experimental design to test how PSF may contribute to *P. angustifolia* range shifts.** **a**, We identified and sampled plants and soils from seven populations across the *P. angustifolia* range that are predicted to have approximately 2–6 °C higher MATs by 2070. **b**, Tree cuttings were collected across 3–5 elevation sites (comprising the interior and edge of their elevation ranges) within each population and allowed to establish and mature for one year in the greenhouse. **c**, Soils were collected from two locations to quantify the effects of plant–soil conditioning by *P. angustifolia* in the field<sup>36,43</sup>. **d**, To test whether conditioning affects plant performance leading to feedback effects, trees were grown in soil inoculated with conditioned or unconditioned soils in a paired live or sterile (gamma irradiated) treatment design that measures the effect of soil communities on tree growth. **e**, For the range-shift PSF experiment, trees were inoculated with conditioned soil communities from their elevation site or from the next-highest-elevation site. As a result, we used three range-shift categories<sup>32</sup>: lower interior trees (I) grown with higher-elevation interior communities (I → I), higher interior trees grown with edge (E) communities (I → E) or edge trees grown with communities beyond (B) current range limits (E → B). Note that edge trees grown with soils beyond current range limits were represented as unconditioned, since no *P. angustifolia*-specific conditioning happened at those sites, but were influenced instead by a suite of heterospecific plant species at higher elevations.

environments in the field (Supplementary Fig. 1), they do alter soil communities in a way that affects their performance.

By examining how specific microbial taxa relate to tree performance, we found that higher Betaproteobacteria abundance in conditioned field soils was positively correlated with a greater aboveground biomass growth of trees in the corresponding live soil inoculum treatment (coefficient of correlation ( $r^2$ ) = 0.5,  $F_{1,11} = 11.1$ ,  $P = 0.01$ ; Fig. 2b). Additionally, there was no effect of range location ( $F_{1,11} = 1.7$ ,  $P = 0.2$ ) or interaction between Betaproteobacteria and range location ( $F_{1,11} = 0$ ,  $P = 0.9$ ), which suggests that variation in how strongly *P. angustifolia* trees influences the abundance of Betaproteobacteria community members may lead to differences in future plant performance, regardless of range location. No other dominant microbial taxon was correlated with tree performance in the greenhouse experiment and there were no interaction effects of microbial abundance and range location on tree growth (Supplementary Table 5). These results show that plant–soil conditioning of soil communities (specifically Betaproteobacteria) relates to the overall positive feedback effect on *P. angustifolia* performance across elevation ranges.

**Range-shift PSF.** To test hypothesis 3, we compared range-shift PSF across three categories (Fig. 1e): lower elevation interior trees grown with higher elevation soil communities, but still within the interior of the range (I → I), highest elevation interior trees grown with edge soil communities (I → E), and edge trees grown with soil communities from beyond current range limits (E → B). This allowed us to compare range-shift PSF using ‘home–away’ and ‘local–foreign’ approaches (that is, soil-centric versus plant-centric approaches for analysing range-shift responses). Specifically, we calculated the log response ratio between: (1) trees grown with soil communities conditioned at their current elevation sites (‘home’) versus trees grown with soil communities conditioned at the next highest elevation site that was within or beyond range limits (‘away’), and (2) trees grown with soil communities conditioned at their current elevation sites (‘local’) versus lower elevation trees grown with the same soil community as the local trees (‘foreign’). In support of hypothesis 3, we found that variation in plant–soil conditioning creates feedback effects by simulating *P. angustifolia* shifts upslope with positive range-shift PSF at lower elevations and negative range-shift PSF at higher elevations (Supplementary Fig. 5). For home–away comparisons (Fig. 3a), we found significant effects of range shift category ( $F_{1,214} = 13.1$ ,  $P < 0.001$ ) and a marginal interaction of range shift category × soil treatment on range-shift PSF ( $F_{1,212} = 2.3$ ,  $P = 0.10$ ). Although these effects were not significant for local–foreign comparisons (Supplementary Table 6), the general patterns of range-shift PSF for local–foreign comparisons matched those from the home–away approach (Fig. 3b).

Interior trees from lower elevations created positive range-shift PSF. Trees from the range interior had larger growth with live soil inoculum from home sites than with live inoculum from higher elevation away sites within the interior (I → I; Fig. 3a), which resulted in a positive average feedback effect of  $0.31 \pm 0.07$  s.e.m. ( $t_{1,57} = 2.4$ ,  $P < 0.01$ ). The local–foreign comparison for I → I range shifts also showed a positive feedback effect (mean =  $0.13 \pm 0.09$ ). Specifically, local interior trees had higher growth than foreign interior trees when grown with the same live soil communities (Fig. 3b), which trended towards positive feedback ( $t_{1,63} = 1.4$ ,  $P = 0.08$ ). Sterilizing the same soil inoculum resulted in neutral feedback effects for both home–away ( $t_{1,50} = 1.2$ ,  $P = 0.12$ ) and local–foreign ( $t_{1,22} = 0.1$ ,  $P = 0.9$ ) comparisons, suggesting that soil communities play a role in shaping the positive feedback effects from live soil inoculum treatments.

Trees at the transition from interior to edge of *P. angustifolia* ranges (I → E) performed equally with soil communities from either range location. Interior trees did not grow significantly better or worse with live home soil communities, compared with higher elevation

**Table 1 | Summary of sampling locations, climate and tree diameter at each field site.**

Site	Elevation (m)	Mean annual temperature (°C)*	Annual precipitation (mm)	Diameter at breast height (cm)†
<b>Blue River (33.68° N, 109.09° W)‡</b>				
Interior (4)§	1,792–2,084	9.1 + 3.0–5.5	467	17.4 ± 3.1
Edge	2,238	7.4 + 1.8–4.3	474	22.2 ± 7.5
Beyond	2,323	7.4 + 1.8–4.3	474	–
<b>Oak Creek (35.02° N, 111.73° W)</b>				
Interior (2)	1,683–1,782	10.0 + 3.8–6.2	574	15.7 ± 6.1
Edge	1982	8.8 + 2.6–5.1	572	17.3 ± 7.5
Beyond	2023	8.8 + 2.5–5.0	572	–
<b>San Juan River (37.30° N, 106.92° W)</b>				
Interior (3)	2,178–2,464	4.8 + 2.4–5.1	496	31.6 ± 3.7
Edge	2,663	2.1 + 3.1–5.7	680	24.6 ± 5.5
Beyond	2,707	2.1 + 1.9–4.6	680	–
<b>San Miguel River (38.00° N, 107.98° W)</b>				
Interior (4)	1,961–2,515	4.3 + 2.8–5.5	578	19.9 ± 3.2
Edge	2,749	1.5 + 2.5–5.1	681	19.8 ± 6.5
Beyond	2,925	–0.7 + 2.1–4.8	825	–
<b>Ogden Canyon (41.37° N, 111.60° W)</b>				
Interior (3)	1,625–2,085	4.5 + 2.4–5.3	531	44.2 ± 5.1
Edge	2,325	3.0 + 1.8–4.7	544	27.4 ± 9.2
Beyond	2,608	2.2 + 1.4–4.2	592	–
<b>Weber River (40.91° N, 111.39° W)</b>				
Interior (3)	1,413–1,958	6.1 + 3.3–6.3	542	30.9 ± 4.2
Edge	2,167	3.0 + 2.6–5.6	573	27.4 ± 6.5
Beyond	2,333	2.1 + 2.1–5.0	643	–
<b>Snake River (43.59° N, 110.60° W)</b>				
Interior (4)	1,695–2,026	1.9 + 2.4–5.2	513	35.7 ± 3.4
Edge	2,209	0.6 + 2.2–5.0	537	14.3 ± 6.9
Beyond	2,488	–0.6 + 1.7–4.5	556	–

\*Data refer to current mean annual temperature averaged for multiple interior sites and projected mean annual temperature in 2070 (mean range of 2.6 to 8.5 representative concentration pathways that predict mean annual temperature increases). †Data shown are mean ± s.e.m.

‡Mean latitudes and longitudes are reported for each population. §Numbers in parentheses refer to how many lower elevation interior sites were sampled.

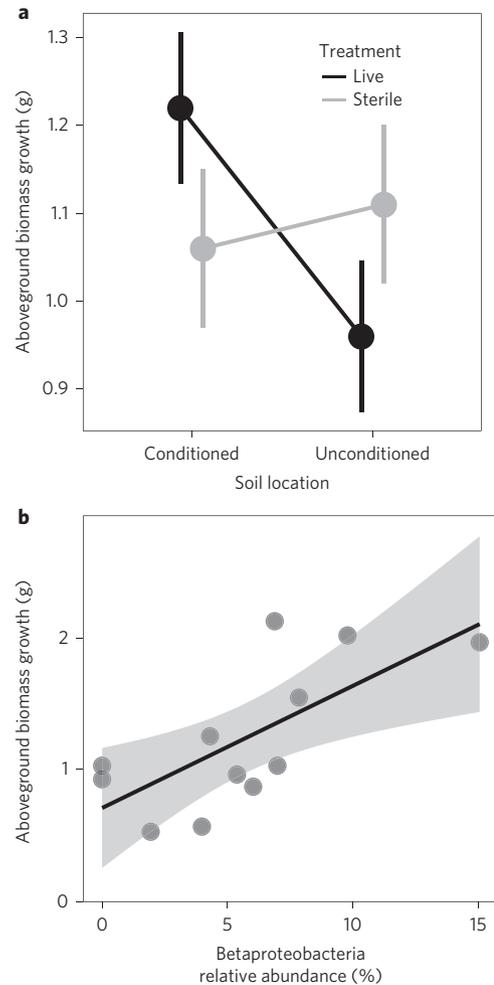
away communities from the range edge ( $t_{1,28} = 0.8$ ,  $P = 0.2$ ; Fig. 3a). In addition, soil communities conditioned by local edge trees in the field did not enhance the growth of edge trees more than foreign interior trees ( $t_{1,26} = 0.4$ ,  $P = 0.3$ ; Fig. 3b). There were no differences for I → E range shift PSF between live and sterile treatments (home–away:  $t_{1,26} = 0.5$ ,  $P = 0.3$ ; local–foreign:  $t_{1,26} = 1.0$ ,  $P = 0.2$ ), indicating that higher elevation interior and edge tree growth may be less dependent on particular soil communities with which they interact, although there may still be positive conditioning effects from soil biota. Together, this shows that the highest elevation trees within the interior performed equally well as edge trees, regardless of whether different soil communities were present.

Edge trees experienced negative range-shift PSF when simulating migration beyond current range limits. Edge trees had reduced growth in soils containing live home communities compared with live soils from beyond current range limits (E → B), resulting in a negative mean range shift feedback of  $-0.75 \pm 0.28$  s.e.m. ( $t_{1,26} = 2.6$ ,  $P = 0.01$ ; Fig. 3a). Consistent with our previous findings,

soil communities appear to create this feedback effect, since an overall neutral feedback was found using sterile inoculum treatments ( $t_{1,26} = 1.0$ ,  $P = 0.2$ ).

**Feedback mechanisms.** In support of hypothesis 4, we found that plant–soil conditioning effects were related to the strength and direction of PSF across elevation ranges (Supplementary Table 7). When predicting feedback effects generated from soil conditioning (quantified as the log response ratio of soil traits between conditioned versus unconditioned locations at the same elevation site in the field; Fig. 1c,d), there was a significant interaction between soil carbon conditioning and range location ( $F_{1,76} = 5.2$ ,  $P = 0.03$ ; Supplementary Fig. 6a), and soil nitrogen conditioning and range location ( $F_{1,73} = 4.8$ ,  $P = 0.03$ ; Supplementary Fig. 6b). Feedback effects in the greenhouse were positively correlated with soil carbon conditioning ( $r^2 = 0.1$ ,  $P = 0.01$ ) and soil nitrogen conditioning ( $r^2 = 0.1$ ,  $P = 0.01$ ) for interior trees. As a result, the most positive feedback effects for interior trees related to the highest levels of soil carbon and nitrogen conditioning by interior trees in the field. Soil carbon and nitrogen conditioning by edge trees did not predict PSF (Supplementary Table 7), probably related to the overall lack of soil conditioning detected for edge trees. Although interior trees had a large impact on soil acidity in the field, pH conditioning did not predict PSF variation, regardless of range location (Supplementary Fig. 6c and Supplementary Table 7). Moreover, Betaproteobacteria abundance was negatively correlated with conditioned soil total carbon ( $r^2 = 0.44$ ,  $P = 0.02$ ) and nitrogen ( $r^2 = 0.38$ ,  $P = 0.03$ ), but not pH ( $r^2 = 0.05$ ,  $P = 0.5$ ), further illustrating a link between soil nutrient conditioning and the abundance of specific biota that relate to plant performance (Supplementary Fig. 7a–c).

Range-shift PSF were predicted by soil conditioning differences across elevation gradients (quantified as the log response ratio of lower versus higher conditioned soil traits in the field). Conditioned and unconditioned soil differences across elevation positively covaried (carbon:  $r^2 = 0.30$ ,  $P < 0.001$ , nitrogen:  $r^2 = 0.45$ ,  $P < 0.001$ ; pH:  $r^2 = 0.15$ ,  $P < 0.001$ ), so we first removed variation attributed to natural soil changes across elevation (unconditioned soil differences) and used the residuals of conditioned soil differences (that is, soil differences across elevation that result from plant–soil conditioning). Residuals of conditioned soil carbon and nitrogen differences did not predict range-shift PSF responses overall (Supplementary Table 8) and there were no soil difference  $\times$  range shift category interactions. Residual conditioned soil pH differences were negatively correlated with range-shift PSF overall ( $F_{1,113} = 15.7$ ,  $r^2 = 0.17$ ,  $P < 0.001$ ) and we found a significant soil pH difference  $\times$  range shift category interaction ( $F_{1,112} = 3.6$ ,  $P = 0.03$ ). Examination of range-shift categories individually showed nonlinear relationships between I  $\rightarrow$  E feedbacks and residuals of conditioned soil carbon and nitrogen (Fig. 4d,e). Here, range-shift PSF were most negative (that is, most favourable for upward shifts) when soil conditioning differences were closest to zero, meaning tree conditioning was relatively ‘matched’ between elevation sites for soil carbon ( $r^2 = 0.30$ ,  $P = 0.002$ ) and nitrogen ( $r^2 = 0.26$ ,  $P = 0.02$ ). Residuals of conditioned soil pH differences also showed a negative correlation with I  $\rightarrow$  E feedbacks (Fig. 4f), where increasingly different levels of soil pH conditioning led to more negative range-shift PSF ( $r^2 = 0.21$ ,  $P = 0.01$ ). For edge trees shifted to soil communities beyond range limits (E  $\rightarrow$  B), there was a nonlinear relationship between residual conditioned nitrogen differences and range shift feedbacks ( $r^2 = 0.20$ ,  $P = 0.05$ ) where more ‘matched’ soil nitrogen conditioning had more positive feedback effects (that is, unfavourable for range shifts) (Fig. 4h). In contrast, greater differences in residual conditioned soil pH were related to more negative range-shift PSF ( $r^2 = 0.20$ ,  $P = 0.02$ ) that would favour upwards range expansion (Fig. 4i). Finally, aboveground biomass growth in the experiment was unrelated to the different soil inoculum treatments carbon,

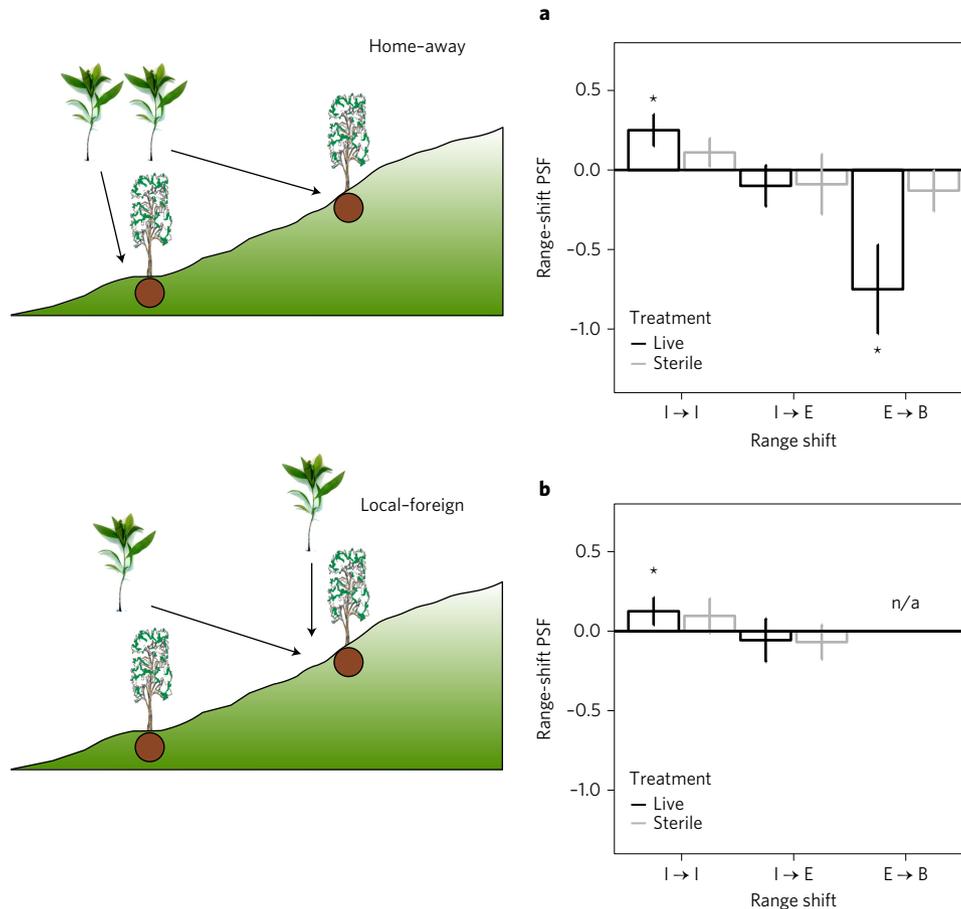


**Figure 2 | Indicative of a positive plant–soil biotic feedback, tree growth relates to conditioned soil communities and the relative abundance of Betaproteobacteria.** **a**, Higher aboveground biomass growth using conditioned versus unconditioned soil biotic communities at the same elevation (that is, positive PSF) was found for *P. angustifolia* trees in live soil treatments (black). No growth differences were found when soil inoculum was sterilized with gamma irradiation (grey). Data are means  $\pm$  1 s.e.m. Growth refers to the difference in total aboveground biomass between the beginning and end of the experiment. **b**, Aboveground biomass growth in conditioned soils was positively related to the relative abundance of Betaproteobacteria from field soils. Data points represent biomass growth in the experiment averaged at the level where soil inoculum treatments were pooled (that is, elevation site); microbial data are from field soils collected beneath a subset of genotypes (from BL, SJ and SNR populations) corresponding to the same elevation sites. Regression line is shown with the shaded area representing the 95% confidence interval.

nitrogen or pH levels from the field (Supplementary Table 9), which shows that feedback effects predicted by soil conditioning were not dependent on any growth correlations with field soil characteristics associated with the various treatments.

## Discussion

Although plant interactions with soil communities are just one factor among many that could alter the pace and direction of plant range shifts, examining the biotic mechanisms that drive plant–soil linkage and feedback differences across elevation ranges will shed light on the relative importance of PSF in shaping plant responses to warming environments. The results of this study suggest that



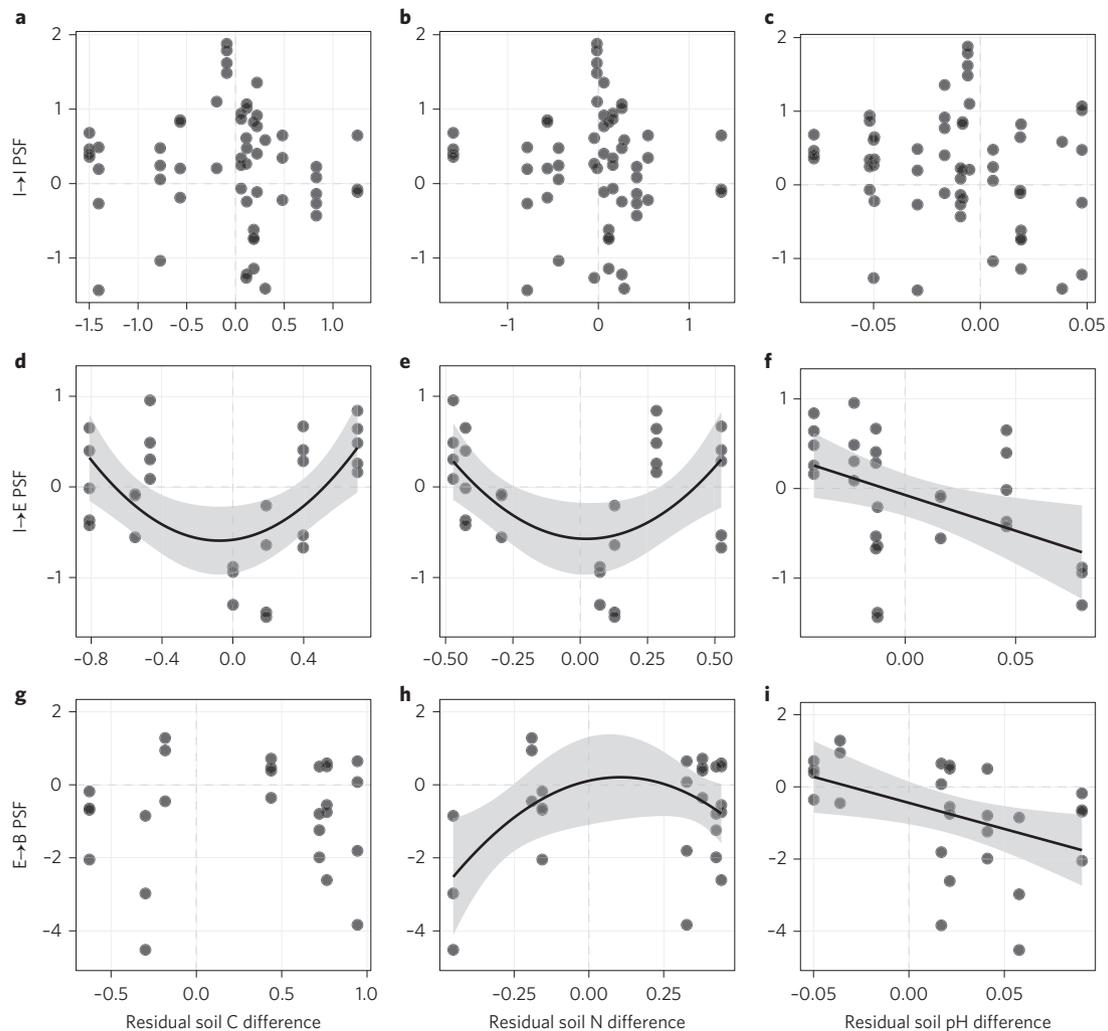
**Figure 3 | Range-shift PSF changed from positive to negative as trees were simulated to move upwards in elevation by interacting with soil communities from higher sites. **a****, Home-away comparisons of plant growth with live soil communities (black bars) at home elevations versus higher elevations showed that interior trees with higher-elevation interior soil communities (I → I) had positive PSF, interior trees with edge communities (I → E) had neutral PSF, and edge trees with communities from beyond range limits (E → B) had negative PSF. **b**, Local-foreign comparisons between higher- versus lower-elevation tree growth with the same soil community produced positive PSF for comparisons of interior trees moving within the interior I → I and neutral PSF for interior trees moving to the range edge (I → E). Sterilizing soil communities (grey bars) led to neutral PSF effects across all range-shift categories and comparison types, indicating that any non-zero PSF were driven by the soil communities and demonstrating the importance of the soil biotic effects on tree growth. Bars depict means  $\pm$  1 s.e.m; asterisks indicate feedbacks that are significantly different from zero ( $*P < 0.05$ ); n/a indicates no possible feedback calculation.

plant–soil biotic interactions could impede range shifts at lower elevations by reducing the performance of plants that shift upwards in elevation relative to plants that remain at lower sites. In contrast, interactions at upper range limits might propel expansions past current range boundaries if abiotic conditions are not limiting and increased growth at these higher sites accelerates upslope movement. What remains unknown is the influence of biotic PSF on plant range dynamics relative to the strength and duration of other environmental forces in the field. It could be that plant–soil interactions are short-term regulators of plant performance and will not play a significant role in determining the long-term success or failure of plant range shifts; in contrast, it may be that PSF accumulate and work synergistically with other factors to impede or improve plant range shifts that may subsequently alter soil nutrient processes and belowground diversity.

Plants modify their local soil environment by regulating the quantity and quality of resources that are delivered belowground<sup>24</sup>, and our study provides rare empirical evidence that variation in the amount of soil conditioning directly corresponds to PSF. In our case, trees from interior elevation sites that improved the average soil nutrient environments in the field relative to adjacent unconditioned soil grew better with live soil communities from conditioned

rather than unconditioned soil locations. We also found that quantifying the difference in conditioned soil properties across elevation gradients predicted the outcomes of plant–soil community interactions with simulated range shifts. Greater standardized differences in soil pH conditioning (and probable microbial composition<sup>25</sup>) between lower and higher sites increased tree growth in the greenhouse with higher-elevation biota than with their lower-elevation home biota (that is, negative range-shift PSF). In certain cases, greater matching of soil carbon and nitrogen conditioning between range-shift sites, shown with standardized soil conditioning differences near zero, were related to the most negative range-shift PSF (favourable for upward shifts), but also the most positive range-shift feedbacks (unfavourable for upward shifts). These nonlinear relationships provide some of the first empirical evidence to support theoretical models that predict the importance of matched and mismatched soil conditioning effects for determining plant performance and the conditions under which feedbacks can evolve<sup>14</sup>. Our results also suggest that ecological niche models that incorporate soil factors may capture part of plant–soil biotic interactions that could be important for defining future plant ranges<sup>1,2</sup>.

The majority of evidence to date shows that negative PSF allow plant migrations past range boundaries<sup>4</sup>, while positive feedbacks



**Figure 4 | Range-shift PSF are related to residual variation in conditioned soil differences between elevation sites after accounting for natural soil variation (unconditioned soils) across elevation gradients.** **a–c**, Range shift PSF variation for interior trees grown with higher-elevation soil communities ( $I \rightarrow I$ ) were not predicted by differences in residual conditioned soil carbon (C), nitrogen (N) or pH across elevation. **d,e**, For interior trees shifted to edge soil communities ( $I \rightarrow E$ ), residual carbon and nitrogen in conditioned soils had nonlinear patterns, where the most negative biotic PSF corresponded to the least amount of residual soil conditioning. **f**, Residual pH differences in conditioned soil were negatively related to the  $I \rightarrow E$  range-shift PSF. **g**, Residual conditioned soil carbon differences were unrelated to feedbacks at the highest range-shift category where edge trees were grown with soil communities from beyond elevation range limits ( $E \rightarrow B$ ). **h**, Residual soil nitrogen showed a nonlinear response, with the lowest  $E \rightarrow B$  range-shift PSF with the most and least amount of conditioned nitrogen differences across elevation. **i**, Residual soil pH differences negatively predicted  $E \rightarrow B$  feedbacks. Regression lines depict significant trends with the shaded areas representing 95% confidence intervals. Residual conditioned soil differences that differ from zero reflect mismatches in conditioned soil environments across elevation.

support plant persistence in harsher environments<sup>26</sup>. Along replicate elevation gradients throughout the *P. angustifolia* species range, on average we similarly found negative range-shift PSF as edge plants were simulated to expand beyond their current elevation range limits (increased performance with soil communities from beyond range limits relative to range edge soil communities) and positive range-shift PSF for the lowest elevation plants mediated by soil communities (possibly related to Betaproteobacteria, but also other taxa not identified in this study). Further experiments identifying potential pathogen build-up in edge soils and comparing soil diversity between lower-elevation sites to trailing edge populations are paramount to understand the generality of enemy release dynamics across elevation and whether community members that improve plant performance under harsh conditions will mitigate increasing environmental stress for *P. angustifolia* populations.

It is unclear whether growth patterns of two-year-old trees correspond to performance differences of longer-lived *P. angustifolia*

in the field (for example, whether conditioning effects or feedback responses change with plant ontogeny or environmental changes across the sites<sup>27</sup>). Because nutrient conditioning positively relates to feedback responses in our study, perhaps continual carbon/nitrogen conditioning by edge trees might gradually shift the range-shift feedback from negative to positive, if decomposition-related nutrient feedbacks becomes more important for plant growth over time. In addition, we know little about whether the potting soil impacted how the inoculated soil communities developed or plant–soil biotic interactions were formed under greenhouse conditions. However, our manipulation with live and sterile inoculum shows that soil biotic effects remain worthwhile to consider and test under field conditions, and our results predict that: (1) negative range-shift PSF might permit *P. angustifolia* expansions past their current range limits as they move away from their conditioned soil communities that may harbour less mutualistic taxa or higher pathogen loads, and (2) lower-elevation interior trees might be inhibited from shifting

upwards to track changing temperatures (due soil biota that reduce tree growth relative to lower-elevation sites and outperformance by higher-elevation interior trees in the same soil community). As a result, investigating plant–soil linkages across elevation gradients may serve as a similarly helpful space-for-time tool as is widely used by climate change studies<sup>28</sup>. Future work conducted in the field will continue to benefit our understanding and predictions of how PSF combine with other environmental factors, which are typically studied in isolation, to influence plant range dynamics.

## Methods

**Study species and sampled populations.** High-elevation riparian ecosystems of the Rocky Mountains are the predominant habitat for *P. angustifolia*<sup>29</sup>. These systems are predicted to experience significant climatic changes due to anthropogenic activities<sup>30</sup> and are critical areas to examine plant–soil responses to increasing temperatures<sup>31</sup>. Moreover, *P. angustifolia* populations span natural elevation gradients that occur along river drainages<sup>29</sup>, creating the opportunity to investigate variation in PSF across replicated gradients on the landscape. Since *P. angustifolia* is a riparian obligate species, this allowed for better identification of suitable habitat beyond current range limits (that is, higher-elevation sites within riparian zones), thus minimizing the risk of choosing inappropriate sites for experimental soil treatments<sup>32</sup>.

Seven populations of *P. angustifolia*, spanning a ~1,500 km latitude gradient that covered a wide range of environmental variation (Fig. 1a and Table 1), were sampled across 980–2,900 m in elevation. Total elevation changes (that is, the difference from the highest to lowest sampling points) across these gradients ranged from 350 to 1,000 m. All sampling points were marked via the Global Positioning System (GPS; Oregon series 550, Garmin), and mean annual temperature (MAT) and annual precipitation data were collected for these coordinates (WorldClim database; [www.worldclim.org](http://www.worldclim.org)). The populations spanned an average of 7°C in MAT and 100 mm in annual precipitation, from the southernmost to northernmost sites and included: Blue River (BL) and Oak Creek (OC), Arizona; San Juan River (SJ) and San Miguel River (SMIG), Colorado; Ogdan Canyon (OGC) and Weber River (WR), Utah; and Snake River (SNR), Wyoming. To quantify the predicted intensity of global warming on these populations, we calculated the MAT predicted for these sites in 2070, based on the average of two global circulation models (GISS-E2-R and HadGEM2-ES) for mild (RCP2.6) and extreme (RCP8.5) representative concentration pathways of greenhouse gases (WorldClim database). Approximately, a 2–6°C increase in MAT is expected to occur over the next 50 years (Fig. 1a and Table 1), indicating that these *P. angustifolia* populations will experience similar temperature changes to those that have been recorded under periods of major species distribution shifts<sup>33</sup>. Moreover, recent work has shown that *P. angustifolia* migrated northward as temperatures warmed after the Last Glacial Maximum<sup>34</sup>, illustrating that this species has the potential to shift geographic ranges in response to rising temperatures.

**Plant collection and elevation ranges.** A total of 310 genotypes (verified with microsatellite data) of *P. angustifolia* were sampled across elevation gradients from distinct populations in June 2012 (BL = 50, OC = 25, SJ = 56, SMIG = 50, OGC = 30, WR = 49 and SNR = 50). Each population comprised an elevation gradient containing 2–4 sites within the range interior, which were separated by ~100 m in elevation, and one site existing at the uppermost range edge, where current population boundaries exist based on visual surveys (Fig. 1b). Ten mature genotypes were sampled at each site; they were identified in the field using morphological indicators and by separating sampled trees over one tree-height distance away, to avoid measuring clones (which was also verified by the microsatellite data). Twenty branch tip cuttings (15 cm) were collected from each *P. angustifolia* tree and stored in a cooler during transport to the greenhouse. In the greenhouse, the bottom 3 cm of each cutting was scored with clippers and treated with rooting hormone to promote establishment (Hormodin 2 with 0.3% indole-3-butyric acid); ten cuttings per genotype were grown together in 3.8 l pots containing general potting mix, composed of equal parts peat, perlite and vermiculite. After 4 months, to reduce crowding and allow further growth under equivalent environmental conditions, trees were transplanted to 6.4 cm × 35.5 cm individual pots (D60 Deepots, Spencer Lemaire) and grown for an additional 10 months with equal water, fertilizer and light regimes to enable root establishment before growth trait measurements. Importantly, we found no relationship between tree size in the field (diameter at breast height; DBH) and growth traits in the greenhouse experiment (see ‘Analysis of maternal effects on tree growth traits’ in Supplementary Information and Supplementary Fig. 3). This supports past work that also found limited maternal effects for *P. angustifolia* growth in common environments<sup>35</sup> and suggests that maternal effects probably played a limited role in determining *P. angustifolia* growth variation in our greenhouse experiments.

**Soil collection and chemical analysis.** Soils were collected from the same populations and field sites in June 2013 to quantify plant–soil conditioning in the field (hypothesis 1) and to use as soil biotic treatments in the feedback experiment (hypotheses 2 and 3). Specifically, soils were sampled in a paired

design for all *P. angustifolia* genotypes, in which conditioned soils were collected directly beneath trees and unconditioned soils were sampled from randomly chosen locations ~5 m from the base of trees (Fig. 1c). This sampling design was previously used to examine patterns of soil conditioning by *Populus* under field conditions<sup>36</sup>. We pooled conditioned and unconditioned soils at the elevation site level because: (1) we wanted to remove possible genotype-specific conditioning effects; (2) recent work showed that site is important for structuring *P. angustifolia* soil fungal communities along an elevation gradient<sup>37</sup>; and (3) elevation site is the level at which soil treatments are applied in the feedback experiment (see ‘Soil conditioning and feedbacks’ and ‘Range-shift PSF’ sections below). To identify suitable habitat at sites beyond current *P. angustifolia* range limits, we walked at least 50 m in elevation above edge populations, while remaining within the riparian zone<sup>29,32</sup>. Soil was then collected from 5–7 random locations and pooled for each population to characterize an average soil environment where *P. angustifolia* might expand beyond current range limits (Fig. 1b). All field-collected soils were sampled to a depth of 10 cm and stored in a cooler during transport to the University of Tennessee, where they were subsequently stored at 4°C until analysis. We measured total soil carbon and total soil nitrogen using chromatography (FlashEA 1112 Elemental Analyzer, Thermo Scientific) after soils had been sieved through 2 mm mesh, ground, and oven-dried at 105°C. Soil pH was measured using a 2:1 slurry of 10 g of soil to 20 ml of 0.2 M CaCl<sub>2</sub> (Denver Instruments). We used a subset of populations (BL, SJ, SMIG and SNR) where soils from the same elevation sites were sampled in 2012, 2013 and 2014 (see ‘Soil microbial analysis’) to test whether soil chemistry varies across elevation (a continuous variable), between populations and by year. We constructed a generalized linear model (GLM) with soil traits (carbon, nitrogen and pH) as the response, elevation, population and year as fixed effects, and all possible interactions as fixed effects. We found no significant three-way interaction between elevation × population × year, indicating that soil traits remained relatively consistent within each population’s elevation gradient across sampling years. Importantly, this result suggests that interannual variation was small and that soils sampled and analysed across years were comparable in this study (Supplementary Table 9).

**Soil microbial analysis.** We collected soils in June 2014 from a subset of *P. angustifolia* genotypes across the same elevation sites as 2012 and 2013 sampling to examine differences in soil microbial communities and how they may relate to feedback effects. Specifically, interior genotypes ( $n = 3$ ) and edge genotype ( $n = 1$ ) were sampled from each of the BL, SJ and SNR populations (Supplementary Table 1). Soils were collected directly from the rhizosphere of genotypes in the field; as a result, microbial diversity should directly reflect conditioning and we did not collect a paired unconditioned soil away from each tree. Soils were stored in a cooler during transport to the University of Tennessee, where they were subsampled for carbon, nitrogen and pH analyses (protocols as detailed in ‘Soil collection and chemical analysis’) to compare how microbial communities relate to soil chemical factors. Soils were then subsequently stored at –40°C before DNA extraction using PowerSoil DNA Isolation kits (MoBio Laboratories). See ‘Amplicon sequencing and bioinformatic processing’ in Supplementary Information for a full description of sequencing and workflow steps. Briefly, sequencing was carried out on a MiSeq Desktop Sequencer (Illumina) running in paired end 2 × 250 mode. We processed 16S amplicon data using *akutils* (<https://github.com/alk224/akutils-v1.2>), which includes modifications to a QIIME 1.9.1 workflow<sup>38</sup>, since it was shown that the default settings can significantly overestimate microbial diversity<sup>39</sup>. Although it is possible that rare taxa could have substantial effects on plants, we focused on the five most abundant bacteria taxa identified by class (representing 58% of the total abundance) across the 12 field samples in this study: Actinobacteria, Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria and Synergistia. These taxonomic groups were also among the most abundant in soil samples collected in 2012 from the same elevation sites, indicating that the identity of dominant taxa in these sites were generally consistent across years (that is, soils collected for experimental inoculum in 2013 should be comparable to the microbial diversity uncovered by sequencing 2014 soils that were collected from the same sites at the same time of year).

**Soil conditioning and feedbacks.** To address hypothesis 1 (that plants vary in their effect on soil environments; Fig. 1c) we compared conditioned and unconditioned soil carbon, nitrogen and pH to investigate this initial premise of PSF<sup>7</sup>. Previous work has shown the effectiveness of conditioned–unconditioned comparisons to measure *Populus* soil conditioning in the field<sup>36</sup> and common garden experiments have shown *P. angustifolia* affects soil nutrient pools, nutrient cycling and belowground microbial communities<sup>6</sup>. Therefore, although an alternative hypothesis could describe that trees selectively colonized sites with certain characteristics, we considered soil measurements directly beneath trees in the field to reflect plant–soil conditioning. Conditioned and unconditioned soils ( $N = 60$ ) were analysed across range locations based on our hypothesis that PSF might impact range shifts if interior and edge genotypes differ in soil conditioning. We constructed a restricted maximum likelihood (REML) model using the *lme4* package with soil carbon, nitrogen or pH, as the response variable; soil location, range location and soil location × range location as fixed effects; and population as a random effect. We used Tukey’s honestly significant difference

test for *post hoc* analyses using the multcomp package in R. In addition, we examined whether the relative abundance of dominant soil bacteria in the *P. angustifolia* rhizosphere differed between the range interior and edge of the three populations. We constructed a GLM with the relative abundance of microbes as the response, and range location, population and range  $\times$  population as fixed effects. Differences in the effect of conditioned versus unconditioned soils (or rhizosphere communities between range locations) were considered to be consistent with the hypothesis that *P. angustifolia* influences its soil abiotic and biotic environment, which may result in PSF. Finally, we tested whether conditioning effects could be related to differences in the amount of time trees in the field have had to change soil environments using DBH as a proxy for tree age. We created a GLM with DBH as the response, and population, range location and population  $\times$  range as fixed effects, to examine whether younger (smaller) trees existed at range edges, while older (larger) trees occurred within range interiors consistently across all populations.

We established a large feedback experiment (initial nitrogen = 858) from September 2013 to May 2015 to address hypotheses 2 and 3: whether conditioned soil communities reciprocally affect plant performance and if such biotic PSF vary with simulated range shifts (see 'Range-shift PSF' below). To address these hypotheses, ~12-month-old trees were grown in soils that received different soil inoculum and were placed in a complete randomized design in the University of Tennessee greenhouse (trees were also given random tag IDs during the experiment to mask their genetic identity, range location and soil treatment). For each site within each population, 3–5 genotypes were selected at random from the pool of the 10 possible genotypes that were collected in 2012 (number of unique genotypes: BL = 41, OC = 15, OGC = 17, SJ = 35, SMIG = 40, SNR = 36, and WR = 27). Each tree was removed from their individual pots and the soil was gently removed from their roots. Trees were then placed back into pots that were filled with 70% (~200 g) general potting mix before receiving soil inoculum treatments. To examine the role of biotic communities in determining feedback effects, one-half of all soils collected underwent gamma irradiation (48 kGy, Steris Isomedix) for subsequent 'live' and 'sterile' treatments. The comparison of live versus sterile soil inoculum provides a direct measure of the effect of soil communities on the growth of *P. angustifolia* trees in the experimental treatments. Approximately 20 g of either live or sterile soil inoculum was added in direct contact with the top of tree root systems and a layer of general potting mix was added above to avoid cross-contamination between pots. Each live soil inoculation treatment had an equivalent, sterilized counterpart for a paired statistical design that directly tests the role of soil communities in affecting plant responses. All trees were measured for initial height and basal diameter as a baseline to quantify plant growth over the course of the experiment that had over 80% survival ( $N = 704$ ). We used height and stem diameter traits from separate *P. angustifolia* trees of similar age and size to create an allometric equation using these growth traits that predicted more than 98% variation in aboveground biomass (Supplementary Information and Supplementary Fig. 2).

Our experimental design using field-collected soils as inoculum is different from the common approach of creating multistage feedbacks (that is, distinct conditioning and response phases<sup>40,41</sup>), but was effective for identifying variation in PSF on the landscape, as it relates to tree species range shifts<sup>41</sup>. Specifically, we used this design because: (1) we sought to simulate biotic plant–soil interactions using soils that most accurately reflected the diversity of soil communities near *P. angustifolia* trees<sup>41,42</sup>; (2) unlike most studies of PSF, where the focal species are short-lived grasses or forbs, mature trees in the field have clear zones of influence beneath their crowns where plant–soil dynamics are formed and attributable to a single individual (for example, conditioned versus unconditioned soil locations<sup>36,43</sup>); and (3) feedbacks created in the field are not necessarily changed by further conditioning in the greenhouse, since trees are long-lived organisms that have already made specific changes to soil environments<sup>44</sup>. Although the length of time needed to destroy these conditioning effects in the greenhouse is typically unknown, if trees responded differently to the various experimental soil treatments (conditioned versus unconditioned soil locations, or range-shift treatments into soil communities that were conditioned at higher elevations) then we presumed these effects were a result of field-based soil changes that were transferred through the inoculum approach. Inoculated soil communities may have also developed or interacted with existing soil biota in the greenhouse or potting mix soil in ways that do not necessarily reflect plant–soil biotic interactions in the field, but we were unable to determine whether this occurred or had any effect on our experimental design, besides comparing live versus sterile treatments. In addition, soil sterilization procedures may result in nutrient pulses from the release of immobilized nitrogen within the biotic community or changes in physicochemical structure<sup>45</sup>; this effect was probably substantially reduced with our use of gamma irradiation versus autoclaving to sterilize and use of a ~10:1 ratio of standard potting mix to sterile soil inoculum, which would have created an exceptionally small nutrient addition or change in soil structure to affect tree growth and performance during the experiment.

We addressed hypothesis 2 (that soil communities drive feedback differences across elevation ranges and that feedbacks are related to soil conditioning; Fig. 1d) using two approaches: (1) by measuring how trees perform when grown with conditioned soil inoculum (beneath trees) and unconditioned inoculum (away

from trees), and (2) by comparing the relative abundance of dominant microbial taxa from genotypes where conditioned soil inoculum was collected to the mean aboveground growth of trees in those corresponding soil treatments. This is a main principle of PSF: that plant-driven changes to the soil (that is, the difference between conditioned and unconditioned soil locations) reciprocally affect plant performance. In the first approach, we used paired live and sterile soil treatments to examine whether soil biota contributed to PSF in *P. angustifolia*. For genotypes at each elevation site, one replicate was grown in soil having been inoculated with live or sterile soil inoculum treatments from the pooled conditioned or unconditioned soil locations at their respective elevations. This led to 215 comparisons of trees grown in soil with live or sterile inoculum from conditioned or unconditioned soil locations across seven *P. angustifolia* elevation ranges (populations). We created a mixed effects model with aboveground biomass growth (the difference between final and initial biomass estimates from the allometric equation) as the response, genotype and population as random effects, and soil location, soil treatment and soil location  $\times$  soil treatment as fixed effects. An interaction between soil location and soil treatment would be evidence that trees in the greenhouse grew differently with conditioned versus unconditioned soil inoculum based on soil biotic effects. We created similar models separated by interior and edge range locations to test whether growth responses to soil locations and treatments varied across elevation gradients. In the second approach, we constructed a GLM with mean aboveground biomass of trees within the same conditioned soil treatment (that is, pooled at the elevation site level) as the response, and the relative abundance of dominant microbial taxa (Actinobacteria, Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria and Synergistia) from the corresponding elevation site, range location and microbial abundance  $\times$  range location as fixed effects. Here, correlations between microbial abundance in field soil (collected in 2014) and tree growth with the corresponding experimental soil inoculum (collected in 2013) would suggest that *P. angustifolia* conditioning of their soil biotic environment is related to variation in growth across soil treatments.

**Range-shift PSF.** We tested hypothesis 3 (that plant–soil conditioning of soil biota feeds back to alter the performance of *P. angustifolia* under predicted range-shift scenarios) by experimentally shifting trees to higher elevation soils in the greenhouse (Fig. 1e). Specifically, trees from replicate genotypes were grown in soil inoculated with live or sterile soil communities that were conditioned at the next highest elevation site by *P. angustifolia* genotypes. Trees from the edge of elevation ranges were grown in soil inoculated with live or sterile communities from soils that were collected beyond current range limits, but still within the dispersal distance of *P. angustifolia*<sup>29</sup>. As a result, we categorized range-shift feedbacks using the following delineations that represent the basic scenario by which *P. angustifolia* range shifts might occur<sup>32</sup> (Fig. 1e): interior–interior, interior–edge and edge–beyond. Specifically, lower-elevation interior genotypes shifted to higher-elevation soils, while remaining within the interior of the range ( $I \rightarrow I$ ), highest elevation interior genotypes shifted to edge soils ( $I \rightarrow E$ ), and edge genotypes expanded beyond current range limits ( $E \rightarrow B$ ). This design allowed for both home–away and local–foreign approaches to compare plant performance (Fig. 4; ref. <sup>45</sup>). The first is soil-centric: 'home' refers to conditioned soils from a given elevation site, while 'away' refers to conditioned soils from the next-highest-elevation site (or unconditioned beyond soils) within each population; the second is plant-centric: 'local' refers to trees from a certain elevation site, while 'foreign' refers to trees from the next-lowest-elevation site.

We assessed range-shift PSF in the greenhouse using the home–away approach, where the growth of trees with soil communities conditioned at their current elevation sites (home) was compared with the average growth of trees with soil communities conditioned at the next-highest-elevation site that was within or beyond range limits (away). Range-shift PSF were also assessed by comparing the performance of local genotypes with their conditioned soil community to the average growth of foreign genotypes from the next-lowest-elevation site in the same soil community. We quantified PSF as the log response ratio between aboveground biomass growth using home–away comparisons ( $N = 219$ ) and local–foreign comparisons ( $N = 169$ ), where larger plant growth in home versus away soil or local versus foreign genotypes would be evidence of positive feedbacks (that is, a positive response ratio). Based on these calculations, neutral feedbacks would arise with similar tree growth between the two categories being compared (which could be a result of simply no feedbacks or a similarity of soil communities and their reciprocal effects on plant growth between soil inoculum treatments). We created mixed effects models with range-shift PSF as the response, range-shift category, soil treatment and range shift  $\times$  treatment as fixed effects, and genotype and population as random effects. To follow, we analysed whether feedback effects differed from zero using one-sample Student's *t*-tests<sup>41</sup>. Different patterns of PSF across range-shift categories and soil treatments would suggest that future *P. angustifolia* migratory responses to climate change could be influenced by the legacy of biotic plant–soil interactions. Range-shift PSF might also occur for trees grown with soil communities collected from ~150 m away from the riparian zone within the same elevation band (that is, equivalent to the distance between edge trees and beyond soils). Although we did not explore this possibility, because our experimental approach focused on upward range shifts within the riparian zone, the obligate riparian life history of *Populus* spp. suggests this is an improbable type of range shift<sup>29</sup>.

**Feedback mechanisms.** We compared soil variation in the field to plant performance across soil treatments in the greenhouse to test hypothesis 4 (that feedback effects should be related to variation in soil conditioning). The strength and direction of feedbacks should be related to variation in soils because feedbacks result from changes to the soil environment<sup>47,46</sup>. We measured variation in soil conditioning in two ways: differences between conditioned and unconditioned soil traits at the same elevation, and differences in conditioned and unconditioned soil traits between elevation sites. This allowed us to test how soil conditioning relates to feedback effects between conditioned and unconditioned soil locations (that is, at the same elevation site), as well as how conditioned soil differences versus natural soil variation across elevation gradients relates to range-shift PSF.

We tested whether the level of soil conditioning relates to the strength and direction of PSF between interior and edge range locations. We calculated soil conditioning effects as the log response ratio between conditioned and unconditioned soil traits (carbon, nitrogen and pH) for each elevation site. Similarly, we calculated feedback effects as the log response ratio between aboveground biomass growth in live conditioned soils versus mean growth in live unconditioned soils for each respective elevation site within populations<sup>41</sup>. We then constructed a REML model with PSF as the response, soil conditioning, range location and soil conditioning × range location as fixed effects, and population as a random effect. If soil conditioning effects positively correspond to feedback effects, then we inferred that trees that increase the average conditioned soil carbon, nitrogen or pH levels relative to unconditioned soils at that site might directly or indirectly affect soil communities that generate positive feedback effects.

For range-shift PSF, we examined whether differences in soil properties across elevation sites might explain the strength and direction of soil biotic feedbacks when plants were grown with lower (home) versus higher (away) conditioned soil communities. Differences in conditioned soil communities across elevation sites could arise from variation in plant–soil conditioning, natural soil changes that occur with elevation, or a combination of these factors. As a result, we calculated standard differences in both conditioned and unconditioned soils across elevation gradients as the log response ratio between lower versus higher elevation soil carbon, nitrogen and pH values (corresponding to each interior–interior, interior–edge and edge–beyond range shifts within populations). If conditioned and unconditioned soil carbon, nitrogen and pH differences across elevations co-varied, then we calculated the residual variation of the linear model between conditioned and unconditioned soil differences to account for variation in conditioned soil differences that may be due to natural differences in soil environments across elevation (that is, isolate how soil conditioning differences are related to range-shift PSF). We then constructed a REML using home–away PSF from live soil inoculum treatments as the response, residual conditioned soil differences, range-shift category and residual conditioned soil differences × range-shift category as fixed effects, and population as a random effect. If residual differences in conditioned soil environments from the field predicted range shift PSF in the greenhouse experiment, then we inferred that differences in plant–soil conditioning change soil communities that reciprocally affects *P. angustifolia* performance.

All analyses were conducted using R version 2.15.1 (ref. <sup>47</sup>), where data met assumptions of normality and variance among groups met assumptions of homoscedasticity using Levene's test.

**Data availability.** Data are stored in the Dryad Digital Repository (<http://doi.org/10.5061/dryad.s5j72>), a free and open-access repository that is the current standard in many areas of ecology, genetics and evolutionary biology. Soil 16S amplicon sequences and associated bioinformatic analyses are currently being used in the preparation of additional manuscripts, but can be made available from the corresponding authors on reasonable request.

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## References

- Coudon, C., Gegout, J. C., Piedallu, C. & Rameau, J. C. Soil nutritional factors improve models of plant species distribution: an illustration with *Acer campestre* (L.) in France. *J. Biogeogr.* **33**, 1750–1763 (2006).
- Beauregard, F. & de Blois, S. Beyond a climate-centric view of plant distribution: edaphic variables add value to distribution models. *PLoS ONE* **9**, e92642 (2014).
- van der Putten, W. H. Climate change, aboveground–belowground interactions, and species' range shifts. *Annu. Rev. Ecol. Evol. S.* **43**, 365–383 (2012).
- van der Putten, W. H. *et al.* Plant–soil feedbacks: the past, the present and future challenges. *J. Ecol.* **101**, 265–276 (2013).
- Bailey, J. K. *et al.* Indirect genetic effects: an evolutionary mechanism linking feedbacks, genotypic diversity and coadaptation in a climate change context. *Funct. Ecol.* **28**, 87–95 (2014).
- Van Nuland, M. E. *et al.* Plant–soil feedbacks: connecting ecosystem ecology and evolution. *Funct. Ecol.* **30**, 1032–1042 (2016).
- Bever, J. D., Westover, K. M. & Antonovics, J. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *J. Ecol.* **85**, 561–573 (1997).
- Morriën, E. & van der Putten, W. H. Soil microbial community structure of range-expanding plant species differs from co-occurring natives. *J. Ecol.* **101**, 1093–1102 (2013).
- Engelkes, T. *et al.* Successful range-expanding plants experience less above-ground and below-ground enemy impact. *Nature* **456**, 946–948 (2008).
- Van Grunsven, R. H. A., van der Putten, W. H., Bezemer T. M. & Veenendaal, E. M. Plant–soil feedback of native and range-expanding plant species is insensitive to temperature. *Oecologia* **162**, 1059–1069 (2010).
- McCarthy-Neumann, S. & Ibáñez, I. Tree range expansion may be enhanced by escape from negative plant–soil feedbacks. *Ecology* **93**, 2637–2649 (2012).
- Gundale, M. J. *et al.* Interactions with soil biota shift from negative to positive when a tree species is moved outside its native range. *New Phytol.* **202**, 415–421 (2014).
- Jump, A. S., Mátyás, C. & Peñuelas, J. The altitude-for-latitude disparity in the range retractions of woody species. *Trends Ecol. Evol.* **24**, 694–701 (2009).
- Schweitzer, J. A. *et al.* Are there evolutionary consequences of plant–soil feedbacks along soil gradients? *Funct. Ecol.* **28**, 55–64 (2014).
- terHorst, C. P. & Zee, P. C. Eco-evolutionary dynamics in plant–soil feedbacks. *Funct. Ecol.* **30**, 1062–1072 (2016).
- Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026 (2011).
- Bridle, J. R. & Vines, T. H. Limits to evolution at range margins: when and why does adaptation fail? *Trends Ecol. Evol.* **22**, 140–147 (2007).
- Angert, A. L. The niche, limits to species' distributions, and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. *Proc. Natl Acad. Sci. USA* **106**, 19693–19698 (2009).
- Ettema, C. H. & Wardle, D. A. (2002). Spatial soil ecology. *Trends Ecol. Evol.* **17**, 177–183 (2002).
- Yang, Y. *et al.* The microbial gene diversity along an elevation gradient of the Tibetan grassland. *ISME J.* **8**, 430–440 (2014).
- Wagg, C., Husband, B. C., Green, D. S., Massicotte, H. B. & Peterson, R. L. Soil microbial communities from an elevational cline differ in their effect on conifer seedling growth. *Plant Soil* **340**, 491–504 (2010).
- Classen, A. T. *et al.* Direct and indirect effects of climate change on soil microbial and soil microbial–plant interactions: what lies ahead? *Ecosphere* **6**, 1–21 (2015).
- Sedlacek, J. F., Bossdorf, O., Cortés, A. J., Wheeler, J. A. & van Kleunen, M. What role do plant–soil interactions play in the habitat suitability and potential range expansion of the alpine dwarf shrub *Salix herbacea*? *Basic Appl. Ecol.* **15**, 305–315 (2014).
- Bardgett, R. D. & Wardle, D. A. *Aboveground–Belowground Linkages: Biotic Interactions, Ecosystem Processes, and Global Change* (Oxford Univ. Press, 2010).
- Fierer, N. & Jackson, R. The diversity and biogeography of soil bacterial communities. *Proc. Natl Acad. Sci. USA* **103**, 626–631 (2006).
- Woolbright, S. A., Whitham, T. G., Gehring, C. A., Allan, G. J. & Bailey, J. K. Climate relicts and their associated communities as natural ecology and evolution laboratories. *Trends Ecol. Evol.* **29**, 406–416 (2014).
- Kardol, P., De Deyn, G. B., Laliberte, E., Mariotte, P. & Hawkes, C. V. Biotic plant–soil feedbacks across temporal scales. *J. Ecol.* **101**, 309–315 (2013).
- Sundqvist, M. K., Sanders, N. J. & Wardle, D. A. Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. *Annu. Rev. Ecol. Evol. S.* **44**, 261–280 (2013).
- Braatne, J. H., Rood, S. B. & Heilman P. E. in *Biology of Populus and its Implications for Management and Conservation* (eds Stettler, R. F. *et al.*) 57–85 (NRC Research, 1996).
- Capon, S. J. *et al.* Riparian ecosystems in the 21st century: hotspots for climate change adaptation? *Ecosystems* **16**, 359–381 (2013).
- Fischer, D. G. *et al.* Plant genetic effects on soils under climate change. *Plant Soil* **379**, 1–19 (2013).
- Hargreaves, A. L., Samis, K. E. & Eckert, C. G. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *Am. Nat.* **183**, 157–173 (2014).
- Ordóñez, A. & Williams, J. W. Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. *Ecol. Lett.* **16**, 773–781 (2013).
- Evans, L. M. *et al.* Geographical barriers and climate influence demographic history in narrowleaf cottonwoods. *Heredity* **114**, 387–396 (2015).
- Holeski, L. M., Zinkgraf, M. S., Couture, J. J., Whitham, T. G. & Lindroth, R. L. Transgenerational effects of herbivory in a group of long-lived tree species: maternal damage reduces offspring allocation to resistance traits, but not growth. *J. Ecol.* **101**, 1062–1073 (2013).
- Madritch, M. D., Greene, S. L. & Lindroth, R. L. Genetic mosaics of ecosystem functioning across aspen-dominated landscapes. *Oecologia* **160**, 119–127 (2009).

37. Gehring, C. A., Mueller, R. C. & Whitham, T. G. Environmental and genetic effects on the formation of ectomycorrhizal and arbuscular mycorrhizal associations in cottonwoods. *Oecologia* **149**, 158–164 (2006).
38. Caporaso, J. G. *et al.* QIIME allows analysis of high-throughput community sequencing data. *Nat. Methods* **7**, 335–336 (2010).
39. Krohn, A. *et al.* Optimization of 16S amplicon analysis using mock communities: implications for estimating community diversity. Preprint at <https://doi.org/10.7287/peerj.preprints.2196v2> (2016).
40. Bever, J. D. *et al.* Rooting theories of plant community ecology in microbial interactions. *Trends Ecol. Evol.* **25**, 468–478 (2010).
41. Brinkman, P. E., van der Putten, W. H., Bakker, E. J. & Verhoeven, K. Plant–soil feedback: experimental approaches, statistical analyses and ecological interpretations. *J. Ecol.* **98**, 1063–1073 (2010).
42. Sykorova, Z., Ineichen, K., Wiemken, A. & Redecker, D. The cultivation bias: different communities of arbuscular mycorrhizal fungi detected in roots from the field, from bait plants transplanted to the field, and from a greenhouse trap experiment. *Mycorrhiza* **18**, 1–14 (2007).
43. Zinke, P. J. The pattern of influence of individual forest trees on soil properties. *Ecology* **43**, 130–133 (1962).
44. McCarthy-Neumann, S. & Kobe, R. K. Conspecific and heterospecific plant–soil feedbacks influence survivorship and growth of temperate tree seedlings. *J. Ecol.* **98**, 408–418 (2010).
45. Blanquart, F., Kaltz, O., Nuismer, S. L. & Gandon, S. A practical guide to measuring local adaptation. *Ecol. Lett.* **16**, 1195–1205 (2013).
46. Ke, P. J., Miki, T. & Ding, T. S. The soil microbial community predicts the importance of plant traits in plant–soil feedback. *New Phytol.* **206**, 329–341 (2015).
47. R Core Team. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2013); <http://www.r-project.org>

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## Author contributions

M.E.V.N., J.K.B. and J.A.S. participated in the study design. M.E.V.N. performed the field work, data collection and statistical analyses. All authors discussed the results. M.E.V.N. wrote the initial manuscript draft, with significant edits from J.K.B. and J.A.S.

## Additional information

**Supplementary information** is available for this paper.

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## Competing interests

The authors declare no competing financial interests.