

## LETTER

# Extensive mismatches between species distributions and performance and their relationship to functional traits

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### Abstract

Mismatches between species distributions and their optimal habitat are predicted by ecological theory and will affect species responses to changing climate. However, empirical tests lack consensus on the prevalence of such mismatches and their underlying mechanisms. Here we present a conceptual framework to quantify the mismatch between optimal conditions for species occurrence and multiple measures of population and individual performance (density, adult growth and survival, and recruitment) and the associated performance reduction, or cost. We quantified these mismatches for 59 tree species in the western US along a soil water balance gradient and found high variability in mismatches among species and among performance measures, often resulting in high costs. We used functional traits to explore how dispersal limitation, migration lags, and competitive exclusion may cause mismatches. Overall, the large variability in mismatches, their costs and the relationship with functional traits highlight the nuanced relationships between species' performance and their distributions.

### Keywords

demography, FIA, forest inventory, niche theory, soil water balance, species distributions, water limitation.

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## INTRODUCTION

The relationship between a species' distribution and performance is fundamental to niche concepts in ecology (Hutchinson 1957), and for understanding how climate change will affect species distributions (Ehrlén & Morris 2015; Petchey *et al.* 2015). It is intuitive to think that species are more likely to occur in the environments where they have greater population growth rates, and most species distribution models rely on this intuition by assuming species' patterns of occurrence reflect environmental suitability. This expectation arises from the basic principle that demographic performance – growth, survival, reproduction and dispersal – are what determine a species' population dynamics and therefore density. However, for long-lived species in particular, historical performance is what gave rise to current distributions, and any process that changes performance over time can cause species distributions to become mismatched from current performance. These processes include anthropogenic management, such as harvesting or planting of species, and temporal variation in the environment, such as changing climate (Pulliam 2000; Guisan & Thuiller 2005; Holt *et al.* 2005). In addition, biotic interactions (e.g. competition), dispersal limitation and source–sink dynamics can also displace species' distributions from their optimal conditions. Such mismatches can bias predictions of species' responses to changing climate (Faurby & Araújo 2018). Despite these reasons to expect mismatches between distributions and performance, and their important implications, there is little consensus among empirical tests of these relationships (Pironon *et al.* 2017a).

Empirical tests of this performance–distribution relationship lack consensus in part because available data all have limitations that may affect their interpretation. The ideal

performance data would be estimates of population growth rates, but these rarely exist across geographic scales. More available are estimates of species' densities or in some cases demographic rates (e.g. growth, survival, recruitment). Density is appealing because it is an integrative measure of population performance, although for long-lived species time lags may cause density to be far from equilibrium. For instance, low densities may indicate newly colonised sites or declining populations (Ehrlén & Morris 2015) and density can be manipulated in managed populations. Demographic rates provide a more contemporary measure of suitability, but may not reflect long-term population dynamics and are rarely collected across large environmental gradients. As a result, studies have used vastly different measures of species performance (Box 1). Moreover, it is unclear how best to quantitatively compare species distributions and performance, leading to a variety of approaches in the literature and making it difficult to make generalisations (Box 1).

Nonetheless, some studies have reported large mismatches between species distributions and their suitable habitat, but with significant variability among species. For example, many species are not consistently most abundant in the centre of their ranges (McGill 2012; Dallas *et al.* 2017), and their individual demographic rates also appear to be only weakly positively related to occurrence probabilities (Canham & Murphy 2016a,b, 2017) or even negatively related (Thuiller *et al.* 2014). The recruitment of new individuals (e.g. tree seedlings or saplings) has been commonly examined because it may indicate whether species show signs of migration. Although there is again mixed evidence among species and studies, recruitment patterns are generally not well matched to adult distributions, and the differences do not tend to suggest directional migration in response to changing climate (Zhu *et al.*

### Box 1. Approaches to quantifying the performance–distribution relationship

Although the relationship between species distributions and performance underlies many basic ecological questions, there are no standard methods for making this comparison. One reason is that a species' distribution and its performance can each be defined and estimated in substantively different ways. A species' distribution can be characterised by patterns of occurrence or abundance, and at a range of scales. Similarly, measures of performance vary from simply abundance to individual demographic rates or population growth rates. Here, we provide a brief overview of the different approaches and methods that have been used to compare species distributions and performance.

#### Abundance – distribution

Perhaps the simplest test of how a species' performance relates to its distribution is to analyse how abundance or density varies within its range. The long-standing 'abundant center,' or 'center-periphery' hypothesis is one example, proposing that species should be most abundant within the centre of their geographic range (Brown 1984). Empirical support for the relationship between occurrence and abundance has been mixed (Dallas & Hastings 2018; Santini *et al.* 2018).

However, abundance can be a poor indicator of a species' performance in response to the environment because it also reflects interactions with other species and intrinsic population processes (e.g. density-dependence). Moreover, source-sink dynamics can result in large population sizes in unsuitable 'sink' habitat (Pulliam 2000). Therefore, the remaining approaches discussed below quantify measures of individual or population performance, typically based in demographic rates.

#### Demographic rates – distribution

Demographic rates (growth, reproduction, survival) are good measures of individual performance. In trees, these rates are affected by climate, stand dynamics (via competition and facilitation), and life stage/ontogeny, so these factors must be accounted for when assessing species' climatic niches. An advantage to working with individual rates is their different responses to environmental gradients can have important consequences for long-term population dynamics (Doak & Morris 2010; Vilellas *et al.* 2015).

Recruitment rates are commonly used to examine performance–distribution relationships because of their importance for species migration (Zhu *et al.* 2012; Serra-Diaz *et al.* 2016). More simply, population structure can be used. Wason & Dovciak (2017) examined the geographic distribution of saplings and adult trees, showing that species varied in their tendencies towards shifting distributions across an elevation gradient.

Adult growth and survival are also important for long-lived species like trees. Canham *et al.* (2016a, 2017) quantified how tree species' demographic rates and their probabilities of occurrence both respond to climate gradients, but made only qualitative comparisons of these response curves. McGill (2012) calculated the Pearson correlations between species' growth rates (from tree ring data) and their importance values (a measure of relative abundance), finding mostly negative correlations between growth rates and importance values.

#### Population dynamics – distribution

Finally, population dynamics integrate the performance across a species' life stages, and therefore help to identify the mechanisms linking performance and distributions (Schurr *et al.* 2012). The relationship between population dynamics and species distributions are theoretically quite clear: in the absence of dispersal, species should only be present in places that support positive population growth rates when the species is rare (Godsoe *et al.* 2017).

The simplest approach to using population dynamics to compare species' distributions and performance is analogous to the 'abundant-center' hypothesis. For example, Aikens & Roach (2014) quantified population dynamics of an endemic Appalachian plant across its range to show a decline in demographic performance towards its range edge, despite there being no such decline in abundance. Similarly, Diez *et al.* (2014) showed that population growth responses to the environment were highly decoupled from an orchid's pattern of distribution.

A more thorough test of the relationship between distributions and population dynamics involves parameterising a fully spatially explicit population model and comparing projections to observed distributions. For example, Merow *et al.* (2014) found that a population model of the shrub *Protea repens* accurately predicted occurrences and absences 71% and 70% of the time respectively. This approach provides a very useful quantitative measure of mismatch, although the requirement for intensive data may limit its applicability across species.

2012; Serra-Diaz *et al.* 2016; Wason & Dovciak 2017). Studies comparing distributions to predicted population growth rates have also shown significant mismatches between where species

are present and where they are predicted to perform well (Diez *et al.* 2014; Merow *et al.* 2014; Csörgő *et al.* 2017). Overall, these studies offer significant evidence that species are

not always distributed where they perform best, but the mechanisms and generality of these relationships remain poorly understood.

The implications of mismatches between population performance and distribution depends on how variable performance is across the species range. For example, a mismatch between population performance and distribution may not result in reduced performance if the species is relatively insensitive to environmental variation. Conversely, even a small mismatch may cause large performance reductions for species with highly variable performance across the gradient (Fig. 1). This can be important in non-equilibrium distribution cases or instances with many absences due to dispersal limitation where the potential distribution of the species is estimated poorly from occurrence data alone (Hattab *et al.* 2017; Merow *et al.* 2017).

In this study, we outline a novel approach for quantifying the relationship between species distributions and performance across environmental gradients, and offer a unique test of these relationships. Our approach and analyses focus on quantifying two complementary measures of the relationship between species' performance and distribution (Fig. 1): (1) the mismatch in climate space between species' optimal performance, measured by density and demographic rates (growth, survival, and recruitment), and their peak probability of occurrence, and (2) the performance cost or the reduction in each performance rate associated with the mismatch, which depends on the shape of a species' response to environmental gradients.

We analyse density and contemporary demographic rates separately as each provides unique information about population and/or individual performance and will refer to all of these responses collectively as performance rates for simplicity. We quantified these relationships for 59 tree species across the Pacific slope of North America in order to ask several questions: (1) How commonly are the optimal conditions for each performance rate mismatched from the optimal conditions for a species based on occurrence? (2) Within species, do mismatches of different performance rates reflect similar

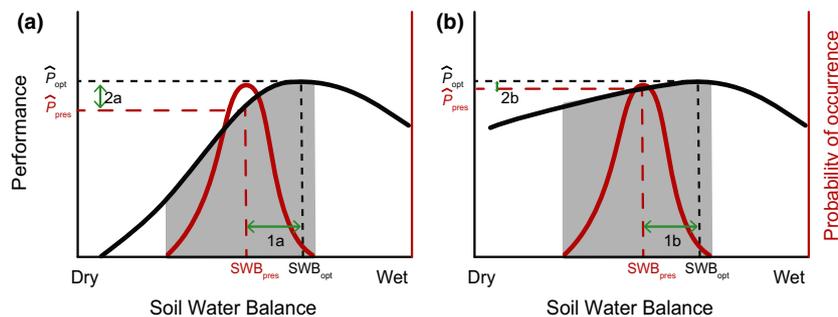
patterns? (3) Do species' traits help explain mismatches between performance and distributions? (4) What are the costs, or declines in performance, associated with these mismatches?

We also used this approach to test several hypotheses about how species' competitive abilities, dispersal, and lifespan affect this mismatch between species performance and distributions. Specifically, we hypothesised that competitively inferior species may exhibit larger mismatches as they are displaced to less than optimum environments (Canham *et al.* 2006; McGill 2012). We also expected that species with poor dispersal abilities or long lifespans may exhibit large mismatches due to an inability to track suitable habitat.

## METHODS

### Study system/data

The US Forest Service's Forest Inventory and Analysis (FIA) program collects individual tree-level data in plots distributed across the United States, making it a unique dataset for analysing the distribution and performance of tree species. Plots are subject to variable management activities such as salvage, selective and clearcut harvesting as well as planting and direct seeding. The gridded design helps to ensure that the data are representative of the forests in the region as a whole. The plot sampling design consists of 1-acre permanent plots in which the diameter at breast height (DBH) and survival of all adult trees are measured and tree recruitment is quantified at 5–10-year intervals (Woudenberg *et al.* 2010). In this study, we analysed the data from the Pacific Northwest (PNW) regional unit which comprises 21 107 plots in California, Oregon and Washington. Many of these trees have distributions that extend past this region, but for simplicity, we will refer to the species distribution within this region as the distribution. Trees are sampled in a nested design, in which each plot consists of four subplots (24.0 ft diameter) where all trees > 5.0 inches diameter at breast height (DBH) are measured. Within each subplot, small trees



**Figure 1** Key measurements for quantifying distribution–performance mismatches for two hypothetical species. The curves are performance (black) and occurrence (red) responses to an environmental gradient, which are estimated from regression models. We calculated mismatch (1) as the difference in SWB between the performance optimum and occurrence optimum ( $SWB_{opt} - SWB_{pres}$ ). These hypothetical species show positive mismatches, meaning that their peak probability of occurrence is in a drier environment than their peak performance. This could be calculated for any environmental axes, but we focus here on SWB due to the overwhelming importance of water availability in western forests. Performance cost (2) is the difference between the predicted performance at  $SWB_{opt}$  ( $P_{opt}$ ) and  $SWB_{pres}$  ( $P_{pres}$ ) divided by the range of performance values to yield % reduction. Here, both species have identical mismatches (1a and 1b), but species a has a larger performance cost (2a and 2b), illustrating how species' different demographic sensitivities to environmental variables may lead to widely varying performance costs given the same mismatch.

(< 5 in. DBH) and seedlings (< 1 in. DBH) are counted within a microplot (6.8 ft diameter). From these data, several measures of performance can be calculated, including density, growth, survival and recruitment rates, as well as species distributions based on occurrence.

The forests analysed in this study span a large geographic gradient in water availability, from semi-arid oak woodlands with as little as 4 cm mean annual precipitation (Davis *et al.* 2015) to pacific temperate rainforests receiving upwards of 100 cm annually (Waring & Franklin 1979). Water availability has been shown to be a key driver of tree performance in California forests (Stephenson 1998), and drought and heat-related mortality has been underestimated even in mesic forests (Allen *et al.* 2015). Therefore, we focused our analyses on species' responses to water availability while accounting for temperature and stand characteristics. For water availability, we used soil water balance (SWB) specifically, the Priestley–Taylor alpha coefficient (Priestley & Taylor 1972), a dimensionless ratio of annual actual evapotranspiration (AET) over potential evapotranspiration (PET). SWB ranges from 0 for completely dry soils to 100 for saturated soils. We extracted the 50-year normal (1950–2000) Priestley–Taylor coefficient from the Global High-Resolution Soil-Water Balance dataset, which has a resolution of 30 arcseconds (~1 km) (Trabucco & Zomer 2010). For temperature, we extracted the 30-year normal (1970–2000) mean annual temperature to the nearest degree Celsius at the same spatial resolution from WorldClim (Fick & Hijmans 2017) (Fig. S1). We estimated stand characteristics from FIA plot data. We processed all GIS raster layers, using the R package *raster* (Hijmans 2018) and all environmental data was extracted for the true plot locations.

### Conceptual framework and modelling overview

Our general framework for quantifying the mismatches between performance and distributions is based on statistical models of how occurrence, density, and demographic rates respond to key environmental gradients. We focused on responses to the SWB gradient, while also accounting for temperature and stand-level variables that could confound estimated relationships with SWB. Thus, our process was to fit statistical models of species occurrence and performance across the SWB gradient, and calculate the mismatches and associated costs as outlined in Fig. 1.

We fit all distribution and performance models (described below) as Bayesian models using Stan (Stan Development Team 2018b) interfaced through R using the *RStan* package (Stan Development Team 2018a). We used non-informative priors for all parameters and convergence was assessed visually and using the Gelman–Rubin statistic. We used Bayesian models to facilitate calculation of the mismatches and performance costs (discussed below). We assessed statistical significance of parameters, using the credible intervals of the parameters. We defined highly significant parameters as having posterior distributions with 95% of its mass on one side of zero, and significant and marginally significant parameters as having 90 and 85%, respectively.

### Distribution models

To estimate how each species' probability of occurrence responds to the SWB gradient, we fit generalised linear models using a Bernoulli error distribution to the plot-level presence/absence data from the most recent survey of all FIA plots in the region. We omitted plots established by artificial regeneration in order to avoid potential biases arising from planting decisions, thereby reducing the number of records by 10.6%. We restricted our analysis to 59 species represented in at least 25 plots (Table S1). Species-specific responses to SWB were estimated using first and second-order terms in order to allow for nonlinear climatic responses. SWB is the only predictor in the distribution models here, although other key gradients could be substituted to ask analogous questions.

### Density models

To estimate patterns of density across the SWB gradient, we fit generalised linear models with a negative binomial error distribution on the plot-level tree density data. Similar to occurrence, we fit first- and second-order terms for the SWB response. Because occurrence was based on plots with at least one tree, density was fit to the same 59 species as the occurrence models (Table S1).

### Demographic models

To estimate demographic responses to the SWB gradient conditional on temperature, competition and stand characteristics, we fit different forms of generalised linear mixed models (detailed descriptions in the Supplement). Because survival and growth data are tree-level data, we also included effects of tree size (DBH). We quantified survival from all records of dead trees, either from standing dead records or from repeat measurements, but tree removals were not considered mortality events. We quantified growth from trees with repeat diameter measurements, and recruitment from counts of seedlings within microplots pooled across subplots. All demographic rates models were restricted to species with data from at least 25 plots (Table S1). The intercept of the survival and growth models varied with species and plot to account for species-specific plot random effects. We included SWB, temperature, adult stem density, average basal area of neighboring trees, and DBH when applicable, as fixed effects. We included second-order coefficients for SWB, temperature and DBH to allow for nonlinearities.

### Calculation of performance mismatch and cost

From the distribution models, we calculated SWB where each species is most likely to occur ( $SWB_{pres}$ , Fig. 1). Similarly, for each performance model, we calculated each species' optimal SWB ( $SWB_{opt}$ ) as the SWB value at the maximum predicted performance. We then calculated predicted performance at  $SWB_{pres}$  ( $P_{pres}$ ) and  $SWB_{opt}$  ( $P_{opt}$ ). These calculations used the partial regressions on SWB, and thus reflect the responses to SWB at mean values of the other variables in the regressions.

Using these values, we quantified each species' mismatch and cost for each performance response. Specifically, we

## Box 2. How functional traits may predict mismatches

Functional traits determine how plants interact with their environment and also serve as easy-to-measure proxies for different 'functions' such as competitiveness (Kunstler *et al.* 2015), dispersal (Greene & Johnson 1993; Thomson *et al.* 2011), environmental tolerance (Loehle 1998; Hacke *et al.* 2001) and succession (Valladares & Niinemets 2008; Wilfahrt *et al.* 2014). Because of this, traits offer a promising approach for generalising patterns of mismatches between a species distribution and performance. Traits associated with effective range shifts at the leading edge might be associated with small mismatches (Angert *et al.* 2011; MacLean & Beissinger 2017). Conversely traits associated with lagging trailing edges may be associated with large mismatches (Hampe & Petit 2005). Mismatches may arise from mechanisms other than failing to migrate. Traits associated with competitiveness may predict mismatches and traits related to environmental tolerance might reflect physiological constraints. In this study, we tested whether the direction and/or magnitude of species' mismatches between their distributions and performance were related to specific functional traits within these three categories. Here we outline our predictions for these relationships.

### Leading edge traits

Using seed mass as a proxy for dispersal (Greene & Johnson 1993), we expect the mismatch magnitude to increase with increasing seed mass due to more limited dispersal distances. However, the relationship between seed mass and dispersal ability may depend on dispersal modality, being more relevant for wind-or gravity-dispersed species and less so for animal dispersed species.

### Trailing edge traits

Longer-lived species are more likely to persist in habitats that become suboptimal over time, resulting in slower climate adaptation (Jump & Penuelas 2005) and lagged climate migration and extinction debts (Talluto *et al.* 2017). We expect long lifespans will correspond to larger SWB mismatches in general. Given that warming since the Little Ice Age is reasonably within the lifespan of many of these trees, we expect that longer lived trees will experience more positive SWB mismatches as a result of slow climate migration upslope or upwards in latitude.

### Competitive and environmental tolerance traits

Higher wood density corresponds to slower growth rates and higher survival rates, and is therefore associated with later successional, more competitive species (Chave *et al.* 2009). Therefore, we expect a negative relationship between wood density and SWB mismatches in general. However, wood density is also particularly related to hydraulic safety margins, as denser wood is often more resistant to drought-induced cavitation (Hacke *et al.* 2001). Because dense-wood species have greater tolerances to dry conditions, we expect that wood density could correspond to more positive SWB mismatches.

High specific leaf area (SLA) indicates a resource-acquisitive or 'fast' strategy (Wright *et al.* 2004), which we would expect to be less competitive in general and correspond to higher SWB mismatches. However, high SLA is also associated with shade tolerance (Hallik *et al.* 2009), which could counteract the pattern expected from being out-competed. Additionally, high SLA species are more likely to be stronger competitors in conditions where resources are more abundant, whereas low SLA species are more likely to be stronger competitors in more resource poor environments. We expect high SLA species to occur more often in wetter than optimal conditions and low SLA species to occur more often in drier than optimal conditions, resulting in a negative relationship between SLA and raw SWB mismatch.

Root depth is an important contributor to performance along water gradients, with deep roots performing better in seasonally dry conditions and shallow roots performing better in moist, frequently waterlogged soils where the water table is shallow (Fan *et al.* 2017). We therefore expect shallow rooted species to occur more often in wetter than optimal environments and deeply rooted species to occur more often in drier than optimal environments, due to their ability to tolerate dry conditions. These differences are expected to result in a positive relationship between root depth and the raw SWB mismatch.

Tree height may influence mismatches in distinct ways. Taller trees are superior light competitors; therefore, we may expect a negative relationship between maximum height and SWB mismatch magnitude. However, this competitive advantage may be context-dependent because of tradeoffs between height and cold-hardiness (Loehle 1998). Additionally, tall trees are more susceptible to soil drying as the water potential gradient required to move water up to the canopy scales with tree height (Koch *et al.* 2000). Because of this, we expect that taller trees will be more likely to have smaller or more negative mismatches as populations would not be able to persist in drier than optimal environments.

quantified the SWB mismatch as the difference between optimum SWB conditions for performance and probability of occurrence, or  $SWB_{opt} - SWB_{pres}$ . We quantified the cost of

an SWB mismatch as the percent reduction in predicted performance at the two key SWB values, or  $P_{opt} - P_{pres} / P_{opt} - P_{min} * 100$  (Fig. 1). To test the hypothesis that

mismatches for different performance responses would be similar within species, we conducted linear regressions of mismatches for density and the demographic rates as well as among pairs of demographic rates. We quantified the strength of the relationship between SWB mismatch and cost separately for positive and negative mismatches with Spearman rank correlations due to non-normal distributions of these data.

### Trait analyses

There are a number of ways that different species traits may influence distribution–performance mismatches (Box 2). First, we tested the relationship between mismatch and median SWB conditions for all of the plots, where a species occurred as a proxy for moisture use strategies with simple linear regressions. Next, to test our specific hypotheses, we used multiple regression models to test the relationship between mismatch and six key quantitative traits related to dispersal, migration lags, competition, succession and water relations. We assembled trait data from multiple data sources: TRY (Kattge *et al.* 2011), Bien (Ackerly 2004; Royer *et al.* 2005; Cornwell *et al.* 2006; Kleyer *et al.* 2008; Zanne *et al.* 2009; Blonder *et al.* 2012; Stevens *et al.* 2015; Ameztegui *et al.* 2016; Maitner *et al.* 2018), and the USDA Plants Database (USDA & NRCS 2018). We included phylogenetic relationships in the models when the 95% credible interval of the phylogenetic signal in residual error of the model ( $\lambda$ ) did not overlap zero. We extracted the phylogenetic tree from (Zanne *et al.* 2014), using the *branching* package in R (Chamberlain 2016) and excluded one species not in the tree. We implemented Bayesian one-step multiple imputation because 14 of the 58 species were missing data for one trait and 5 species were missing data for two or more traits. This approach minimises any bias arising from non-randomly distributed missing data among species. We built the trait-mismatch multiple regression models in the *brms* package in R (Bürkner 2017).

## RESULTS

### Performance responses

Performance responses to the SWB gradient varied substantially among species and among density and demographic rates. Because we included quadratic terms for the SWB regression coefficient in the models, species responses could be monotonically increasing or decreasing or a parabolic shape concave up (unimodal) or concave down (U-shaped). Within each of the performance measures, all four shapes were represented. We considered a variable to have a significant effect if either its first- or second-order term (or both) was significantly different from zero because either term signals a significant response when working with centred predictor variables. For density, SWB was the only predictor variable and was significant in 71.19% of species (42 out of the 59). In the demographic models which included other covariates, SWB was a significant predictor for at least one demographic rate in 82.76% and 37.50% of those species had significant responses to SWB across all of the modelled demographic rates. There

was considerable variability among species and among other variables in the demographic models (Figs S3–S6). Temperature was a significant predictor of performance for at least one demographic rate in 82.76% of species. Stand characteristics, measured by stem count and average basal area, were modelled with only first-order terms and were significant predictors for at least one demographic rate in 87.93 and 70.68% of species respectively. Out of the significant regression coefficients, 82.82% of stem count and 86.11% basal area effects were negative. Tree diameter was only included as a predictor for growth and survival and was significant (first- or second-order term) for at least one of the demographic rates in 94.82% of species.

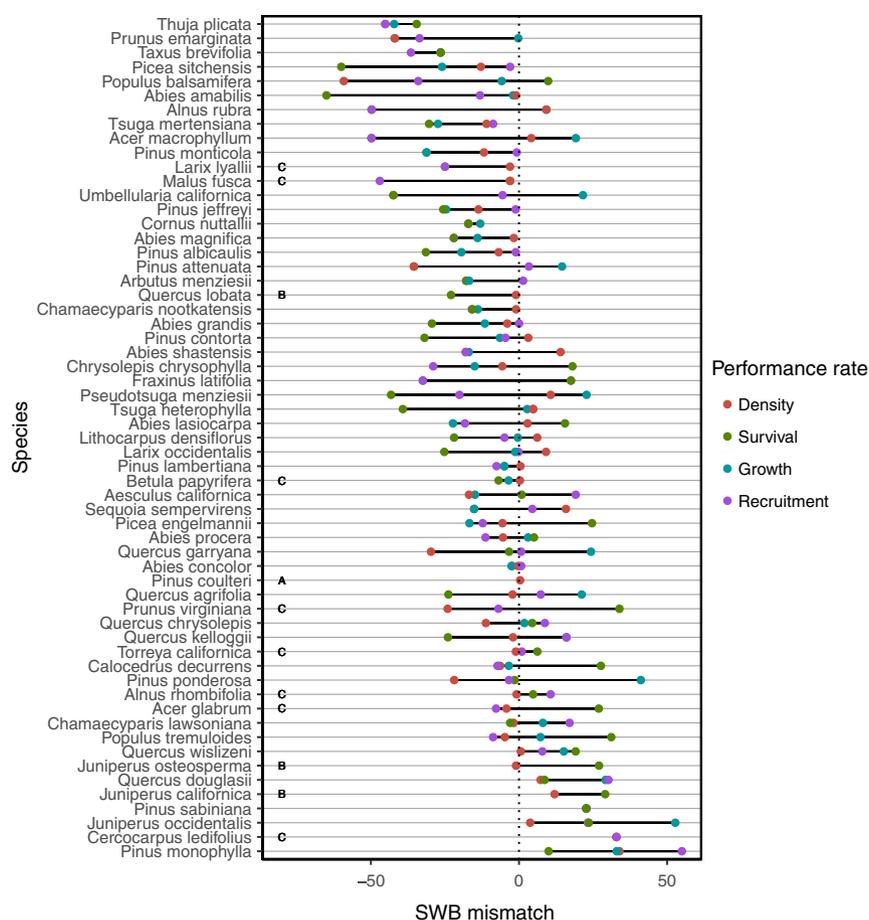
### SWB mismatch

The mean mismatches along the unitless SWB gradient were negative for all performance rates: density, survival, growth and recruitment ( $-5.00 \pm 17.55$ ,  $-9.34 \pm 25.9$ ,  $-1.35 \pm 20.58$ ,  $-6.20 \pm 21.16$ , mean  $\pm$  1SD), meaning that many species' maximum probabilities of occurrence were in wetter than optimal environments (Fig. S7, Tables S2–S3). However, the substantial variability in mismatches and the high prevalence of species to have mixtures of positive and negative mismatches (36 of 58 species with more than one modelled performance rate) show that interpreting these results as evidence that in general species are most likely to occur in wetter than optimal environments could be misleading (Fig. 2). Survival had the largest median mismatches regardless of sign, mismatch magnitude hereafter, followed by growth, recruitment, and density (23.69, 12.03, 10.98, and 6.64 respectively). Density mismatches were weakly positively correlated with demographic rates (Fig. S8; not significant for density-survival or density-growth comparison) and also among demographic rates, indicating that species have somewhat similar mismatches among their different performance measures (Fig. S8 not significant for growth-survival comparison).

### Relationship between traits, phylogeny and mismatch

The relationship between the median SWB of plots where a species was present and the mismatch was significant ( $\text{Pr} > 95\%$ , where  $\text{Pr}$  is the proportion of the posterior distribution on one side of zero) and negative for all performance measures. This suggests that xeric-adapted species are often most likely to occur in drier than optimum conditions for some or all of the performance measures and conversely that mesic-adapted species are often most likely to occur in wetter than optimal conditions for some or all of the performance measures (Fig. 3, Fig. S9). These patterns are consistent with the predictions of hypothetical tradeoffs between competition and tolerance but may also be susceptible to random sampling effects.

Despite the strong relationship between median SWB and mismatch, only few functional traits significantly affected mismatch. Maximum height had a significant negative effect on raw mismatch for survival ( $\text{Pr} > 95\%$ ), indicating that taller species tended to have more negative survival mismatches.



**Figure 2** Each species' SWB mismatch with respect to each performance measure. Each point represents the estimated mismatch for a particular performance measure, and the line connecting them simply represents the variability among different performance measures for a given species. Not all species had data available for all four performance measures; thus, the letters on the left hand side of the panel indicate the total number of performance measures estimated for that species (A = one, B = two, and C = three). Species on the y-axis are ordered by increasing mean mismatch value.

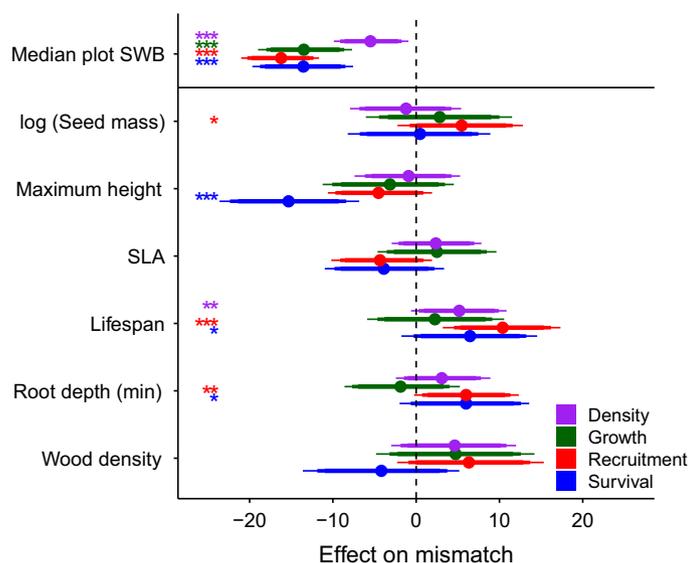
Lifespan had a positive effect on the raw SWB mismatch for density, recruitment, and survival ( $P > 85\%$ ), indicating that long lived species tended to have more positive mismatches. Minimum root depth also had positive effects on survival and recruitment mismatch ( $P > 85\%$ ) and seed mass on recruitment mismatch ( $P > 85\%$ ) (Fig 3). The only significant effects of any traits on mismatch magnitude were a negative effect of maximum height on recruitment mismatches ( $P > 85\%$ ) and a positive effect of lifespan on growth mismatches ( $P > 85\%$ ) (Fig. S10). Phylogenetic signal ( $\lambda$ ) was significant for all models but weak, ranging from 0.082 to 0.18.

#### Performance cost and relationship with SWB mismatch

For each performance rate, the cost measured in percent decline ranged from 0 to 100%. The median decline in performance was greatest for growth (43.35%), followed by survival (31.66%), recruitment (10.21%), and density (9.72%) (Table S4). We found significant ( $P < 0.05$ ) relationships between mismatch magnitude and cost across all performance rates and regardless of sign, so while there was still quite a bit of variation, in general, large mismatches were associated with substantial performance declines (Fig. 4).

#### DISCUSSION

Our analyses show that mismatches between species' distributions and density or demographic rates along the SWB gradient are common, but highly variable among species. These results extend a growing body of research, suggesting that patterns in occurrence do not necessarily match current patterns in density and demographic rates (Diez *et al.* 2014; Thuiller *et al.* 2014; Csergő *et al.* 2017; Pironon *et al.* 2017b). Because current densities of long-lived species are determined by past demographic performance, any factors that lead to changes in performance over time may lead to mismatches between current performance and distributions. In addition, competitive displacement, dispersal limitation or 'over-dispersal' into sink habitats can also all cause mismatches. These mismatches can cause large biases in predictions of species' responses to ongoing climate change (Faurby & Araújo 2018) and in some cases may indicate extinction debts (Talluto *et al.* 2017). This may be particularly important for hybrid spatial-demographic methods that attempt to infer demographic performance from habitat suitability estimated from occurrence patterns (Akçakaya & Sjögren-Gulve 2000; Nenzén *et al.* 2012).



**Figure 3** Effects of functional traits and the average SWB conditions which a species encounters on the SWB mismatch. Positive relationships mean that increasing trait values are associated with positive mismatches, meaning that their peak probability of occurrence is in a drier environment than their peak performance, whereas negative relationships mean that increasing trait values are associated with negative mismatches. For average SWB conditions, small values indicate dry conditions and large values indicate species wet conditions, so the negative relationship there means that species from dry environments are more likely to have positive mismatches and species from wet environments are more likely to have negative mismatches. Significance is based on credible intervals from Bayesian multiple regression models, results from separate models are divided by horizontal line. Asterisks denote high probabilities that the effect of a trait is greater or less than zero (\*\* = probability > 95%; \* = probability > 90%; \* = probability > 85%). We also tested these same effects on mismatch magnitude, results for effects on mismatch magnitude are shown in Fig. S10.

### Relationships among performance measures

Mismatches between demographic rates and occurrence may arise as an artifact of demographic compensation; i.e. when opposing responses of a species' demographic rates to an environmental gradient stabilise population growth rates (Villemas *et al.* 2015; Pironon *et al.* 2017b). In this study, 62.07% of species had demographic rates with mismatches in opposing directions suggestive of demographic compensation, although raw plot-level demographic data correlations were mixed (Fig. S11). To fully evaluate this, accurate measures of long-term population growth rates are required. Density is a more integrative measure of performance than demographic rates, and reflects longer-term dynamics; nonetheless, density and occurrence were also often mismatched.

### Functional traits

These broad patterns of species mismatches appear to be at least partly driven by functional traits associated with life history tradeoffs, such as competition vs tolerance. Different species may have optimal performance under similar conditions, but the less competitive or more tolerant species can be

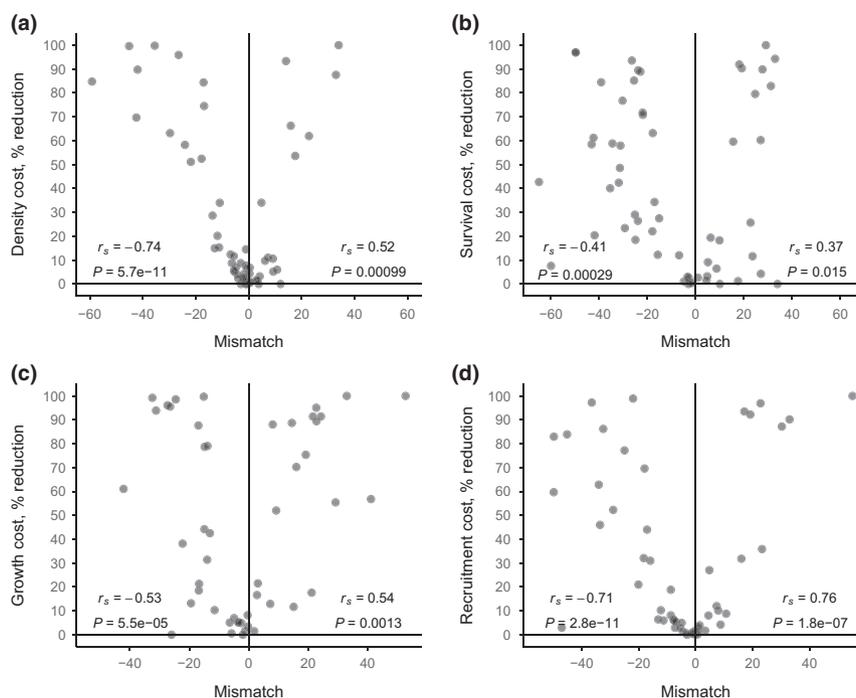
relegated to suboptimal conditions (Loehle 1998; Wisheu 1998; McGill 2012). For example, we found that deeply rooted species have maximum occurrence rates in drier than optimal environments for recruitment and survival, likely because they can tolerate seasonally dry conditions by tapping into deep water sources (Fan *et al.* 2017). Tree height is associated with competitive ability and may help explain why taller trees had smaller recruitment mismatches (King 1990; Loehle 1998). However, traits such as height may affect multiple processes simultaneously. As trees grow taller, leaf water stress increases due to the difficulty of moving water along longer paths against gravity (Koch *et al.* 2000), leaving taller trees more sensitive to changes in soil water. This may therefore increase the chances that taller species occur in locations that are wetter than optimal for survival.

We also found evidence traits associated with climate-tracking may affect mismatches. Species with longer lifespans are more likely to have larger mismatches and specifically maximum occurrence rates in drier than optimal environments (Fig. S8). Long-lived species are likely to remain in suboptimal conditions due to slow population turnover rates and higher tolerance to environmental variability (Morris *et al.* 2008). For such species, distributions may reflect demographic suitability from years or centuries previous. Although precipitation in the western US over the past centuries have been extremely variable, rising temperatures have increased the vapor pressure deficit, effectively making conditions drier for plants, possibly causing these positive mismatches for long lived species. We also predicted that traits related to dispersal distance, such as seed mass and plant height, would influence mismatches through their effects on climate tracking at the leading edge. Plant height is also often a better predictor of seed dispersal than seed characteristics (Thomson *et al.* 2011), suggesting an additional mechanism through which height could produce smaller recruitment mismatches.

We focused our study on water availability because of its importance in this region, but species may be simultaneously limited by other abiotic conditions which may complicate patterns with functional traits. For example, *Pinus attenuata* (Lemmon), a closed-cone pine species endemic to serpentine soils has large negative density and survival mismatches, indicating that occurrence rates peak in wetter environments and density and survival rates peak in drier environments. These negative mismatches likely arise because serpentine soils retain more water than neighbouring chaparral soils where *P. attenuata* is likely to be outcompeted (Vogl 1973).

### Performance costs

In general, larger mismatches between a species' distribution and its performance should result in greater costs. However, this relationship need not be linear because it depends on the shape of the performance and distribution responses to the environment. Our results in fact show a remarkable amount of variability in this mismatch–cost relationship, highlighting the variability among species responses (Fig. 4). In particular, the strength of the mismatch–cost relationship depends on both the performance measure and the direction of the mismatch (Fig. 4).



**Figure 4** Costs to species performance (percent reduction) as a function of SWB mismatch for (a) density, (b) survival, (c) growth, and (d) recruitment. Each point represents the estimated mismatch and cost for a particular species. Spearman rank correlations were calculated separately for species with negative mismatches and positive mismatches and show that costs increase significantly with larger mismatches. Negative mismatches signify when occurrence rates peak in wetter environments than the performance rates, whereas positive mismatches signify when occurrence rates peak in drier environments than the performance rates.

Although somewhat counter-intuitive for water-limited ecosystems, many of the species in our study did have negative mismatches. Wetter than optimal environments can be detrimental to performance for various reasons, including poor soil aeration and increased pathogen loads. Poor soil aeration can lead to slower root development, root rot and root tissue death. Fungal pathogens, mainly of the genus *Phytophthora*, are an increasing threat to western forests and have higher rates of infection in moist conditions (Hansen 2015; Lockman & Kearns 2016). White pine blister rust, *Cronartium ribicola* (Fisch), requires cool moist conditions for the fungus to sporulate and spread (Geils *et al.* 2010). Although infections are not always lethal, they often weaken trees for years before they finally die from the disease or a multitude of stressors, which could explain the higher growth and recruitment costs associated with equivalent negative mismatches in comparison to survival.

On the other end of the water gradient, declines in performance due to water limitation are well studied. Drought avoidant trees conserve water through stomatal regulation at the cost of reduced photosynthesis and growth (McDowell *et al.* 2008). Trees that maintain stomatal conductance in dry conditions often grow dense wood that is more resistant to cavitation, but this also poses a cost to growth in dry conditions (Anderegg & Hille Ris Lambers 2016). High costs to growth and survival from positive mismatches could be caused by aggressive stomatal regulation or steep reductions in xylem conductivity after reaching threshold xylem pressures.

### Challenges and future directions

Despite being a unique quantitative test of distribution–performance mismatches, a number of inherent difficulties with this type of analysis could influence our results. First, even with the extraordinary spatial extent of individual tree data in the FIA dataset, rare species are still poorly represented. The 34 rare species excluded from our analyses might exhibit particularly interesting performance–distribution mismatches precisely due to their restricted distributions. Even for widespread species, there is less performance data in areas where a species is rare, risking inflated influence of the few records towards the environmental extremes. Nonetheless, there did not appear to be a bias in the estimated mismatch related to species rarity (Fig. S12). Second, management activity inevitably influences forest dynamics and may influence observed mismatches and their relationships to functional traits, both directly through altered abundances and/or indirectly through modified competition and disturbances. Our inclusion of stand density and average basal area as predictors of the demographic rates should account for many effects of stand history, but nonetheless could miss any legacies of disturbance or management that are not manifest in these stand characteristics. Additionally, assessments of mismatch can be sensitive to which variables are included in models. We focused on responses to soil water because of its importance for trees in this region, and across North America (Copenhaver-Parry *et al.* 2017), however other environmental variables may be uniquely important for different species. We

chose to model all of the species with the same predictors to enable better comparisons. However, it would also be interesting to quantify the variation among species in which environmental predictors were most important, and their mismatches from those variables. Finally, acquiring environmental data that accurately reflects the conditions experienced by individual trees is always challenging. Fine-scale microclimates associated with small drainages and riparian zones may be particularly important within relatively dry climates, but may not be captured by a 1 km<sup>2</sup> SWB grid cell. Additionally, species that root into deep water sources may effectively experience different conditions than those calculated for water availability in more shallow soil horizons (Baldocchi *et al.* 2004). In such cases, the estimated SWB could appear drier than the conditions actually experienced by trees, leading to over-estimation of occurrence and performance in dry environments.

Two extensions to our approach could further broaden its utility. First, it would be powerful to quantify how population growth rates are related to distributions, in addition to density and individual demographic rates. With population models, the relative importance of individual demographic rates for species persistence can be quantified, further clarifying the mechanisms underlying distribution–performance mismatches (Ehrlén & Morris 2015; Csergő *et al.* 2017). Population models for long-lived trees are challenging, but within reach given new quantitative tools (Needham *et al.* 2018). Second, this approach could be used to examine species' past shifts in distributions (Kelly & Goulden 2008; Crimmins *et al.* 2011) and identify vulnerabilities to ongoing change. In particular, the mismatch and performance cost calculated in our framework may help indicate which species are under the greatest pressure to track environmental changes, and which demographic rates are the most sensitive to these changes. These mismatches and costs could be quantified in spatially explicit analyses to identify, for example, either vulnerable portions of a species range or promising locations for conservation or assisted migration.

## CONCLUSION

Historically, trees have been extremely successful at tracking changes in climate (Clark 1998), however evidence of climate tracking does not necessarily imply that species are in equilibrium with their climatic niche (Ordonez & Williams 2013). Moreover, the pace of contemporary change and potential for no-analog climates (Williams & Jackson 2007; Loarie *et al.* 2009) make future predictions more challenging. Our results highlight a widespread, contemporary lack of congruence between patterns of species occurrence and patterns in density and demographic performance across an important soil moisture niche axis. Additionally, our results suggest that life-history strategies can be useful in understanding mismatches, as made evident by the complex relationships between mismatches and functional traits. These kinds of mismatches, particularly when associated with large declines in performance, suggest the need for cautious interpretation of predictions of how climate change will affect species distributions.

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## AUTHORSHIP

TB and JD designed the research. TB analysed the data. TB wrote the first draft of the manuscript and TB and JD revised the manuscript.

## DATA AVAILABILITY STATEMENT

No new data were used in this work.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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