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LETTER

Tree species diversity increases with conspecific negative density dependence across an elevation gradient

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Abstract

Elevational and latitudinal gradients in species diversity may be mediated by biotic interactions that cause density-dependent effects of conspecifics on survival or growth to differ from effects of heterospecifics (i.e. conspecific density dependence), but limited evidence exists to support this. We tested the hypothesis that conspecific density dependence varies with elevation using over 40 years of data on tree survival and growth from 23 old-growth temperate forest stands across a 1,000-m elevation gradient. We found that conspecific-density-dependent effects on survival of small-to-intermediate-sized focal trees were negative in lower elevation, higher diversity forest stands typically characterised by warmer temperatures and greater relative humidity. Conspecific-density-dependent effects on survival were less negative in higher elevation stands and ridges than in lower elevation stands and valley bottoms for small-to-intermediate-sized trees, but were neutral for larger trees across elevations. Conspecific-density-dependent effects on growth were negative across all tree size classes and elevations. These findings reveal fundamental differences in biotic interactions that may contribute to relationships between species diversity, elevation and climate.

KEYWORDS
biodiversity, conspecifics, density dependence, elevational gradient, environment–diversity relationship, species interactions

INTRODUCTION

A synthetic understanding of the processes that shape biodiversity patterns across spatial and temporal scales is a fundamental goal of ecology (Humboldt & Bonpland, 1807; Tilman & Pacala, 1993; Wright, 2002). Differences in climate, particularly temperature and moisture, play an important role in shaping biodiversity patterns, evidenced by strong associations between climate and species diversity for multiple taxa at local, regional and global scales (Gaston, 2000; Zellweger et al., 2020). Several hypotheses have been proposed that emphasise the importance of historical and biogeographic processes in shaping climate–diversity relationships (e.g. Ricklefs, 1987). Other hypotheses emphasise the importance of biotic interactions in shaping climate–diversity relationships, positing that warmer, wetter and more aseasonal climates favour biotic interactions that maintain higher species diversity (Schemske et al., 2009). A comprehensive evaluation of all potential hypotheses for diversity–environment relationships is beyond the scope of this study. However, a critical first step in evaluating the importance of biotic interactions to climate–diversity relationships is to test whether climatic differences associated with elevation influence the strength of biotic interactions that are thought to maintain species diversity.

Substantial debate has surrounded the contribution of local biotic interactions to patterns of tree species diversity, especially at larger spatial scales (Bagchi et al., 2014; Connell, 1971; Detto et al., 2019; Hülsmann et al., 2020; Janzen, 1970; Jia et al., 2020; LaManna, Mangan, et al., 2017; LaManna et al., 2021; Levi et al., 2019; Ricklefs, 1987). Biotic interactions are thought to maintain higher species diversity if they limit population growth of common species and provide a relative demographic advantage to less abundant species. One such process, known as conspecific negative density dependence (CNDD), is generated by interactions that act in a relatively species-specific way to reduce per-capita tree performance (e.g. survival or growth) when a species is at high abundance and enhance performance when a species is at low abundance (Comita et al., 2014). Such interactions include intraspecific competition for resources and host-specific interactions with mutualists and natural enemies, including pathogens, parasites and predators (Bagchi et al., 2014; Bennett et al., 2017; Bever et al., 1997; Mangan et al., 2010; Packer & Clay, 2000). CNDD is the traditional name for this process, referring to when conspecific density-dependent effects on survival or growth are more negative than heterospecific density-dependent effects (CDD–HDD <0). This results in conspecific suppression (reduced survival or growth in areas of high conspecific density). However, density-dependent effects of conspecifics on survival or growth can also be more positive than heterospecific effects (CDD–HDD >0), resulting in conspecific facilitation. Hereafter, we use the acronym CDD–HDD instead of CNDD to acknowledge that conspecific-density-dependent effects can be more negative or more positive than heterospecific effects.

Yet, we currently lack a comprehensive understanding of how CDD–HDD may vary across environmental gradients. In particular, we know little about how the strength of biotic interactions that generate CDD–HDD might shift with local climate and other factors associated with elevation. Lower elevations are often associated with warmer temperatures and greater relative humidity. Increases in temperature can intensify antagonistic interactions between trees and their parasites (Bell et al., 2020) and cause some fungal associates of trees to switch from mutualists to pathogens (Manter et al., 2005). Disease transmission for plants can also be greater where relative humidity is higher, the climate is more aseasonal and more precipitation falls as rain, all of which can favour fungal pathogen dispersal and activity (Milici et al., 2020). At higher elevations, greater amounts of precipitation as snow, freezing temperatures, shorter growing seasons and greater seasonality likely reduce disease risk, synchronise plant phenology and reduce host specificity of plant pathogens (Busby et al., 2014; Milici et al., 2020). These findings collectively suggest that stronger host-specific effects of pathogens on plants might generate stronger negative CDD–HDD at lower elevations.

Effects of climate on tree–mycorrhizae interactions may also contribute to differences in CDD–HDD across elevations. Relatively host-specific mutualists, such as ectomycorrhizae, provide important limiting nutrients to trees and can alleviate negative CDD–HDD caused by host-specific pathogens (Jiang et al., 2020; Liang et al., 2021). Ectomycorrhizae are thought to be more important to trees at higher elevations where decomposition rates are slower and nutrients less available to trees (Thébault et al., 2014). If so, then ectomycorrhizae may contribute to neutral or even positive CDD–HDD at higher elevations.

While a few studies have shown that CDD–HDD can change over time with climate (e.g. dry years vs. wet years; Bachelot et al., 2015; Lin et al., 2012; Song et al., 2018), relatively few studies have tested whether elevational differences in climate affect CDD–HDD. One previous study in the subtropics found that CDD–HDD in seedling survival (based on 1 year of data) was more negative at 300 m than 600 m, and linked these effects to soil biota (Xu & Yu, 2014). However, whether differences in CDD–HDD are evident across larger elevation gradients or persist into larger size classes remains uncertain. CDD–HDD effects on intermediate to larger size classes are more likely to have greater overall influences on population growth rates for long-lived organisms like trees (Green et al., 2014). Recent spatial analyses of tree recruitment indicate that CDD–HDD may be more negative in tropical than temperate forests and may be more negative in warmer/wetter environments at landscape and regional scales (LaManna, Belote, et al., 2017; LaManna et al., 2016). These findings suggest that spatial differences in climatic factors associated with elevation and latitude may alter CDD–HDD (Figure 1). However, the hypotheses that climate or elevation mediate CDD–HDD remain unresolved in part because of recent debate about how to measure CDD–HDD (Detto et al., 2019; Hülsmann et al., 2020; LaManna, Mangan, et al., 2017). The disagreements include concerns about potential bias in analyses that use spatial data (as opposed to temporal data on survival or growth) or that do not test multiple functional forms of the relationship between local densities and vital rates (Detto et al., 2019; Hülsmann et al., 2020). While we have addressed critiques of spatial CDD–HDD analyses elsewhere (LaManna et al., 2021), an emerging consensus solution is to examine CDD–HDD using long-term dynamic data on plant survival and growth and to explicitly examine multiple functional forms for CDD–HDD (Comita et al., 2010; Detto et al., 2019; Hülsmann et al., 2020; LaManna et al., 2021).

We, therefore, used long-term forest dynamic data to evaluate the following predictions: (1) CDD–HDD is more negative in lower elevation forests associated with greater tree species diversity; and (2) CDD–HDD is more negative in areas experiencing microclimatic conditions that favour greater relative humidity (Figure 1). We tested these predictions using long-term demographic data from 23 old-growth forest plots situated along a

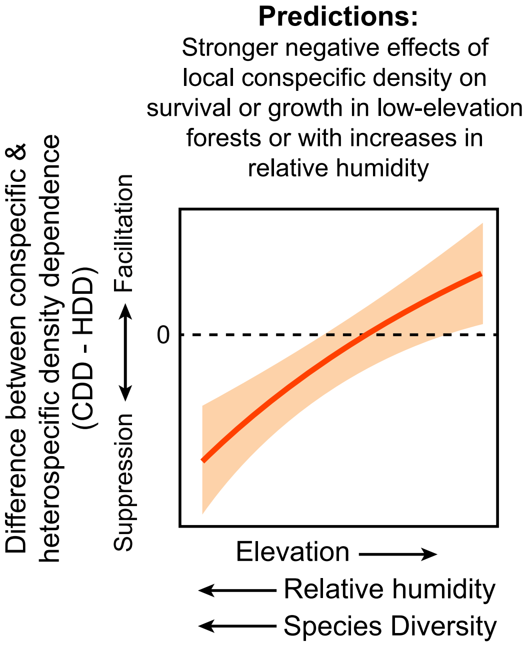

FIGURE 1 Key predictions evaluated in this study, which are generated from the hypothesis that increases in relative humidity associated with elevation alter interactions among plants and their host-specific enemies/mutualists and generate stronger negative effects of conspecific density on survival and growth. CDD–HDD is measured as the effect of local conspecifics on survival or growth (i.e. CDD) minus the effect of local heterospecifics (i.e. HDD; Comita et al., 2010; Hülsmann et al., 2020; LaManna, Mangan, et al., 2017). Mean CDD–HDD across species (orange line) is predicted to be stronger in lower elevation forests associated with greater relative humidity and greater tree species diversity. Negative CDD–HDD is generated by intraspecific competition or interactions with host-specific natural enemies. Disease risk is greater and growing seasons longer at lower elevations which may generate negative CDD–HDD by favouring host-specific pathogens. At higher elevations, freezing temperatures, lower humidity, greater seasonality, more precipitation falling as snow and lower nutrient availability may generate neutral or positive CDD–HDD by reducing pathogen loads and favouring host-specific mutualists

1,000-m elevational gradient in the western Cascade Mountains of Oregon, USA (Figures 2, S1 and S2). Our findings are restricted to trees ≥5 cm diameter-at-breast height (DBH) because smaller trees and seedlings were not surveyed in these long-term plots. Our results indicate that the survival and growth of focal trees were suppressed more by large conspecific trees than large trees of other species (i.e. CDD–HDD <0), and that CDD–HDD in survival of trees 5–25 cm DBH and CDD–HDD in growth of trees 15–25 cm DBH were more negative in low-elevation forests characterised by higher species diversity, greater relative humidity and greater aseasonality than high-elevation forests. Our results reveal elevational and climatic differences in the type and intensity of biotic interactions that generate CDD–HDD and suggest that these differences may be important contributors to relationships between species diversity, elevation and climate.

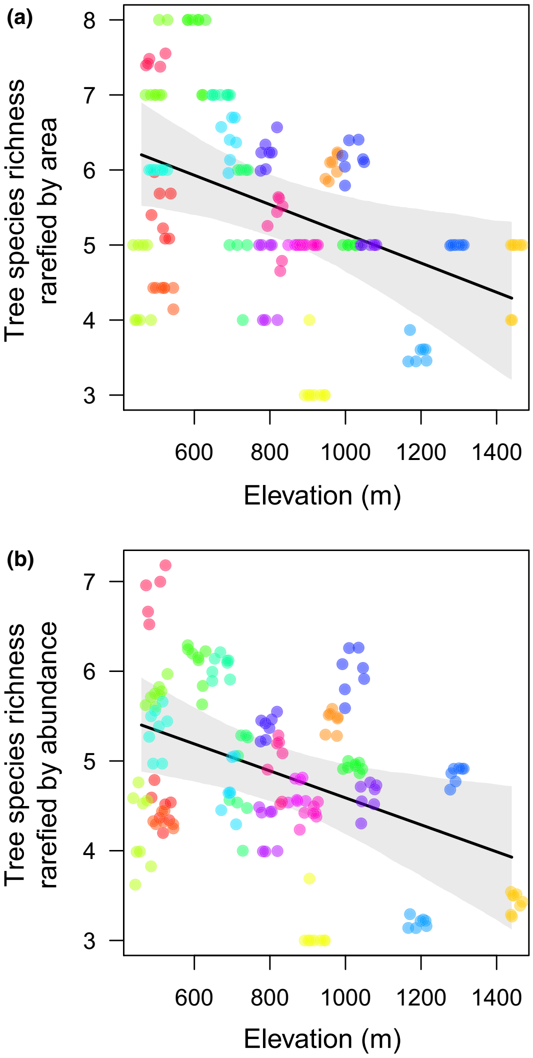

FIGURE 2 Relationships between rarefied species richness and elevation across forest plots in the H. J. Andrews Experimental Forest between 1971 and 2014. (a) Species richness in each census of each forest plot rarefied to 0.25 ha area, the minimum area across forest plots. (b) Species richness in each census of each forest plot rarefied to 51 individuals, which was the minimum abundance across forest plots and censuses. Values of rarefied species richness from the same forest plot (i.e. from different censuses of the same forest plot) have the same colour. The 95% credible interval of the posterior distribution for the slope is shown in grey. Bayesian inference from mixed-effects models that contain random effects of forest plot and census to account for temporal and spatial autocorrelation indicated that slope of the fixed-effects relationship had a 98.2% and 98.6% probability of being less than zero in panels (a) and (b) respectively. Values are slightly adjusted (± 5–30 m elevation) on the x-axis and points transparent for ease of visualisation

MATERIALS AND METHODS

Study sites

We examined 44 years of data (Franklin et al., 2021) collected from 23 old-growth forest plots situated along a 1,000-m elevational gradient in the H. J. Andrews Experimental Forest long-term ecological research site

(HJA) in west-central Oregon, USA. The 6,400-ha HJA encompasses an entire watershed and spans an elevational gradient from 410 m to 1,590 m (Figures S1, S2), characterised by differences in mean annual temperature (range =7.4°C to 10.3°C) and precipitation (range =2,040 mm/yr to 2,354 mm/yr; Wang et al., 2016). The research plots (0.25–4 ha in size; mean size =0.81 ha) along this gradient have been mapped, censused and resurveyed every 5–6 years since the 1970s (Franklin et al., 2021). These forests have some of the tallest trees and largest above-ground biomass of any in the world, with species including Douglas-fir (*Pseudotsuga menziesii*), western red-cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), other conifers including several *Pinus* and *Abies* species and many broadleaf tree species including big-leaf maple (*Acer macrophyllum*) and Pacific dogwood (*Cornus nuttallii*).

Long-term meteorological stations situated near the bottom (436 m) and top (1,268 m) of the elevation gradient show that low-elevation valleys generally have higher mean-spring temperatures and greater relative humidity throughout most of the year than higher elevations (Figure S3). At lower elevations, more moderate temperatures and adequate moisture provide a long growing season for evergreen plant species, even during favourable conditions in winter (Waring & Franklin, 1979). At higher elevations, a short pulse of water from snowmelt in spring/early summer, a dry summer and freezing temperatures throughout the wet season shorten the growing season. Cold-air drainage and pooling are common throughout the year and cause frequent temperature inversions (i.e. lower temperatures at lower elevations) at both the basin-wide scale (entire watershed) and the cross-valley scale (from valley bottom to ridge top within an elevational band; Daly et al., 2010; Rupp et al., 2020). Inversions at these two spatial scales become most decoupled in spring and summer when night-time inversions are common at the cross-valley scale but not the basin-wide scale (Rupp et al., 2020). Importantly, relative humidity varies nearly as much at the cross-valley scale as it does across the entire basin (Figure S3). Thus, we examined differences in CDD–HDD across elevations (reflecting basin-wide differences in relative humidity) as well as across differences in relative humidity between valley bottoms and midslopes/ridges within elevation bands.

Tree species richness across the elevational gradient

Species richness for each forest plot and each census was calculated in two ways to account for differences in species abundances and area surveyed: (1) rarefied to 51 individuals (minimum total abundance across forest plots and censuses) using the 'rarefy' function in the vegan R package; and (2) rarefied to a sampled area of 0.25 ha, which was the minimum sampled area across forest plots using the 'specaccum' function in the vegan R package (Oksanen et al., 2019; R Core Team, 2020). We tested for associations between elevation and tree species richness across forest plots with linear-mixed models that had random intercepts for plot and census using Bayesian approaches in the STAN and 'rstan' R package (Carpenter et al., 2017; Stan Development Team, 2020).

Measuring density dependence (CDD–HDD)

Recent literature has called for estimating density dependence with long-term data on organismal survival and growth (Detto et al., 2019; Hülsmann et al., 2020). Therefore, we used long-term data to assess changes in CDD and HDD across the elevational gradient. We measured CDD–HDD as the effect of local-conspecific density on tree survival and growth minus the effect of local-heterospecific density (Figure S4), which is the recommended approach to disentangle effects attributable to greater numbers of local conspecifics from effects attributable to greater numbers of neighbours in general (i.e. crowding; Comita et al., 2010; Hülsmann et al., 2020; LaManna, Mangan, et al., 2017). If negative per-capita effects of local conspecifics on survival/growth equal negative per-capita effects of local heterospecifics (i.e. CDD = HDD), then these effects are not species specific. Only species-specific negative effects of local conspecifics (beyond background crowding, i.e. CDD–HDD <0) are thought to maintain species diversity (Connell, 1971; Janzen, 1970).

We used Bayesian hierarchical generalised linear mixed models (GLMM) to measure CDD and HDD in annual survival and diameter growth. This approach generated posterior distributions for CDD and HDD for each tree species in each forest plot. We then used average-predictive comparisons with Bayesian bootstrap (Gelman & Pardoe, 2007; Gustafson, 2007; Rubin, 1981) to make inferences on the posterior distributions of CDD–HDD in different elevational bands and microclimates. Using this approach allowed us to calculate CDD–HDD in real-parameter space so that CDD–HDD was comparable among plots and species with different mean values of survival or growth (Breen et al., 2018; Hülsmann et al., 2020).

Our Bayesian GLMMs used flexible local-density indices (LDI) that allow for size dependence, distance dependence and nonlinearities in the responses of tree survival and growth to increasing local density (Comita et al., 2010; Uriarte et al., 2004). We used the long-term forest data to fit parameters for size dependence (controls weighting of tree size in LDI), distance dependence (controls weighting of trees at different distances from a focal tree in LDI) and nonlinearities (threshold responses of survival/growth to increasing local densities; Table S1). This approach allowed evaluation of different functional forms of CDD–HDD to avoid biases that might be generated if we did not account for such dependencies (Hülsmann et al., 2020). Preliminary analyses and a priori reasoning suggested that these dependencies likely differed among trees as a function of size, with survival/growth of larger trees likely affected by other large local trees and smaller trees likely affected by all local trees regardless of size. Thus, we separated the data into size classes that were partially determined by sample design. Trees 5–14.99 cm DBH were only surveyed in subplots that represented 50%–100% of the larger forest plots, so they constituted one size class. Trees ≥15.00 cm DBH were split into three size classes so that approximately equal numbers of individuals would be in each class. This resulted in four size classes: 5–15 cm DBH, 15–25 cm DBH, 25–52 cm DBH and 52–220 cm DBH.

Live trees were surveyed and measured every 3–7 years (mean census interval =5.44 years, SD of census intervals =0.74), and annual mortality assessments were conducted in some plots in some years when logistically feasible. Accordingly, we used approaches that explicitly incorporate variability in census intervals to estimate annual rates of survival (piecewise-exponential survival models; Holford, 1980) and growth (cm-diameter/year). Piecewise exponential survival approaches, which measure mortality rates by modelling time-to-death for each individual, were advantageous because their likelihood function explicitly accounts for multiple observations of the same individual through time and they can incorporate time-varying covariates (Holford, 1980).

The Bayesian GLMMs estimated survival and growth as functions of initial size, census year, distance-weighted abundance of large conspecific and heterospecific adults (≥ 15 cm DBH) within 10-m radii of focal individuals, and interactions of DBH with local conspecific and heterospecific densities. We measured survival and growth for all trees that were >10 m from a plot boundary due to the use of 10-m neighbourhood radii based on the spatial extent of CDD–HDD effects in previous studies (Comita & Hubbell, 2009; Comita et al., 2010; LaManna, Mangan, et al., 2017) and lack of information on large trees outside the plot. We fit our models using the STAN Hamiltonian Monte-Carlo program and R package 'rstan' with 'log' link functions ('log' link functions for survival are equivalent to piecewise-exponential survival models when used with an offset for log-transformed exposure time, and growth data were log-transformed prior to analyses due to right skew). We determined a priori that we would include random intercepts for each species, each plot, each plot-by-species combination and each plot-by-census combination to allow for differences in mean vital rates at each of these levels. These random intercepts also accounted for spatial and temporal autocorrelation in the data. For growth models, we also included random intercepts for each individual. As described above, piecewise-exponential survival models do not require individual random intercepts to appropriately account for multiple observations of individuals (Holford, 1980). We also determined a priori that our models should include a measure of CDD and HDD for each species, each plot and each plot-by-species combination, meaning that models contained a random slope for local-conspecific density and local-heterospecific density at each of these levels. This allowed us to estimate how intercepts and slopes of regressions varied between species and forest plots and to account for dependencies in observations (Gelman et al., 2013). We did not include elevation or microclimate variables in these models because we were interested in comparing how CDD–HDD differed across elevations/microclimates in real-parameter space (in units of real changes in survival and growth) and not in the link-transformed model-fit space given that unit changes in link-transformed space do not reflect consistent changes in real-parameter space (Breen et al., 2018; Hülsmann et al., 2020). We assessed goodness-of-fit with Bayesian residual plots (Hartig, 2021) and posterior-predictive checks (Gelman et al., 2013).

After fitting Bayesian GLMMs for survival and growth and assessing model fit, we transformed posterior distributions for CDD and HDD into real-parameter space using average-predictive comparisons (Gelman & Pardoe, 2007; Gustafson, 2007). For each species in each plot, we calculated the average-predictive value of CDD–HDD as the difference in survival or growth between being in a conspecific stand and a heterospecific stand (at a standardised mean total tree density) averaged across all trees in the data for each posterior sample. To calculate average-predictive comparisons across elevations/microclimates, we applied Bayesian bootstraps (Gustafson, 2007; Rubin, 1981) to make inference across forest plots. Weighted means were calculated at low, mid and high elevations as well as at low, mid and high values of PC2 (described below), weighting each plot by its area and by a randomly determined weight applied iteratively at each posterior sample using the Bayesian bootstrap approach (Gustafson, 2007). We split plots into elevational bands and groups based on PC2 so that an approximately equal number of forest plots was in each group.

Because we did not have relative-humidity data for each forest plot, elevation was used as a proxy for basin-wide differences in relative humidity, and differences in understory microclimate temperature (i.e. minimum spring and mean summer temperatures) were used as a proxy for cross-valley differences in relative humidity (Figure S3). Both of these microclimate variables are related to spring and summer cold-air drainage and pooling that is associated with differences in relative humidity between valleys and ridges that is largely decoupled from broader scale elevational differences (Daly et al., 2010; Rupp et al., 2020). Microclimate variables were obtained from spatial analysis of long-term temperature data (10 years) from 183 understory loggers placed systematically throughout the HJA watershed (Frey et al., 2016; Wolf et al., 2021). We used the second principal component (PC2) from principal components analyses (PCA) to isolate positive covariation between elevation and either minimum spring ($PC2_{MinSpring}$) or mean summer temperatures ($PC2_{MeanSummer}$). Low values for these two variables reflected low-elevation valley bottoms, intermediate values reflected low-elevation midslopes and higher elevation valley bottoms and high values reflected low-elevation ridges and higher elevation midslopes/ridges. PC1 was highly correlated with elevation and was not examined here because of redundancy with how CDD–HDD varies with elevation. See supplemental methods for more details on all of our approaches.

RESULTS

Species rarefied richness decreased with increasing elevation (Figure 2). CDD–HDD in survival differed along the elevation gradient for smaller trees, being more negative in higher diversity, lower elevation sites (Figure 3). At low elevations, CDD–HDD in survival was strongly negative for smaller trees (5–15 cm DBH), less negative for intermediate-sized trees (15–25 cm DBH) and CDD in survival was approximately equal to HDD for trees ≥25 cm DBH (Figures 3a, 4a-c, 5a-c, S6–S8, Tables S1–S4). In contrast, CDD–HDD at higher elevations was only negative for smaller trees, and we found no evidence that CDD in survival differed from HDD for trees >15 cm DBH at high elevations (Figure 3a). CDD–HDD in survival was more negative at lower than higher elevations for smaller trees (Figure 3a, Table S3). For survival of smaller trees (5–15 cm DBH), CDD–HDD generally resulted from negative effects of conspecifics and slight facilitation from heterospecifics (Figure S7 and S8).

Differences in CDD–HDD across the elevation gradient were also associated with microclimate. CDD–HDD in survival for trees 5–25 cm DBH was more negative in low-elevation valley bottoms than at either low-elevation ridges or higher elevation midslopes/ridges, which were locations associated with higher minimum spring temperatures (i.e. $PC2_{MinSpring}$; Figures 3–5) and lower relative humidity (Figure S3). For survival of intermediate-sized trees (15–25 cm DBH), differences in CDD–HDD with microclimate generally resulted from stronger negative effects of conspecifics and greater facilitation from heterospecifics in valley bottoms compared to ridges (Figure S7 and S8).

CDD–HDD in diameter growth was negative for all size classes examined, but especially for trees 15–52 cm DBH (Figure 3c,d). CDD–HDD in growth did not appear to differ across elevations for smaller (5–15 cm DBH) or larger trees (≥25 cm DBH). For trees 15–25 cm, there was a 90.8% probability that CDD–HDD in growth was more negative in low-elevation valley bottoms than at either low-elevation ridges or higher elevation midslopes/ridges, which were locations associated with higher mean summer temperatures (i.e. $PC2_{MeanSummer}$; Figures 3, 6, Figures S6–S8, Tables S1–Table S4) and lower relative humidity (Figure S3).

DISCUSSION

Our analyses of long-term dynamic data on tree survival and growth provide evidence that CDD–HDD shifts along elevation and microclimate gradients associated with plant species diversity and relative humidity. For trees 5–25 cm DBH, CDD–HDD in survival was most negative in lower elevation valley bottoms characterised by greater relative humidity and tree species diversity. In contrast, CDD–HDD in survival was generally weakly negative or neutral at higher elevations (Figure 3). Whereas negative CDD–HDD is thought to maintain species diversity, neutral CDD–HDD is not expected to maintain diversity (Connell, 1971; Janzen, 1970; Mangan et al., 2010; Stump & Comita, 2018). We found that CDD–HDD for 5–15 cm DBH trees at low elevations reduced annual survival probability by an average of 3% (Figure 3). When compounded over the time a tree will typically spend in this size class in our system (50 years based on mean-growth rates), this represents a decrease in cumulative-survival probability from 61% when in the vicinity of large heterospecific trees to only 13% when in the vicinity of large conspecific trees. This substantial decrease in survival of small trees near large conspecifics reduces the probability that the large tree will be replaced by a conspecific upon death. Such effects on small size classes can have disproportionate effects on population and community dynamics of trees later in life (Green et al., 2014). These findings support the idea that fundamental differences in local biotic interactions that generate CDD–HDD, including intraspecific competition and host-specific interactions with natural enemies and mutualists, contribute to larger scale relationships between the abiotic environment and plant species diversity. While beyond the scope of our study, we note that other processes, including historical and biogeographic processes, likely also contribute to such diversity–environment relationships (May et al., 2020; Mittelbach et al., 2007; Ricklefs, 1987).

Our findings of more negative CDD–HDD in lower elevation forest stands support the hypothesis that microclimatic conditions lower CDD–HDD by increasing pressure from host-specific natural enemies, reducing assistance from host-specific mutualists or generating intraspecific competition (Bachelot et al., 2020; LaManna, Belote, et al., 2017). We hypothesised that several mechanisms could lead to more negative CDD–HDD at lower elevations. First, our findings support the idea that aseasonal climates and greater relative humidity generate more negative CDD–HDD (Comita et al., 2014; Milici et al., 2020). Warmer temperatures combined with greater relative humidity can increase disease risk for

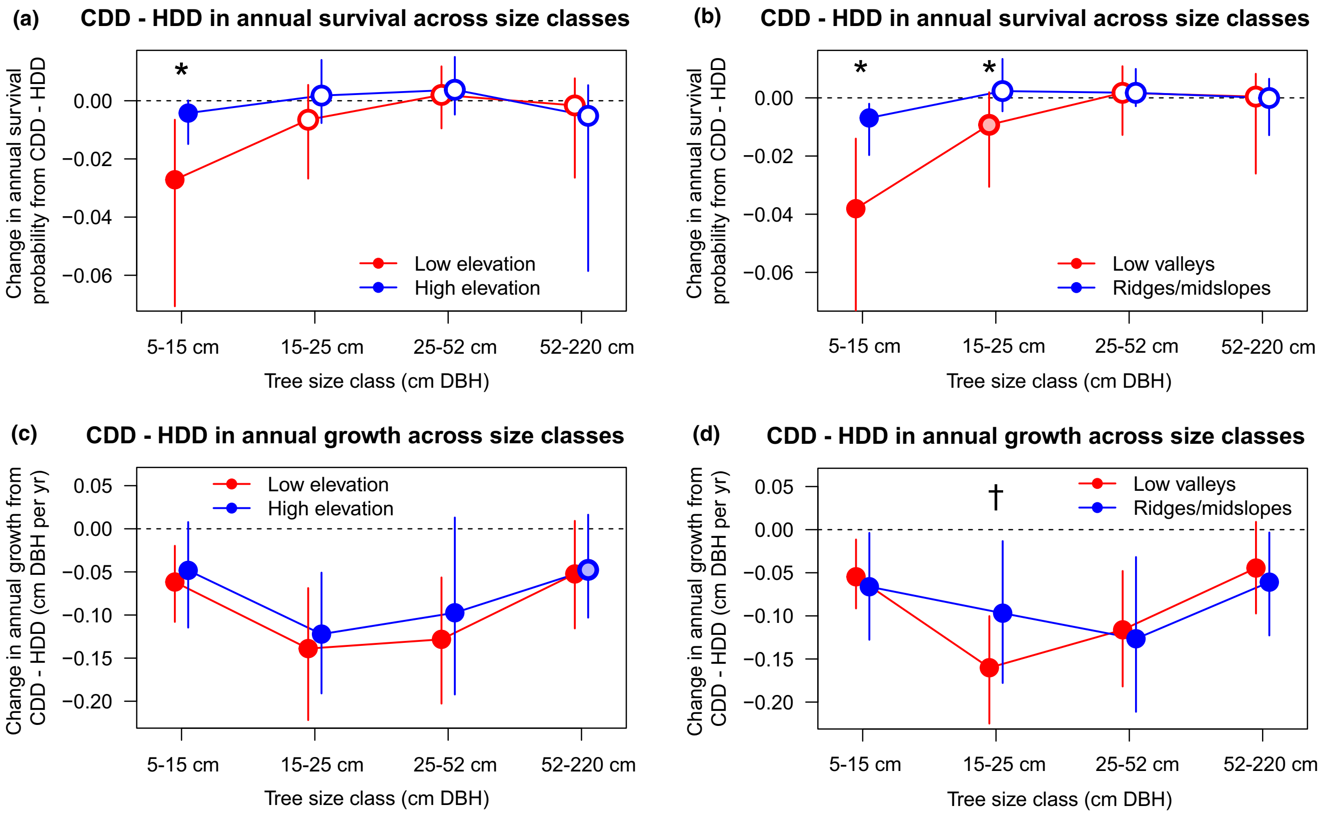

FIGURE 3 Average-predictive comparisons of CDD–HDD in survival (a and b) and growth (c and d) across tree size classes. (a) Differences in CDD–HDD in survival across size classes at high (1,450 m) and low (450 m) elevations. (b) Differences in CDD–HDD in survival between forest plots with lower values of $PC2_{MinSpring}$, indicative of lower elevation valley bottoms that experience colder minimum spring temperatures associated with greater relative humidity, and forest plots with higher values of $PC2_{MinSpring}$, indicative of low-elevation ridges and higher elevation midslopes/ridges that experience warmer minimum spring temperatures associated with lower relative humidity (Figures S1 and S3). (c) Differences in CDD–HDD in growth across size classes at high (1,450 m) and low (450 m) elevations. (b) Differences in CDD–HDD in growth between forest plots with lower values of $PC2_{MeanSummer}$, indicative of lower elevation valley bottoms that experience colder mean summer temperatures associated with greater relative humidity, and forest plots with higher values of $PC2_{MeanSummer}$, indicative of low-elevation ridges and higher elevation midslopes/ridges that experience warmer mean summer temperatures associated with lower relative humidity (Figures S1 and S3). Solid-filled values have ≥95% probability of being different from zero, lightly filled points have a 90%–95% probability of being different from zero, and open points have a <90% probability of being different from zero. Error bars reflect 95% credible intervals. Stars indicate highly probable differences (≥95%), and crosses indicate probable differences (90%–95%) across elevations or PC2 (i.e. difference between red and blue values)

trees (Busby et al., 2014; Milici et al., 2020). Long-term climate data from our site indicate that lower elevations are characterised by warmer mean-spring temperatures and greater relative humidity throughout most of the year (Figure S3), potentially contributing to our observation of more negative CDD–HDD at lower elevations. Relative humidity can also be enhanced by cold-air drainage and pooling, which generates substantial cooling of valley bottoms in the HJA (Daly et al., 2010; Rupp et al., 2020) and may also direct fungal-pathogen spore dispersal into valley bottoms (Edmonds & Driver, 1974). This valley cooling is most decoupled from basin-wide temperature inversions during spring nights and during the summer, likely accounting for observations of more negative CDD–HDD with decreasing minimum-spring and mean-summer temperatures (i.e. PC2). More moderate climates with greater relative humidity, such as in low-elevation valleys, likely favour host-specific pathogens that generate negative CDD–HDD (Milici et al., 2020). In contrast, freezing temperatures and lower relative humidity at higher elevations likely reduce pathogen abundance and dispersal as well as decomposition rates, making fewer nutrients available to trees at higher elevations and increasing the importance of relatively host-specific mutualists like mycorrhizae (Thébault et al., 2014). Similar mechanisms to the ones described here may also drive differences in CDD–HDD across latitudes or across humidity gradients in the tropics (Milici et al., 2020); however, more study in this area is needed. We emphasise that our analyses cannot determine whether differences in CDD–HDD across elevations are due to host-specific pathogens, mutualists or intraspecific competition. Experimental tests are the next step to determine which of these mechanisms is responsible for generating differences in CDD–HDD with elevation and microclimate.

Our findings provide a potential explanation for apparent contradictions between results of two recent

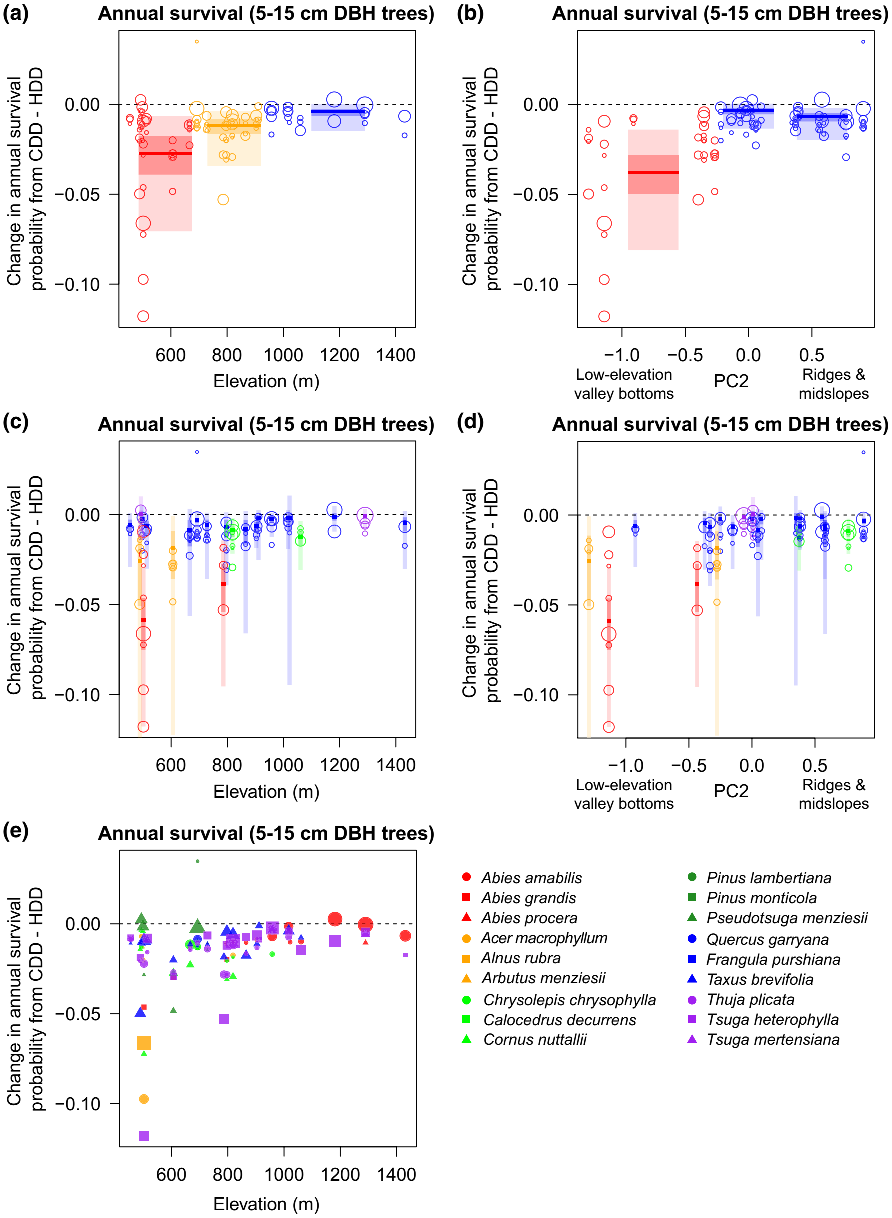

FIGURE 4 Average-predictive comparisons of CDD–HDD in survival of 5–15 cm DBH trees across elevation and microclimate variables. CDD–HDD in survival was defined as the difference in annual survival probability for a focal tree in a stand of conspecific trees (at mean tree density) versus in a stand of heterospecific trees (at mean tree density). (a and b) Average-predictive comparisons were calculated across forest plots at low, intermediate and high values of elevation (a) and $\mathrm{PC2}_{\mathrm{MinSpring}}$ (b) using a Bayesian bootstrap approach to make inference to other forest plots within each group (see text for details). (c and d) Average-predictive comparisons were also calculated at the forest-plot level to show probable differences among the forest plots used in this study. (a–d) Average-predictive values for each species-by-plot combination (circles) are sized according to their sample size (number of individuals). Median values (dark strip), 50% credible intervals (i.e. interquartile range; darker bar) and 95% credible intervals (lighter bar) of the group- or plot-level average-predictive values are also shown. (a and b) Red groups have ≥95% probability of difference from blue groups; orange group has ≥90% probability of difference from blue groups. (c and d) Colours indicate highly probable differences (≥95% probability of difference) among forest plots (red =lower than ≥5 plots; orange =lower than ≥1 plot; grey =no differences from other plots; green =lower than ≥1 plot and higher than ≥1 plot; blue =higher than ≥1 plot; purple =higher than ≥5 plots). (e) Average-predictive values for each species-by-plot combination across elevations

experimental studies. One found more positive and the other found more negative CDD–HDD in seedling survival following warming experiments (Bachelot et al., 2020; Liu & He, 2021). Our findings suggest that warming may generate more positive CDD–HDD if warming also decreases relative humidity (which is expected without an increase in air moisture). However, experimental warming may generate more negative CDD–HDD if relative humidity increases. Our findings are also consistent with one other study of tropical seedling survival finding more positive CDD–HDD in dry than in wet forests (Inman-Narahari et al., 2016). The combined findings from these and our study suggest that projections of increased evapotranspiration and associated declines in

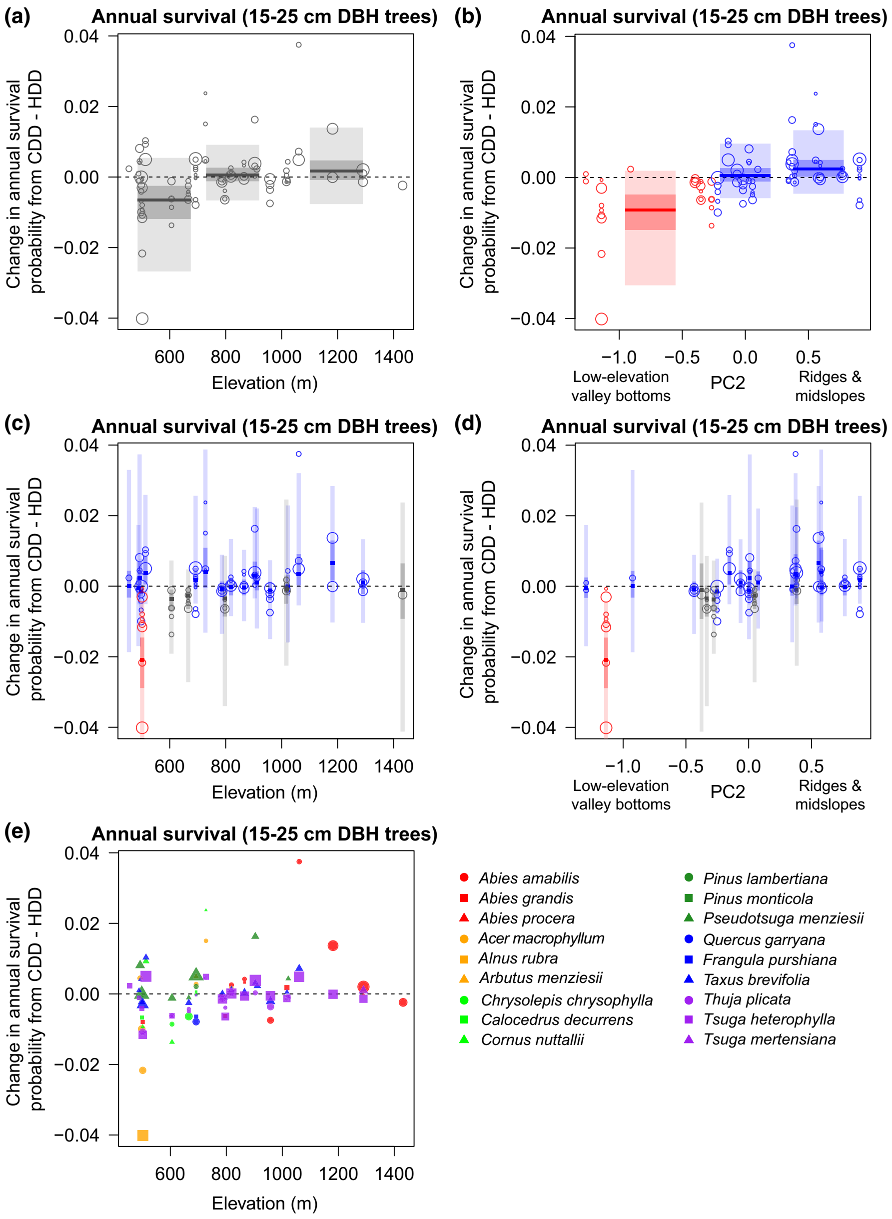

FIGURE 5 Average-predictive comparisons of CDD–HDD in survival of 15–25 cm DBH trees across elevation and microclimate variables ($PC2_{MinSpring}$). CDD–HDD in survival was defined as the difference in annual survival probability for a focal tree in a stand of conspecific trees (at mean tree density) versus in a stand of heterospecific trees (at mean tree density). See Figure 4 for description of panel details; all panel details here are the same as in Figure 4, except data here are for survival of 15–25 cm DBH trees

relative humidity with global climate change (USGCRP, 2017) may cause CDD–HDD to become more positive. Positive CDD–HDD may erode species diversity in the short-term (e.g. by increasing local extinction rates) and potentially in the long-term as well depending on whether new species enter the ecosystem or not.

CDD–HDD in survival was more negative for smaller size classes than for larger size classes, as observed in previous studies (Comita et al., 2014). However, our findings were seemingly contradictory: CDD–HDD in survival was most negative for smaller trees (5–15 cm DBH), whereas CDD–HDD in growth was most negative for intermediate-sized trees (15–52 cm DBH; Figure 3). This apparent inconsistency likely indicates that larger trees are better able to handle increased pathogen loads and other pressures that accompany high local-conspecific densities. Whereas smaller trees are not likely to survive such pressures, intermediate-sized trees may respond by shifting resources from growth to defence in order to survive (Brown et al., 2020). Given strong effects of CDD–HDD on seedling survival observed in previous studies (Comita et al., 2014; Song et al., 2021), our findings suggest that effects of CDD–HDD on tree survival diminish and effects of CDD–HDD on tree growth increase as trees grow larger. Effects of CDD–HDD on growth are important to consider because even

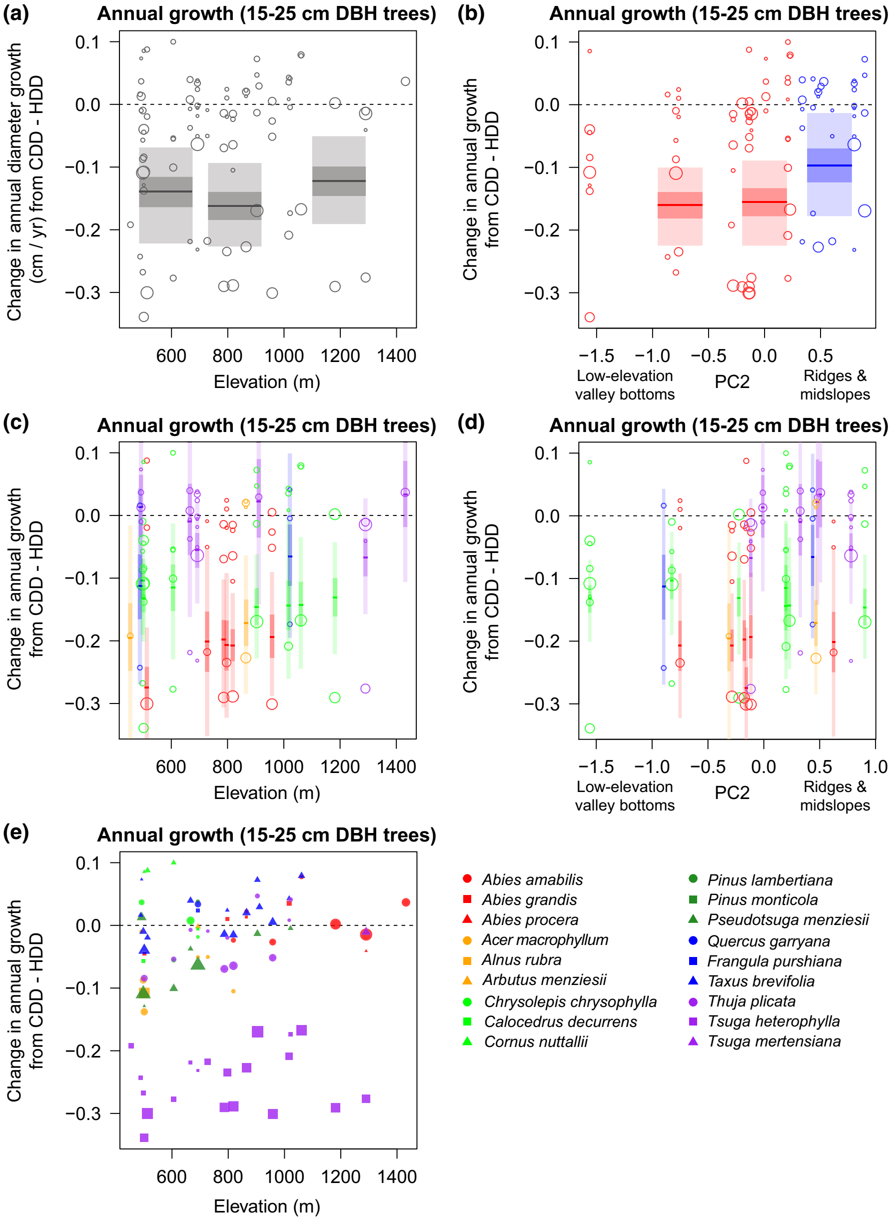

FIGURE 6 Average-predictive comparisons of CDD–HDD in growth of 15–25 cm DBH trees across elevation and microclimate variables ($\mathrm{PC2}_{\mathrm{MeanSummer}}$). CDD–HDD in growth was defined as the difference in annual diameter growth rate (cm per year) for a focal tree in a stand of conspecific trees (at mean tree density) versus in a stand of heterospecific trees (at mean tree density). See Figure 4 for description of panel details; all panel details here are the same as in Figure 4, except data here are for growth of 15–25 cm DBH trees and PC2 is $\mathrm{PC2}_{\mathrm{MeanSummer}}$. The red and blue colours in panel B indicate a 90.8% and 89.1% probability that CDD–HDD in growth was more negative at low and intermediate values of $\mathrm{PC2}_{\mathrm{MeanSummer}}$, respectively, than at high values of $\mathrm{PC2}_{\mathrm{MeanSummer}}$ (as opposed to colours in panels (a) and (b) in Figures 4 and 5, which indicate a ≥95% probability of difference between groups)

if CDD–HDD does not cause mortality, strong negative effects of large trees on the growth of other conspecific trees will likely reduce the probability that these conspecifics will replace the canopy tree. These results highlight the importance of examining density dependence in multiple fitness metrics when measurement of CDD–HDD in population growth rates is not feasible, as with trees and other long-lived organisms (Hülsmann et al., 2020; LaManna et al., 2021). Importantly, we found that negative CDD–HDD on tree growth persisted into the largest size classes (Figure 3), which are responsible for sequestering the vast majority of carbon. This finding suggests that diverse forest stands may be able to sequester carbon at higher rates than less-diverse stands, although more study is needed.

We found notably strong negative CDD–HDD in growth for *Tsuga heterophylla*, a common shade-tolerant species (Figure 6). Shade-tolerant species may experience negative CDD–HDD because they are more likely to be infected by aggressive necrotrophic fungal pathogens than by less-aggressive biotrophs (García-Guzmán & Heil, 2014). However, negative CDD–HDD in growth for *T. heterophylla* did not translate into negative CDD–HDD in survival for this species relative to others. These findings may reflect a strategy of shifting resources from growth to defence for shade-tolerant species experiencing high local-conspecific densities (Brown et al., 2020). However, similarly low CDD–HDD in growth was not observed for other shade-tolerant species (e.g. *Thuja plicata*, *Taxus brevifolia*), likely reflecting a unique strategy of *T. heterophylla*.

While negative CDD–HDD is expected to maintain higher species diversity (Adler et al., 2007; Levi et al., 2019), theoretical and simulation studies suggest that the ability of negative CDD–HDD to maintain diversity may be weakened if CDD–HDD is more negative for rare than common species (Stump & Comita, 2018). However, neither CDD–HDD in survival nor growth was associated with species abundance in our study after accounting for species-level differences (Figure S9). These findings indicate that observed differences in mean CDD–HDD with elevation and microclimate are consistent with theoretical expectations for how CDD–HDD might contribute to elevational patterns in tree species diversity. We acknowledge that links between negative CDD–HDD and coexistence are still a subject of debate (Hülsmann et al., 2020), and the ability of CDD–HDD to affect coexistence is dependent on a number of other factors including fitness hierarchies (Chisholm & Fung, 2020). Other mechanisms, such as differential responses to spatial and temporal environmental heterogeneity, also may play a role in diversity maintenance across elevations (Adler et al., 2006).

Elevational and climatic shifts in CDD–HDD highlight the need for experimental studies to test mechanisms for how and why these shifts occur. A better understanding of the mechanisms by which microclimate alters species interactions and CDD–HDD along elevational gradients will provide important insights into how populations, communities and ecosystems will respond to global climate change. Yet, mechanistic explanations for such shifts have rarely been tested experimentally along climatic, elevational or latitudinal gradients. Replicated experiments with plants along gradients of temperature, humidity, elevation or latitude should ideally manipulate the presence and abundance of agents responsible for CDD–HDD, including host-specific natural enemies, host-specific mutualists and conspecifics (Bagchi et al., 2014; Mangan et al., 2010; Packer & Clay, 2000). Further tests using long-term data on survival and growth, in addition to replicated experiments across different climatic contexts (Bagchi et al., 2014; Jia et al., 2020), will be essential to further our understanding of why CDD–HDD and species diversity shift with changes in climate, elevation and latitude.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

JAL conceived the study, conducted all analyses and wrote the first draft. DMB, RJP and DCS administered data from the forest reference plots across the H. J. Andrews used in this paper. All authors contributed to revisions of the manuscript.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13996.

DATA AVAILABILITY STATEMENT

Data and R code to reproduce all of our analyses are available at: https://doi.org/10.5281/zenodo.6284270 (https://doi.org/10.5281/zenodo.6284270).

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