Functional diversity affects tree vigor, growth, and mortality in mixed-conifer/hardwood forests in California, U.S.A, in the absence of fire

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ABSTRACT

Mixed tree-species forest management can increase forest resilience by reducing the impacts of disturbances that disproportionately affect a single tree species or closely related groups of tree species. Beyond disturbance-risk reduction, tree-species diversification may foster functional-diversity effects (e.g., complementarity or facilitation) that alter the performance of a given tree species in mixed versus pure stands, potentially benefitting carbon sequestration and wildlife habitat. Tree species-mixture effects have been explored to only a limited degree in western US forests and, particularly, in California. Establishing whether vigor, growth, and mortality of common tree species vary with stand composition would help inform restoration and modeling of these forests under climate change. Using data from USDA Forest Service Forest Inventory and Analysis (FIA) plots from California, we examined how individual-tree vigor, as indicated by live crown ratio (LCR), periodic basal area increment (BAI), and mortality odds varied with functional dissimilarity (FDis). We quantified FDis using an index based on 11 traits related to resource acquisition, competition, environmental tolerances, and fire ecology. We classified major tree species into ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), incense-cedar (*Calocedrus decurrens*), true firs (*Abies* spp.), Douglas-fir (*Pseudotsuga menziesii*), live oaks (*Quercus* spp.), and deciduous oaks (*Quercus* spp.) response groups. We tested for the main effects of FDis on tree responses, as well as interactions with tree, site, stand, and climate factors. We found that initial tree height modulated the effects of FDis on ponderosa pine, Jeffrey pine, incense-cedar, and true fir LCR, whereas FDis interacted with climate to alter live oak and deciduous oak LCR. FDis decreased BAI in ponderosa pine and increased BAI in live oaks. FDis interacted with tree size to influence BAI for Jeffrey pine, Douglas-fir, and true firs. We found no evidence that climate or site quality modulated FDis effects on BAI for any species group. Tree mortality was not responsive to FDis, except for the true firs, where both initial tree height and competition interacted with FDis to increase and decrease mortality odds, respectively. FDis effects commonly shifted from positive to negative along gradients of stand structure and site quality, indicating that these effects vary with site and stand conditions. Our results have implications for balancing the ecosystem benefits of mixed stands, such as disturbance risk, carbon sequestration, and habitat during forest restoration projects in the region, as well as for more accurate modeling of complex stands.

1. Introduction

Ecologists have long examined the relationships between productivity and species diversity (Feng et al., 2022), and foresters have planted multiple tree species to enhance production of timber, ecosystem services such as wildlife habitat, and resilience to disturbance (Tang et al., 2022). Planting tree-species mixtures has been found to enhance aboveground productivity in a variety of forest types worldwide (Ammer, 2019; Pretzsch and Schütze, 2021; Feng et al., 2022). Neutral or negative species interactions are also possible, with notable examples from the European Scots pine (*Pinus sylvestris*) and Southeastern United States loblolly pine (*Pinus taeda*) ecosystems (Ruiz-Peinado et al., 2021; Willis and Blazier, 2022). Enhanced tree growth in

species mixtures relative to monocultures can reflect a range of interactions. Complementarity in resource niche (i.e., contrasting species traits that promote more efficient resource use) may reduce competition. For example, diversity in canopy traits, such as phenology and crown shape, can enhance light-use efficiency in mixed-species stands (Forrester et al., 2018; Ishii and Asano, 2010). Alternately, facilitation may occur via improved nutrition, litter characteristics, and hydraulic lift of deep soil water (Forrester and Bauhus, 2016). Species mixtures can also increase forest resilience by reducing the impacts of stressors and disturbances that disproportionally affect a single tree species or groups of closely related species (Yachi and Loreau, 1999; Jactel and Brockerhoff, 2007; Jactel et al., 2017) to better ensure continuation of forest ecosystem function.

Species-mixture effects can range from positive to negative for a given community based on site quality factors (e.g., soil fertility), terrain, and climate (Mina et al., 2018). The stress-gradient hypothesis predicts that facilitation becomes increasingly important relative to competition with declining site quality (Bertness and Callaway, 1994). Consistent with this hypothesis, data from temperate western European forests provide support for stronger positive mixture effects on lower-quality sites (Toïgo et al., 2015). The influence of climate is less clear. A study of Scots pine and Norway spruce (*Picea abies*) mixtures found that species-mixture effects did not consistently vary across European climatic gradients (Ruiz-Peinado et al., 2021), whereas climate positively influenced species-mixture effects in sessile oak (*Quercus patrea*)-European beech (*Fagus sylvatica*) stands (Pretzsch et al., 2013). An experimental study of temperate Ontario, Canada, tree species that manipulated both functional diversity and water availability found no support for the stress-gradient hypothesis in young stands (Belluau et al., 2021), and a global *meta*-analysis found that greater precipitation increased the strength of positive species-mixture effects but temperature was not significant (Jactel et al., 2018).

Forest structure can also exert important controls on species-mixture effects (Toïgo et al., 2015; Zeller et al., 2018). A study of European Mediterranean and temperate forests found that larger tree size measured as stand basal area strengthens positive mixture effects under high evapotranspiration in Mediterranean systems, whereas smaller trees exhibit positive mixture effects under low evapotranspiration in temperate systems (Madrigal-González et al., 2016). Positive mixture effects decline with increasing stand density in temperate, subalpine Swiss mixed-species forests (Mina et al., 2018). In contrast, mixture effects become increasingly positive with density-related competition in plantations of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) (Amoroso and Turnblom, 2006) and in European silver fir (*Abies alba*)-Norway spruce stands (Forrester et al., 2013). Positive mixture effects often reflect efficient light partitioning in stratified mixtures of overstory shade-intolerant and shade-tolerant lower canopy species (Cordonnier et al., 2018; Forrester et al., 2018). By affecting growth and stratification of different tree species in a stand, climate can indirectly alter species-mixture effects (Condés et al., 2022).

Although studies of species-mixture effects have most commonly examined tree growth responses (Grossiord, 2020), mixtures may also promote changes in the forest canopy that influence tree vigor (Jucker et al., 2015) and ecosystem services such as wildlife habitat (Himes and Puettmann, 2019). Depending on species composition, trees may exhibit plasticity of tree crown size and shape (Jucker et al., 2015; Pretzsch, 2014). Where species-mixture effects improve crown condition (e.g., in respect to live crown ratio, foliage transparency, or crown width), such changes are expected to reduce tree mortality risks and improve growth potentials (Dobbertin, 2005; Wykoff, 1990), as well as enhance the ability of suppressed trees to respond to release via thinning or disturbance (Oliver and Larson, 1996). By supporting greater leaf area and evapotranspiration, however, species mixtures may also increase stand water use and stress (Grossiord, 2020). Thus, managing for high tree-species diversity may not improve drought resilience in all forests (Grossiord et al., 2014).

On the Iberian Peninsula, Jucker et al. (2014) found that pine species show greater plasticity in crown condition in response to neighboring tree-species composition than oak species, which corresponds with stronger positive mixture effects on pine biomass increment. Mixed pine-oak forests on average produce ∼ 48% more aboveground woody biomass annually than pine or oak monocultures, except in drought years (Jucker et al., 2014). A study of red alder (*Alnus rubra*)-conifer plantations in Oregon, U.S., found that live crown length and tree growth do not differ between mixtures and monocultures (Himes and Puettmann, 2019). In contrast, Erickson et al., (2009) found that western hemlock planted in mixtures with Douglas-fir had lower live crown ratio (LCR, i.e., the percentage of total tree height populated by branches that support live green foliage) than in pure stands, suggesting an

antagonistic effect on tree vigor (i.e., the potential to withstand stress, particularly from insect attacks, and respond positively to release when thinned). However, tree growth was not reduced. The prospect that LCR may mediate species-mixture effects raises the possibility that routinely collecting these measurements could simplify growth and yield modeling of mixed stands. However, the extent to which landscape variation in factors such as forest structure, climate, and site quality simultaneously alter species-mixture effects on LCR, growth, and mortality needs to be more fully investigated.

In the mixed-conifer/hardwood forests of California, U.S., fire suppression, drought, bark-beetle outbreaks, and wildfires have interacted with complex physiography to alter forest succession, tree population structure, and site quality over large areas (North et al., 2007). In the Sierra Nevada, the odds of pine species' mortality declines with both the absolute and relative density of conspecific neighbors (Das et al., 2008; Koontz et al., 2021). While lower tree density and relative abundance of bark beetle hosts likely reduces beetle aggregation and attack success (Jactel et al., 2018; Koontz et al., 2021), whether higher tree diversity reduces tree mortality by promoting higher tree vigor (defined as combined growth and survival) remains unclear. Oaks are the dominant hardwood species in these forests and may improve conifer drought resistance in mixtures via hydraulic lift of deep soil moisture based on studies of similar species mixtures in European (Forrester and Bauhus, 2016; Pretzsch et al., 2013) and southern U.S. forests (Klockow et al., 2020; Willis and Blazier, 2022). In California savannahs, hydraulic lift by oaks appears to buffer their rhizosphere hyphae against the impacts of severe soil drying during the summer drought period (Querejeta et al., 2007). Phenological contrasts among species, particularly between evergreen and deciduous species, could also drive seasonal partitioning of light use (Forrester and Bauhus, 2016). Species-mixture effects may not necessarily be positive or easily predictable in many California ecosystems. For example, hardwood competition has been demonstrated to reduce conifer growth in plantations in California (McDonald and Fiddler, 2010), while hardwoods in mature California stands on federal lands managed for non-timber objectives are declining under heavy competition from conifer encroachment (Cocking et al., 2014; Long et al., 2018). Better understanding how species-specific functional differences in conifer and hardwood resource-use affect tree growth, vigor, and mortality would aid the restoration, post-fire recovery, and climate change adaptation of forest ecosystems in California.

Studies of U.S. Pacific Coast tree-species mixtures have focused historically on forest stands or experimental plantations with just two or three tree species in the Pacific Northwest, which is characterized by less severe summer droughts compared to California (e.g., Amoroso and Turnblom, 2006; Himes and Puettmann, 2019; Maguire and Mainwaring, 2021). Thus, the available research examines a limited gradient of functional diversity over a small range of structures and site qualities under less strongly seasonal precipitation patterns. Furthermore, the stand-level analyses used in these studies may not detect subtle species mixture effects that could be resolved with more powerful individual-tree analyses (Forrester and Pretzsch, 2015). We examined tree vigor (as indicated by live crown ratio (LCR)) and tree growth (measured as periodic basal area increment, BAI) using USDA Forest Service Forest Inventory and Analysis (FIA) data across California. Our objectives were to better understand how (1) functional diversity affects individual-tree vigor, growth, and mortality within a variety of important species response groups in California's Mediterranean climate, (2) how tree, stand, site, and climate characteristics modulate functional diversity effects on individual-tree vigor, growth and mortality, and (3) whether LCR mediates functional diversity effects on individual-tree growth and mortality.

2. Methods

2.1. Study area and plot selection

This study used FIA data from California (Fig. 1), which features a diversity of floristic provinces that share a common FIA sampling protocol (USDA Forest Service, 2021). The climate is Mediterranean, with warm summers and most precipitation occurring in winter as rainfall that turns to snow at higher elevations and east of the Sierra Nevada Mountains (Western Regional Climate Center, 2021). Mean annual temperature across sampling plots ranged from 4.1 to 17.4 °C, while precipitation ranged from 276 to 3913 mm year^{-1}. Plot locations ranged from 33.6° to 42.0° north in latitude, −124.3° to −116.7° west in longitude, and 30 to 2957 m in elevation above sea level. These plots
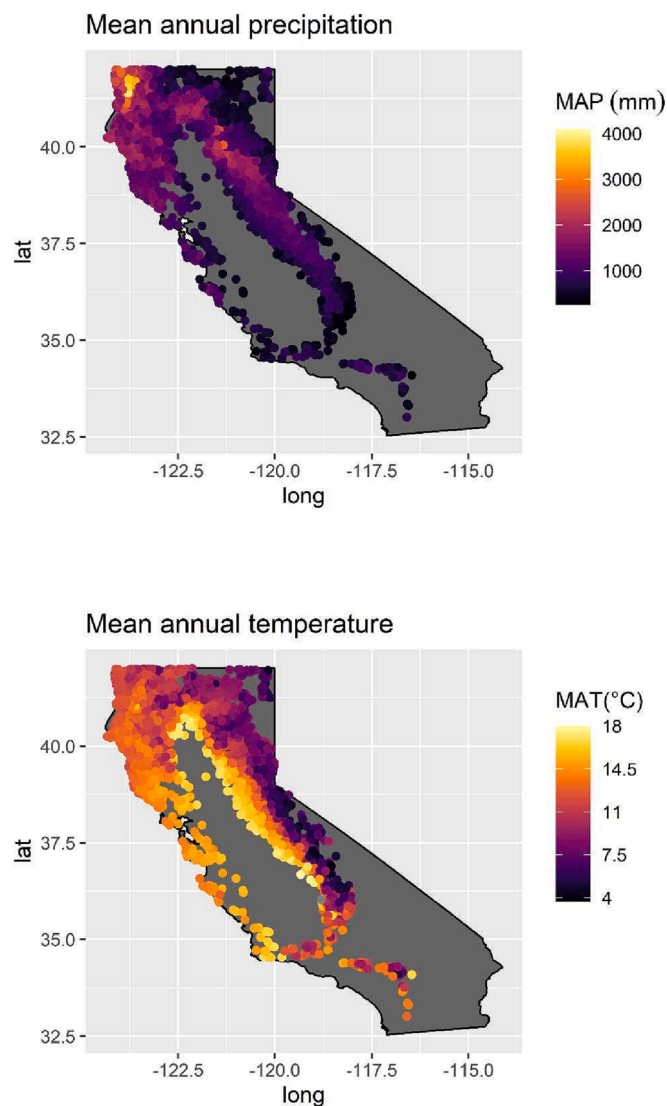

Fig. 1. Map of the distribution of selected Forest Inventory and Analysis (FIA) plots in California, USA. Plots are color coded by mean annual precipitation (MAP, top panel) and mean annual temperature (MAT, bottom panel).

spanned 18 FIA forest type groups, with California mixed-conifer being the most common.

We queried the FIA database to extract forested[1] plots that were not subdivided and mapped into separate "conditions" (similar to stands) owing to discontinuities in forest type, owner class, stand size or density classes, forest/nonforest status or reserve status. This assured that sampling units across the dataset were consistently sized and that functional diversity was reasonably consistent within a plot, though it also limits the scope of inference to more interior stand conditions, under-representing stand edges. We included plots subject to all natural disturbances except for fire. We excluded plots with evidence of prescribed fire ("TRTCD1=="0"), as well as natural fire events (DSTRBCD1==30,32, or 31), as the intricacies of fire behavior and effects warrant a more focused analysis as the subject of a future study. We also excluded plots with evidence of management, including treatment > 0.4 ha in size, occurring within 5 years of plot establishment, ignoring activities associated with minor non-timber forest products extraction (Woudenberg et al., 2021).

The FIA annual inventory program's plot design consists of four points, each associated with three nested sampling circles for assessing trees of different diameters: a 0.101-ha macroplot for "large" trees – in California, the large-tree threshold is 60.1 cm diameter at breast height (DBH), a 0.016-ha subplot for small-to-medium trees (12.7 – 60.1 cm DBH), and a 0.0013-ha microplot for saplings (2.54 cm ≤ DBH < 12.7 cm). Plots are targeted for remeasurement every 10 years, and we included only plots remeasured within 8 to 12 years of initial (time 1) measurement for consistent growth estimates. When queried on 5 April 2022, intended sampling years for time 1 measurements of selected plots in the FIA data ranged from 2001 and 2009, and for time 2 remeasurement ranged from 2010 to 2019. We downloaded database tables using the rFIA package (Stanke et al., 2020) for R (R Core Team, 2022) and manually joined tables into a flattened dataset. We relied on the growth, removals, and mortality tables FIA TREE_GRM_COMPONENT and TREE_GRM_BEGIN for growth and mortality analysis. These tables provide a full reconciliation of all trees at both visits (including missed and improperly sampled trees from time 1), offering a more definitive basis for mortality estimation over the remeasurement period. They also provide corrected values of initial observations of attributes such as species, diameter, volume and biomass where actual errors were detected or the height at which diameter was measured had to be changed due to swellings at DBH, forking rules, or other considerations during the remeasurement visit (Woudenberg et al., 2021).

2.2. Quantifying functional diversity

We followed the example of Belluau et al. (2021) and quantified plot-level (based on the aggregate data of all four FIA subplots) functional diversity using the functional dissimilarity index (FDis) of Laliberté and Legendre (2010). This index accounts for species' relative abundances by calculating the Gower multivariate species distance to the centroid, weighted by species' relative abundances, for each plot. Functional dissimilarity values, therefore, reflect multivariate species traits and are weighted by relative abundances within each plot, rather than comparisons across plots. The use of Gower multivariate distance accommodates a mixture of categorical, ordinal, and continuous scale traits. Communities consisting of a single species would simplify to FDis = 0, while FDis has no theoretical upper limit. Key advantages of this index include an insensitivity to species richness, a meaningful 0 value, and weak sensitivity to outliers (Laliberté and Legendre, 2010). We dropped 40 plots with rare species, such as California nutmeg (*Torreya*

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[1] "Forested" criterion before 2011 was ≥ 10% stocking; post-2011 it was ≥10% canopy cover; in both eras, a previously forested plot that was not currently forested but was expected to return to forest within 30 years retained its forested status and was sampled as such.

californica) and cypresses (*Cupressus spp.*), out of an initial sample of 3181 plots, due to a lack of published trait data. Although resulting in a slight loss of inference (1.3% of plots dropped), we prioritized the accurate assembly of trait values. We assembled a list of 11 traits commonly available for the remaining 65 tree species in the data. Several traits were selected to represent contrasts in resource use: crown shape, deciduousness, mycorrhizal symbiont type, wood specific gravity, growth rate (as represented by height at age 20), and mature height (Table S1). A second set of traits was selected to represent tolerances to stress, disturbance, and regeneration ecology: shade tolerance, drought tolerance, fertility requirement, bark thickness, and fire strategy (Agee, 1993). Following Harvey et al. (2016), we modified Agee's (1993) classification of species' fire strategy as either avoiders, resisters, endurers, or invaders to accommodate species exhibiting a combination of two strategies (e.g., resister/invader for Douglas-fir). Although we excluded plots with a recent history of prescribed or natural fire, we included these traits given the pivotal role of fire in the evolution of California forest ecosystems and frequent covariation with traits related to growth rate, growth form, and stress tolerances (Stevens et al., 2020). We calculated plot-level proportions for each species in terms of stand density index (SDI; calculated via the summation method with stems ≥ 2.54 cm DBH; Reineke, 1933; Long and Daniel, 1990), in order to weigh traits by species relative abundance. Stand density index is a relative density metric that integrates tree size and density information to more meaningfully represent site occupancy compared to basal area or stems ha^{-1} (Shaw et al., 2005), expressing stand density in terms of the number of 25 cm DBH-equivalent trees ha^{-1}. Functional dissimilarity was calculated based on traits and relative abundance by SDI at the time of the first plot visit, using the FDis function of the dbFD package (Laliberté et al., 2014). We retained plots where 100% of live tree SDI consisted of species for which we had trait data. We calculated FDis for the initial plot visit rather than averaging over both plot visits.

2.3. General model structure and variables

We focused our analyses on all trees (initial DBH ≥ 12.7 cm) that were live at the time 1 visit. We developed separate sets of models for each of 7 tree species or groups of tree species. We modeled each species group separately to facilitate interpretation, as species groups differed widely in terms of the range of tree, site, and stand factors. We also wished to avoid complex three-way interactions that confound clear ecological interpretation and could potentially contribute to collinearity issues. Conifers included ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), Douglas-fir, true firs (a pooled category including white fir (*Abies concolor*), red fir (*Abies magnifica*), grand fir (*Abies grandis*), and Shasta red fir (*Abies magnifica* var. *shastensis*)), and incense-cedar (*Calocedrus decurrens*). For oaks, we pooled the most common evergreen oak species, (coast live oak (*Quercus agrifolia*), canyon live oak (*Quercus chrysolepis*), and interior live oak (*Quercus wislizeni*) into a single live oak category. We also pooled the principal winter-deciduous species in the region (California black oak (*Quercus kelloggii*), valley oak (*Quercus lobata*), and Oregon white oak (*Quercus garryana*) into a deciduous oak category. We did not analyze the low-elevation species, blue oak (*Quercus douglasii*), because it diverged from winter-deciduous oaks in its intermittent summer-drought deciduousness. From an initial sample of 3141 plots meeting selection criteria, our FIA database queries returned a total sample of 2468 FIA plots also hosting at least one of these response-species groups. Plots were not mutually exclusive, meaning that plots hosting multiple response-species groups were included in multiple analyses. (See Table 1 for summaries of tree and

plot characteristics for each species group).

For each species group, we fit generalized linear mixed models of LCR, periodic annualized basal area increment (BAI) as our indicator of tree growth, and tree mortality using an individual-tree modeling approach (Forrester and Pretzsch, 2015), incorporating tree, stand, and site-level information (Table 2). Compacted LCR[2], the ratio of live crown length to total tree height, served as our indicator of crown condition (Schomaker et al., 2007). Increasing LCR is associated with improved tree growth and survival (Zarnoch et al., 2004) and is an integral parameter in forest growth and yield models such as the Forest Vegetation Simulator (FVS, Crookston and Dixon, 2005). We dropped trees without detectable (non-positive) BAI from growth analyses, assuming these trees were growing within measurement error (Fenn et al., 2020) or were subject to minor disturbances not recorded in the data by FIA field crews (e.g., trees below the 25 percent impact threshold required to code them). This resulted in dropping 6% of trees from BAI analysis. This decision inflated BAI estimates but was necessary to assure proper model fit as these data showed evidence of strong zero inflation and yielded models with poor residuals diagnostics when trees with non-positive growth were included. As a mitigating measure, we used BAI rather than periodic annual volume increment (PAI), where additional error in height measurements led to a greater proportion of trees with non-positive growth (10%). The tree mortality analysis consisted of all stems that were alive and tree-sized (≥12.7 cm DBH) at the time 1 visit that were classified as either survivor or new mortality trees by the second plot measurement, with the binary outcome of tree status coded as 0 = live and 1 = dead.

We constructed a null model of LCR, BAI, and tree mortality as functions of the fixed effects of initial tree size (diameter), the SDIL competition index (described below), site quality, mean annual precipitation (MAP), and mean annual temperature (MAT) (Table 3). Initial tree height was used in LCR models, as larger tree size is commonly associated with lower LCR (Ritchie and Hann, 1987; Temesgen et al., 2005). Stem slenderness, as indicated by tree height/diameter ratio, is also a strong predictor of LCR. However, we excluded stem slenderness from LCR models because tree height/diameter ratio is responsive to species-mixture effects (Pretzsch and Biber, 2016). We used a peaking DBH function consisting of both log-transformed initial tree DBH and initial DBH2 to represent tree size in BAI models, a model form that has been applied to range-wide analyses of ponderosa pine (Uzoh and Oliver, 2008). For mortality models, we included both linear and quadratic polynomial DBH terms to account for commonly U-shaped mortality-DBH relationships (Yang et al., 2003), a pattern confirmed in preliminary residual diagnostics. For both BAI and mortality models, we included LCR as a predictor because it is well known to influence growth and mortality odds (Zarnoch et al., 2004), and is commonly used in individual tree based forest projection models such as the FVS. Because crown condition may be responsive to species-mixture effects (Jucker et al., 2014), including LCR both as a predictor in these models and as an analyzed response in its own right potentially allowed us to infer direct vs. LCR-mediated effects of functional diversity. We quantified site quality in terms of FIA site class (Woudenberg et al., 2021), an ordinal variable characterizing potential annual volume production ranging from highest quality at a value of 1 to lowest quality at a value of 7 (1 = > 15.7 m^3 ha^{-1} yr^{-1}; 7 = < 1.3 m^3 ha^{-1} yr^{-1}). We opted to use site class to avoid potential errors surrounding different base ages in site index curves, and considered site class to be sufficiently accurate, given that the uneven-aged and mixed-species character of many stands would reduce the utility of site index (Skovsgaard and Vanclay, 2008). Our model approximates the ordinal site class attribute as a continuous

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[2] The compacted crown ratio (CCR) is estimated by field crews by "ocularly transferring live branches lower in the crown to fill large gaps in the upper portion of the tree until a full, homogeneously distributed crown can be visualized" (USDA Forest Service PNW Research Station FIA, 2022).

Table 1

Site, stand and tree characteristics for seven tree-species response groups (mean and standard deviation).

	Ponderosa pine	Jeffrey pine	Douglas-fir	True firs	Incense-cedar	Live oaks	Deciduous oaks
Number of trees	2669	1972	6432	9211	2347	4274	2148
Number of plots	340	229	504	512	281	346	292
BAI (cm^2 yr^{-1})	31.9 (24.9)	28.9 (21.0)	54.1 (42.3)	30.7 (26.3)	25.6 (22.4)	8.9 (11.9)	10.8 (11.9)
Mortality (%)	9.9 (2.5)	5.0 (1.7)	3.9 (1.4)	13.8 (1.3)	2.1 (1.1)	9.1 (2.5)	10.7 (2.3)
Stand age (yr)	102.0 (58.7)	124.7 (75.3)	109.0 (77.0)	134.2 (75.4)	121.0 (65.6)	105.7 (64.1)	97.3 (48.8)
Site class	4.4 (1.3)	5.1 (1.1)	4.0 (1.4)	4.2 (1.2)	4.0 (1.1)	5.4 (1.6)	4.8 (1.6)
MAT (°C)	11.3 (2.3)	8.6 (0.1.8)	12.3 (1.7)	9.2 (1.2)	11.0 (1.9)	13.6 (2.0)	12.9 (1.9)
MAP (mm)	1160 (475)	1013 (508)	1594 (562)	1318 (540)	1331 (551)	1197 (541)	1249 (441)
LCR (%)	51.1 (15.6)	57.0 (14.5)	61.6 (16.5)	60.8 (19.7)	58.0 (16.5)	50.3 (16.2)	42.8 (16.8)
FDis	0.15 (0.07)	0.12 (0.07)	0.16 (0.05)	0.14 (0.06)	0.17 (0.05)	0.14 (0.07)	0.17 (0.06)
SDIL (trees ha^{-1})	55.1 (48.9)	43.7 (39.5)	77.8 (54.1)	91.2 (61.2)	91.9 (64.1)	92.3 (65.8)	76.2 (58.1)
SDI (trees ha^{-1})	462.3 (282.8)	475.9 (306.8)	629.8 (373.0)	609.8 (330.9)	610.5 (296.2)	404 (279.9)	426.5 (261.8)
Basal area (m^2 ha^{-1})	25.6 (16.5)	28.9 (17.7)	34.6 (21.1)	37 (20.9)	36.2 (19.2)	20.7 (15.3)	23.3 (16.6)
Initial height (m)	24.0 (12.7)	21.3 (10.1)	22.5 (10.2)	18.1 (10.2)	16.5 (8.1)	9.2 (4.4)	13.0 (5.8)
Initial DBH (cm)	51.0 (27.2)	59.4 (27.5)	45.2 (27.2)	39.2 (21.0)	43.7 (24.6)	21.5 (10.9)	32.0 (17.4)
Elevation (m)	1311.1 (383.4)	1933.0 (390.0)	941.9 (456.3)	1772.5 (507)	1432.5 (363.7)	928.9 (487.6)	1027.9 (433.9)

Abbreviations: BAI = basal area increment; MAT = mean annual temperature; MAP = mean annual precipitation; LCR = live crown ratio; FDis = functional dissimilarity; SDIL = stand density index of larger neighbors; SDI = stand density index; DBH = diameter at breast height.

Table 2

Variables used in live crown ratio (LCR), basal area increment (BAI), and mortality (M) modeling.

Variable	Category	Description	Level	Analysis
BAI	Response	Periodic annual basal area increment	Tree	BAI
Status	Response	Tree status code: 0 = live tree, 1 = mortality tree	Tree	M
LCR$_2$	Response	Live crown ratio (crown length / total height): indicator of tree vigor, assessed at Time 2	Tree	LCR, BAI, M
Plot ID	Sample strata	Random effect, synonymous with stand	Stand	LCR, BAI, M
DBH	Stand structure	Initial diameter at breast height	Tree	BAI, M
Height	Stand structure	Total tree height	Tree	LCR
LCR$_1$	Stand structure	Live crown ratio (crown length / total height): indicator of tree vigor, assessed at Time 1	Tree	BAI, M
SDIL	Stand structure	Stand density index of larger neighbors	Tree‡	LCR, BAI, M
siteclcd	Site quality	FIA site class code (1 = high, 7 = poor)	Stand	LCR, BAI, M
MAT	Climate	Mean annual temperature	Stand	LCR, BAI, M
lMAP	Climate	Mean annual precipitation	Stand	LCR, BAI, M
FDis	Functional diversity	Functional dissimilarity based on relative SDI-weighted species traits	Stand	LCR, BAI, M

Table 3

Hypothesis models with constituent criteria and indicator variables.

Resp.	Hyp.	Response varies as a function of:
LCR	0	Ht + SDIL + Siteclcd + MAP + MAT
LCR	1	Ht + SDIL + Siteclcd + MAP + MAT + FDis
LCR	2	Ht + SDIL + Siteclcd + MAP + MAT + FDis + FDis × Ht
LCR	3	Ht + SDIL + Siteclcd + MAP + MAT + FDis + FDis × SDIL
LCR	4	Ht + SDIL + Siteclcd + MAP + MAT + FDis + FDis × MAP
LCR	5	Ht + SDIL + Siteclcd + MAP + MAT + FDis + FDis × MAT
LCR	6	Ht + SDIL + Siteclcd + MAP + MAT + FDis + FDis × Siteclcd
BAI	0	lDBH + DBH^2 + SDIL + Siteclcd + MAP + MAT
BAI	1	lDBH + DBH^2 + SDIL + Siteclcd + MAP + MAT + FDis
BAI	2	lDBH + DBH^2 + SDIL + LCR$_1$ + Siteclcd + MAP + MAT + FDis × lDBH + FDis × DBH^2
BAI	3	lDBH + DBH^2 + SDIL + LCR$_1$ + Siteclcd + MAP + MAT + FDis + FDis × SDIL
BAI	4	lDBH + DBH^2 + SDIL + LCR$_1$ + Siteclcd + MAP + MAT + FDis + FDis × MAP
BAI	5	lDBH + DBH^2 + SDIL + LCR$_1$ + Siteclcd + MAP + MAT + FDis + FDis × MAT
BAI	6	lDBH + DBH^2 + SDIL + LCR$_1$ + Siteclcd + MAP + MAT + FDis + FDis × Siteclcd
Mort.	0	DBH + DBH^2 + SDIL + LCR$_1$ + Siteclcd + MAP + MAT
Mort.	1	DBH + DBH^2 + SDIL + LCR$_1$ + Siteclcd + MAP + MAT + FDis
Mort.	2	DBH + DBH^2 + SDIL + LCR$_1$ + Siteclcd + MAP + MAT + FDis + FDis × Ht
Mort.	3	DBH + DBH^2 + SDIL + LCR$_1$ + Siteclcd + MAP + MAT + FDis + FDis × SDIL
Mort.	4	DBH + DBH^2 + SDIL + LCR$_1$ + Siteclcd + MAP + MAT + FDis + FDis × MAP
Mort.	5	DBH + DBH^2 + SDIL + LCR$_1$ + Siteclcd + MAP + MAT + FDis + FDis × MAT
Mort.	6	DBH + DBH^2 + SDIL + LCR$_1$ + Siteclcd + MAP + MAT + FDis + FDis × Siteclcd

Abbreviations are as follows: Resp. = response, Hyp. = hypothesis, LCR = live crown ratio (time 2), LCR$_1$ = live crown ratio (time 1), BAI = periodic annual basal area increment, Mort. = mortality, Ht = total height, SDIL = sum of stand density index (additive method) of subplot neighbors larger than a given subject tree, Siteclcd= FIA site class code, FDis = functional dissimilarity, MAP = mean annual precipitation, MAT = mean annual temperature.

variable. For ease of interpretation, we reversed this scale so that site quality increases from low-to-high values. We used MAT and MAP to represent climate at each plot location. As alternatives to MAP and MAT, we also evaluated climatic moisture deficit for generic all-species models but found no substantial improvements to BAI or mortality models and considerably poorer fit for LCR (Table S2). For climate data, we used norms (1991 – 2020) of gridded MAP and PPT which were downscaled to 800 m resolution while adjusting for elevation (Wang et al., 2016).

We used neighborhood competition indices to represent the competitive environment for individual trees within a given subplot (Crookston and Dixon, 2005; Larocque et al., 2012). We used the SDIL (the sum of stand density index of neighboring plot trees larger than a given subject tree) competition index of del Río et al. (2014), which we based on subplot-level SDI (Reineke, 1933). We modified this index to use the summation SDI method of Long and Daniel (1990) to quantify competition across both even and uneven-aged stands. This distance-independent index only considers subplot neighbors larger than each

subject tree to be competitors, so our estimates of local competition are conservative:

$$SDIL = \sum_{\substack{j=1 \\ D_j > D_i}}^{n} \left(\frac{D_j}{25}\right)^{1.605}$$

where D_i is the diameter of target tree i, D_j is the diameter of plot neighbor tree j, and n is the total number of subplot neighbors. We used

initial SDIL as a predictor for all three responses. This index is analogous to the basal area level (BAL) of Wykoff (1990). We selected this index because it showed moderate-to-strong performance across responses versus total plot-level SDI or BAL (Table S3), as well as for its conceptual similarity to BAL, which is commonly used in Forest Vegetation Simulator equations for silvicultural planning on U.S. National Forest System lands.

2.4. Alternative hypothesis models

We created a series of analogous competing models for the LCR, BAI and mortality responses, building upon the respective null model stems for each response separately by species group. Following the general recommendations of Burnham and Anderson (2002), we built a set of distinct a-priori hypothesis models iteratively examining either the FDis main effect or a single two-way interaction between FDis and other terms, while excluding potentially more complex alternatives featuring multiple two-way or three-way interactions. We also did not examine three-way interactions to maintain clarity of ecological interpretation, help limit the number of a-priori candidate models and avoid likely issues with collinearity. Although Mina et al. (2018) use backwards elimination with AIC for model building rather than through comparisons of a-priori models, their evaluation of suites of two-way interaction terms separately by species groups motivated our model comparison approach. The first alternative model investigated whether FDis had a simple main effect on each response variable. The second alternative model evaluated whether initial tree size modulated the FDis effect. The third alternative model examined whether competition modulated the FDis effect. The fourth and fifth alternatives evaluated whether FDis effects varied with MAP and MAT, respectively. The sixth alternative investigated the FDis × site-class interaction.

2.5. Statistical analysis

We compared the alternative hypothesis models for each response variable following the information-theoretic approach (Burnham and Anderson, 2002). We evaluated relative support for the hypothesized models using multi-model inference with corrected Akaike's Information Criterion (Burnham and Anderson, 2002; Sugiura, 1978). Models with ΔAICc < 6 of the best-approximating model that a) did not contain simpler nested models with stronger AICc support, and b) increased log likelihood were considered plausible (Richards, 2008). More complex models (i.e., models with added parameters) that were within 2 AICc of simpler nested alternatives were also excluded (Burnham and Anderson, 2002). For interaction term model support, we required at least a 2 AICc reduction versus the FDis main effect model and a 4 AICc reduction versus the null (6 for two-term DBH models) to warrant consideration. Models satisfying these criteria warranted inclusion in inference.

We used the glmmTMB package (Magnusson et al., 2018) in R (R Core Team, 2022) for all modeling. For LCR, we used a logit link function to a beta-binomial error distribution. We used a log-gamma error distribution to model strongly right-skewed volume increment data (Lindsey, 1997). We used a logit link to the binomial distribution to model binary mortality data. Live crown ratio and BAI models included the random effects of FIA plot to properly stratify the stand-level FDis variable and account for residual variation in growing conditions. In the case of pooled-species models (i.e., the true firs and oak groups), we included a random species effect to account for changes in species along environmental gradients. All models were fit with maximum likelihood. We used plots of simulated residuals to graphically verify model assumptions of linearity, dispersion, and the suitability of error distributions using simulated residuals plots (Hartig, 2018). Based on these diagnostics, we retained the peaking DBH function in BAI models and quadratic DBH function in mortality models. We log-transformed MAP in LCR, BAI, and mortality models to meet model assumptions. Except for height and diameter, predictor variables were not highly correlated,

and height and diameter were never included simultaneously in models. Lack of variance inflation factors (VIF) in excess of 5 for all models indicated low-to-moderate collinearity (James et al., 2013).

Although we relied on AICc for inference, we report conditional (combined fixed and random effects) pseudo-R^2 for each model with substantial AICc support. We used the MuMIn package (Bartoń, 2017) to perform multi-model inference for all models. We calculated pseudo-R^2 statistics via Nakagawa et al. (2013) trigamma and theoretical methods for log-gamma BAI and logit-binomial mortality models, respectively. For logit-beta LCR models, we followed the pseudo-R^2 approach of Ferrari and Cribari-Neto (2004). We converted all predictor variables to Z-scores to help interpret relative effect sizes and facilitate model convergence.

We interpreted substantial AICc support in terms of the strength and sign of FDis and interaction coefficients. A positive FDis term signified a positive mixture effect of greater local functional dissimilarity, where BAI or LCR in functionally diverse mixtures was higher compared to functionally equivalent communities. A negative FDis term signified a negative (antagonistic) mixture effect translating into lower BAI or LCR of a given species group in functionally dissimilar mixtures compared to functional monocultures. In the case of mortality, we interpreted negative and positive FDis coefficients, corresponding with reduced mortality odds, as evidence of positive and antagonistic mixture effects, respectively. In case of substantial evidence supporting functional dissimilarly interactions with other covariates, we interpreted FDis as contingent on other factors rather than as a main effect. In the event of interactions, we plotted predicted response values vs. FDis on the × axis, holding the second predictor variable at the 25th and 75th percentile values for a given species (Lüdecke and Schwemmer, 2017).

3. Results

3.1. Live crown ratio models

The best-approximating LCR models for ponderosa pine, Jeffrey pine, incense-cedar, and the true firs included the main effect of FDis and the FDis × initial tree height interaction (Table 4). Under these models, the LCR of short ponderosa pines, Jeffrey pines, and incense-cedars declined with increasing FDis (Fig. 2). The LCR of tall ponderosa pines and incense-cedars increased with higher plot FDis, while the LCR of tall Jeffrey pines did not vary with FDis. For the true firs, the LCR of short firs did not vary with FDis, while the LCR of tall firs increased with FDis. For the true fir group, a plausible alternative model featured the FDis × competition interaction. Under low competition, true fir LCR increased with greater FDis. Under high competition, LCR did not vary with FDis. The FDis × MAP interaction was included in a plausible alternative model for Jeffrey pine, with LCR decreasing with FDis on low MAP plots and increasing on high MAP plots (Table S4). We found evidence of a weak FDIS × MAP interaction for the live oaks, suggesting LCR increased with FDis on low-MAP plots and decreased on high-MAP plots. However, this model did not represent a clear improvement over the null model (Table S4), which was also plausible, indicating that support for this interaction was equivocal. For deciduous oaks, we found that the effect of FDis on LCR was contingent on MAT. LCR increased with FDis for deciduous oaks on low MAT and declined with FDis on high MAT plots. The null model was the best-supported for Douglas-fir.

In terms of null model effects, LCR declined with competition for all species. LCR declined with initial height for species groups besides Douglas-fir and the two oak groups. LCR declined with increasing MAP in species groups other than Jeffrey pine, the true firs, and incense-cedar. LCR declined with MAT for conifer species groups but not oaks, which showed no response. Lower site quality was associated with higher LCR in the Jeffrey pine, Douglas-fir, true fir, and deciduous oaks groups, lower LCR in live oaks, and no response in the incense-cedar group. LCR increased with stand age for live oaks, was neutral for the deciduous oaks, true fir, Jeffrey pine, and ponderosa pine groups, and

Table 4
Summary of model comparison results for live crown ratio (LCR).

Group	Hyp.	Model terms*	LogLik	ΔAICc	R^2
Ponderosa pine	2	Ht + SDIL + siteclcd + MAP + MAT + FDis + FDis × Ht	−2590.2	0.0	0.51
Ponderosa pine	0	Ht + SDIL + siteclcd + MAP + MAT	−2580.8	9.5	0.51
Jeffrey pine	2	Ht + SDIL + siteclcd + MAP + MAT + FDis + FDis × Ht	931.8	0.0	0.51
Jeffrey pine	4	Ht + SDIL + siteclcd + MAP + MAT + FDis + FDis × MAP	930.0	3.6	0.51
Jeffrey pine	0	Ht + SDIL + siteclcd + MAP + MAT	925.9	7.9	0.51
Douglas-fir	0	Ht + SDIL + siteclcd + MAP + MAT	3588.5	0.0	0.52
True firs	2	Ht + SDIL + siteclcd + MAP + MAT + FDis + FDis × Ht	3730.3	0.0	0.37
True firs	3	Ht + SDIL + siteclcd + MAP + MAT + FDis + FDis × SDIL	3727.9	4.8	0.37
True firs	0	Ht + SDIL + siteclcd + MAP + MAT	3719.9	17.0	0.37
Incense-cedar	2	Ht + SDIL + siteclcd + MAP + MAT + FDis + FDis × Ht	939.1	0.0	0.40
Incense-cedar	0	Ht + SDIL + siteclcd + MAP + MAT	933.7	6.9	0.40
Live oaks	4	Ht + SDIL + siteclcd + MAP + MAT + FDis + FDis × MAP	2725.9	0.0	0.42
Live oaks	0	Ht + SDIL + siteclcd + MAP + MAT	2721.8	4.2	0.42
Deciduous oaks	5	Ht + SDIL + siteclcd + MAP + MAT + FDis + FDis × MAT	1201.1	0.0	0.48
Deciduous oaks	0	Ht + SDIL + siteclcd + MAP + MAT	1195.4	7.4	0.48

Note: Only plausible models are displayed in this table. Please see Table S4 and Fig. S1 for additional model results. Other abbreviations: Hyp. = hypothesis model, LogLik = log-likelihood, AICc = corrected Akaike's information criterion, R^2 = coefficient of determination. See Table 2 for model term abbreviations and Table 3 for the list of hypotheses.

declined in older stands for Douglas-fir and incense-cedar.

3.2. Periodic annual BAI models

We found substantial support for a simple main effect of FDis for both ponderosa pine and the live oaks group (Table 5). Ponderosa pine BAI declined with FDis, while live oak BAI increased (Fig. 3). We found evidence that the FDis effect on Jeffrey pine, Douglas-fir, and the true firs varied with initial DBH. The BAI of small-medium Jeffrey pines (<70 cm DBH) was relatively higher on low FDis plots, where BAI peaked at smaller tree sizes. The BAI of large Jeffery pines was relatively higher on high FDis plots. Jeffrey pine BAI also peaked at smaller tree sizes on low FDis plots. Large-diameter (>100 cm DBH) Douglas-fir and true firs exhibited relatively higher BAI on low vs. high-FDis plots. We found no evidence that FDis interacted with MAT, MAP, or site quality for any species group. The null model omitting any FDis effects was the best-supported model for incense-cedar and the deciduous oaks.

Among the null model fixed effects, BAI for all species increased with LCR. BAI decreased with site class for ponderosa pine but did not vary for all other species. BAI increased with MAP for ponderosa pine, Jeffrey pine, Douglas-fir, and the live oaks, while remaining neutral for true firs and the two oaks groups. BAI increased with MAT for all species except Jeffrey pine. BAI with DBH showed a curvilinear relationship peaking at intermediate tree sizes for all species except oaks. BAI declined with SDIL for all species.

3.3. Tree mortality models

We did not find widespread support for FDis as a factor in tree mortality, either as a main effect or in interaction with other factors, with only the true firs showing evidence of mortality-FDis relationships (Table 6). The FDis × DBH interaction was included in the best-approximating model of true fir mortality. Under this model, true fir mortality odds showed a U-shaped relationship with tree size on low-diversity plots, with minimum values at approximately 100 cm DBH and higher values at extremes of tree size. In contrast, true fir mortality odds did not substantially vary with tree size on high-diversity plots (Fig. 4). The FDis × competition interaction was included in a second true fir model with nearly equivalent support. Under this model, true fir mortality odds for trees growing in low competition neighborhoods increased with FDis, while the mortality odds of trees growing in high competition neighborhoods did not vary. The null model was the best-approximating model for ponderosa pine, Jeffrey pine, Douglas-fir, incense-cedar, live oaks, and deciduous oaks groups.

In terms of the null model fixed effects, mortality odds decreased with increasing LCR in all species, and increased with SDIL across all species except the true firs, where mortality did not vary with SDIL. Mortality odds increased with MAT in all species except Douglas-fir, which did not vary substantially. Higher MAP was associated with lower mortality in the live oaks. Mortality odds declined with increasing site quality in the true firs. Neighborhood competition was associated with higher mortality odds in ponderosa pine and deciduous oaks, while mortality declined with competition in the true firs.

4. Discussion

4.1. Live crown ratio responses to functional diversity

We found evidence that individual-tree LCR varied with conifer diversity in California forests, although responses differed by species and interactions were evident between FDis and stand structure and/or site quality. In ponderosa pine, incense-cedar, and the true firs, large-tree vigor, as indicated by high LCR, improved on plots with higher FDis. This is somewhat consistent with research in natural, mature forest stands in Europe, where Jucker et al. (2014) found that crown volume, another indicator of tree vigor, increased in Scots pine and Austrian pine (*Pinus nigra*) in mixtures with functionally dissimilar oaks. However, we found that mixture effects were commonly antagonistic for short-statured ponderosa pine, Jeffrey pine, and incense-cedar (and neutral for small true firs), with small-tree LCR declining with functional diversity. Our LCR results are similar to those of Madrigal-González et al., 2016 for individual-tree BAI in European Mediterranean forests, where large trees of all species showed a positive functional-diversity effect on large-tree growth and a negative functional diversity effect on small-tree growth. Madrigal-González et al. (2016) hypothesized the negative effect of diversity on small trees reflected shifts in growth allocation away from roots, and in the case of conifers, competition with sprouting hardwood species with higher small-tree carbohydrate reserves. Both mechanisms are plausible drivers of reduced small-tree LCR under high functional diversity in our forests, where sprouting hardwood species, such as tanoak (*Notholithocarpus densiflorus)* and madrone (*Arbutus menziesii*), are aggressive competitors that restrict conifer crown ratio and width (Oliver, 1990). Where management objectives make perpetuating large ponderosa pine, Jeffrey pine, and incense-cedar a priority (e.g., for habitat or wildfire risk reduction), functional diversity could promote higher LCR.

That tall-tree LCR improves or is maintained in functionally diverse stands may be explained by enhanced light environment or lack of physical restriction through stratification. Yachi and Loreau (2007) developed a model to assess the effects of species diversity on light competition and total plant biomass. They showed that reductions in average light-competition intensity due to differences in foliar
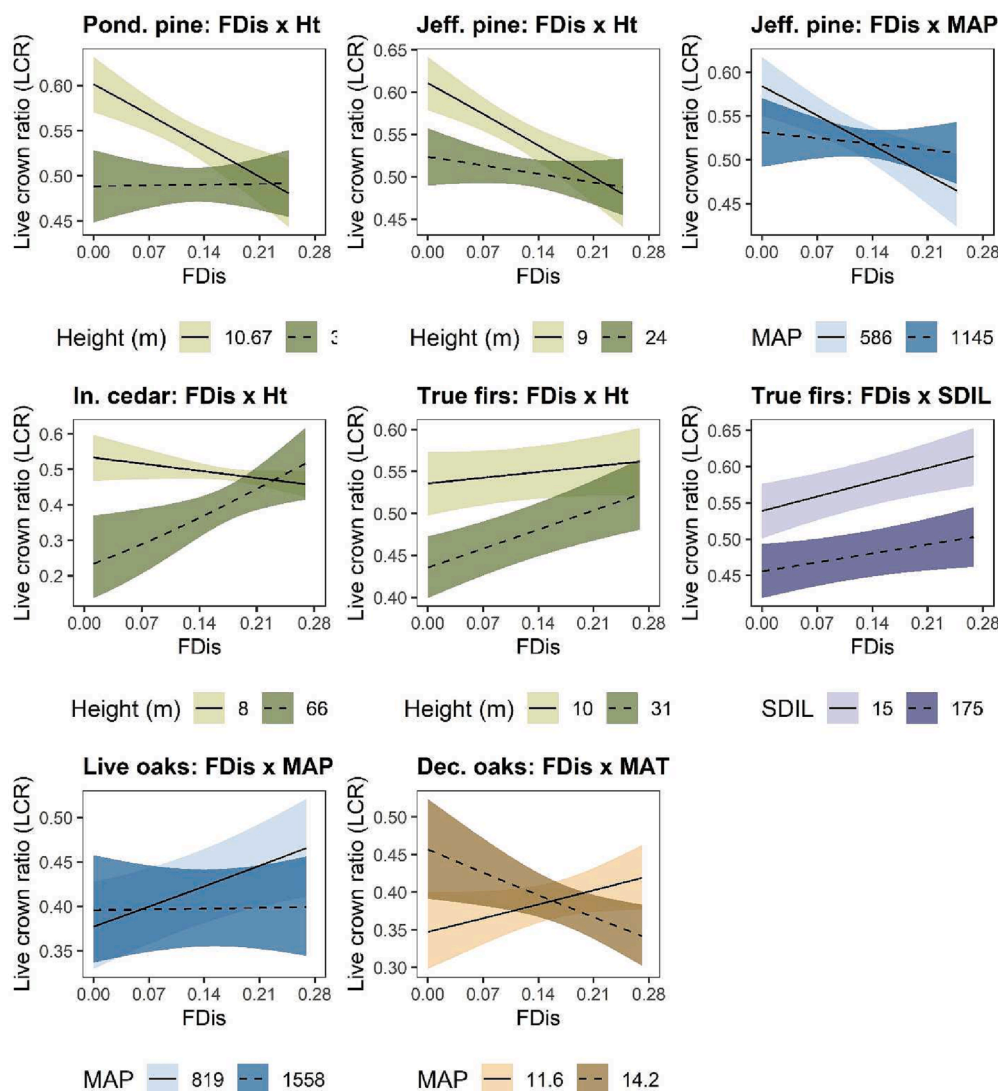
Fig. 2. Predicted value of modeled individual tree live crown ratio (LCR) at the end of the 10 yr observation period, based on the best-supported model for each species group. All models involved interactions between functional dissimilarity (FDis) and covariates. Predicted values are presented as the 25th and 75th percentile values of covariates. Abbreviations are as follows: Pond. pine = ponderosa pine; Jeff. Pine = Jeffrey pine; In. Cedar = incense-cedar; Dec. oaks = deciduous oaks; MAP = mean annual precipitation, MAT = mean annual temperature. Note that as a response, LCR is analyzed as a static measurement at the time of second plot measurement and does not represent change over the observation period.

architecture among species enhanced total plant biomass in mixtures, but that competitive balance among species also plays an important role. The true firs have higher shade tolerance than the other conifer species in our study, and both small and large true firs responded positively to functional diversity. For the true firs, in particular, high shade tolerance combined with cone-shaped crowns may allow for more efficient use of growing space in stands with rounded or irregularly crowned, shade-intolerant neighbors (Burkhart and Tomé, 2012; Jucker et al., 2015).

In addition to an interaction with tree size in three of the four conifer species groups (ponderosa pine, Jeffrey pine, and incense-cedar), we found strong support for competition playing a modulating role in the FDis-LCR relationship in the true firs. LCR increased most markedly with FDis for true firs growing under low competition. The relationships between stand density and positive species mixture effects are commonly nonlinear, ranging from negligible at low densities where interactions among trees are uncommon, to strongest at an intermediate range of stand densities, and decline again under high densities where competitive interactions overwhelm complementarity effects (Bauhus et al., 2017). Shifts to antagonistic mixture effects with increasing competition have been observed in forests in Switzerland (Mina et al., 2018). In European plantations of shade-intermediate Douglas-fir and shade-tolerant European beech, Douglas-fir showed evidence of a shift from negative mixture effects in young stands (<15 yr) to positive mixture effects in old stands (Thurm and Pretzsch, 2016). Once

outgrowing the shade-tolerant hardwood layer, Douglas-fir crowns benefitted from a lack of physical growing space restriction (Thurm and Pretzsch, 2016). In our study, true fir trees with low competition would have similarly been freer to expand their crowns over lower canopy strata, which may have fostered complementarity in light use (Ishii and Asano, 2010).

Beyond tree size and neighborhood competition, we found evidence that functional diversity interacted with climate to alter LCR for Jeffrey pine, the live oaks, and deciduous oaks groups, but that these interactions had different implications for tree vigor. In Jeffrey pine, functional diversity had a negative effect on LCR on plots with low-precipitation and a positive effect on high-precipitation plots. LCR of deciduous oaks declined with FDis on plots with higher MAT but decreased on plots with low MAT. Jeffrey pine, which commonly occurs in the arid montane rain shadow east of the Sierra Nevada-Cascade crest (Safford and Stevens, 2017), occupies the lowest precipitation plots in this study. Our finding of a negative interaction between FDis and precipitation in Jeffrey pine, in particular, is inconsistent with the stress-gradient hypothesis, which predicts that positive interactions among species will become more evident on stressful sites (Bertness and Callaway, 1994). However, subsequent research has found widespread evidence for the opposite pattern, with positive species-mixture effects intensifying with increased MAP (Jactel et al., 2018). Diverse stands may exacerbate stand water loss under drought conditions (Grossiord

Table 5

Model comparison results for basal annual increment (BAI) for 7 species response groups.

Species group	Hyp.	Model terms*	LogLik	ΔAICc	R^2
Ponderosa pine	1	$lDBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT + FDis$	−9004.3	0.0	0.71
Ponderosa pine	0	$lDBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT$	−9010.4	6.6	0.71
Jeffrey pine	4	$lDBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT + FDis + FDis*lDBH + FDis*DBH^2$	−6591.0	0.0	0.73
Jeffrey pine	0	$lDBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT$	−6603.7	19.4	0.73
Douglas-fir	2	$lDBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT + FDis + FDis*lDBH + FDis*DBH^2$	−25549.7	0.0	0.76
Douglas-fir	0	$lDBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT$	−25574.3	43.2	0.75
True firs	2	$lDBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT + FDis + FDis*lDBH + FDis*DBH^2$	−31496.4	0.0	0.76
True firs	0	$lDBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT + FDis$	−31521.7	44.8	0.76
Incense-cedar	0	$lDBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT$	−7471.3	0.0	0.72
Live oaks	2	$lDBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT + FDis + FDis*lDBH + FDis*DBH^2$	−9567.2	0.0	0.53
Live oaks	1	$lDBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT + FDis$	−9571.6	4.8	0.52
Live oaks	0	$lDBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT$	−9577.0	13.6	0.52
Deciduous oaks	0	$lDBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT$	−5141.8	0.0	0.66

Note: Only plausible models are displayed in this table. Please see Table S4 and Fig. S2 for additional model results. Other abbreviations: Hyp. = hypothesis model, LogLik = log-likelihood, AICc = corrected Akaike's information criterion, R^2 = coefficient of determination. See Table 2 for model term abbreviations and Table 3 for the list of hypotheses.

et al., 2014), which could offset positive mixture effects in Jeffrey pine and the live oak species groups. Our finding of a weak opposite relationship for the live oaks, where greater functional diversity was associated with higher LCR on low-MAP plots and reduced LCR on high-MAP plots, was more consistent with the stress-gradient hypothesis. However, this model did not represent a clear improvement over the null model, which was also plausible, indicating that support for this interaction was equivocal.

4.2. Basal area increment

Functional diversity influenced individual-tree BAI of ponderosa and Jeffrey pine, Douglas-fir, true firs, and live oaks. For ponderosa pine and the live oaks, there was evidence of a simple main effect. Ponderosa pine BAI declined with functional diversity. For Jeffrey pine, we found that functional-diversity effects were also negative except under high competition, where the BAI response to FDis was neutral. Research has generally found deleterious effects of competing hardwood species on ponderosa pine growth and vigor in California (McDonald and Fiddler,

2010; Oliver, 1990). For the live oaks group, trees growing in mixtures with deciduous neighbors may benefit from seasonal canopy gaps during leaf-off (Ishii and Asano, 2010), while contrasting rounded or irregular crown shapes of the live oaks and conical conifer crowns could foster stratified mixtures that are efficient in terms of light use (Ishii and Asano, 2010).

For Jeffrey pine, Douglas-fir and the true firs, the FDis effect was contingent on initial DBH. In Jeffrey pine, low values of FDis were associated with more rapid growth in medium-sized trees, while high FDis was associated with faster growth in large trees. For Douglas-fir and the true firs, large tree BAI responded negatively to functional diversity. Our findings that FDis effects in large Jeffrey pine generally shifted from negative to positive with increasing tree size are consistent with the results of Madrigal-Gonzales et al. (2016) for general-species models in European forests. Given the typical occurrence of Jeffrey pine in arid forests east of the Sierra-Cascade crest (Stevens et al., 2016), the positive effect of FDis on large-tree BAI may reflect complementarity in soil resource use. Potential drivers may include differential use of soil resources and facilitative effects of litter from diverse neighbors (Forrester and Bauhus, 2016). In contrast, the adverse effects of FDis on large-tree BAI in Douglas-fir and the true firs could reflect higher leaf area contributing to drought stress in these species (Grossiord et al., 2014). Antagonistic BAI-FDis relationships in tall trees may also emerge if functional diversity contributes to crown shyness. Crown shyness, related to increased abrasion against the crowns of neighboring species, is typically most acute in larger trees (Smith and Long, 2001). Although causal mechanisms are unclear from our data, our results suggest functional diversity may potentially accelerate or accentuate the age-related growth decline (Smith and Long, 2001) in the Douglas-fir and true fir components of California forests, while sustaining large Jeffrey pine BAI across a larger range of maximum tree sizes.

Our findings have several potential implications for the restoration of California forests subject to densification and shifts towards shade-tolerant conifers under fire exclusion (Safford and Stevens, 2017). For ponderosa pine, the antagonistic effect of FDis on growth suggests simplifying species composition during thinning could help sustain individual-tree carbon sequestration and vigor. Because positive FDis effects on Jeffrey pine growth were confined to large trees, thinning and fuels reduction treatments that also simplify community functional diversity could be particularly effective in terms of promoting residual Jeffrey pine BAI in small-medium-sized trees. Meanwhile, larger Jeffrey pine with high ecological value might be more effectively perpetuated by managing for higher functional diversity. Simplifying functional diversity during thinning could also help sustain large-diameter Douglas-fir and true firs, which have both higher ecological value and fire resistance than small trees (Johnston et al., 2019; North et al., 2009). Conversely, thinning treatments preserving compositional complexity could benefit the growth of live oaks, which could be important for promoting habitat for wildlife that depend upon oaks (Long et al., 2016). Our results also suggest that uneven-aged management, which subjects regenerating trees to forest edge effects from mature neighbors, would require careful application in compositionally diverse stands where maintaining shade-intolerant pine is a key objective. In the Southern Cascades (Taylor, 2010) and central Sierra Nevada (Lydersen et al., 2013), tree species historically tended to form compositionally homogeneous patches within stands, inspiring the "unit area control" method of uneven-aged management (LeBarron, 1958) and contemporary approaches to fuels management in California (Knapp et al., 2017; Ritchie, 2005). Managing for distinct within-stand, compositionally homogeneous units could minimize antagonistic diversity-growth relationships on the BAI of pine species and large Douglas-fir or true firs, while otherwise maintaining the ecosystem benefits of compositionally diverse stands. Examples from European Douglas-fir and beech forests illustrate how spatial or temporal separation of tree species could be used to potentially maximize positive diversity effects and minimize antagonistic interactions (Bauhus et al., 2017).
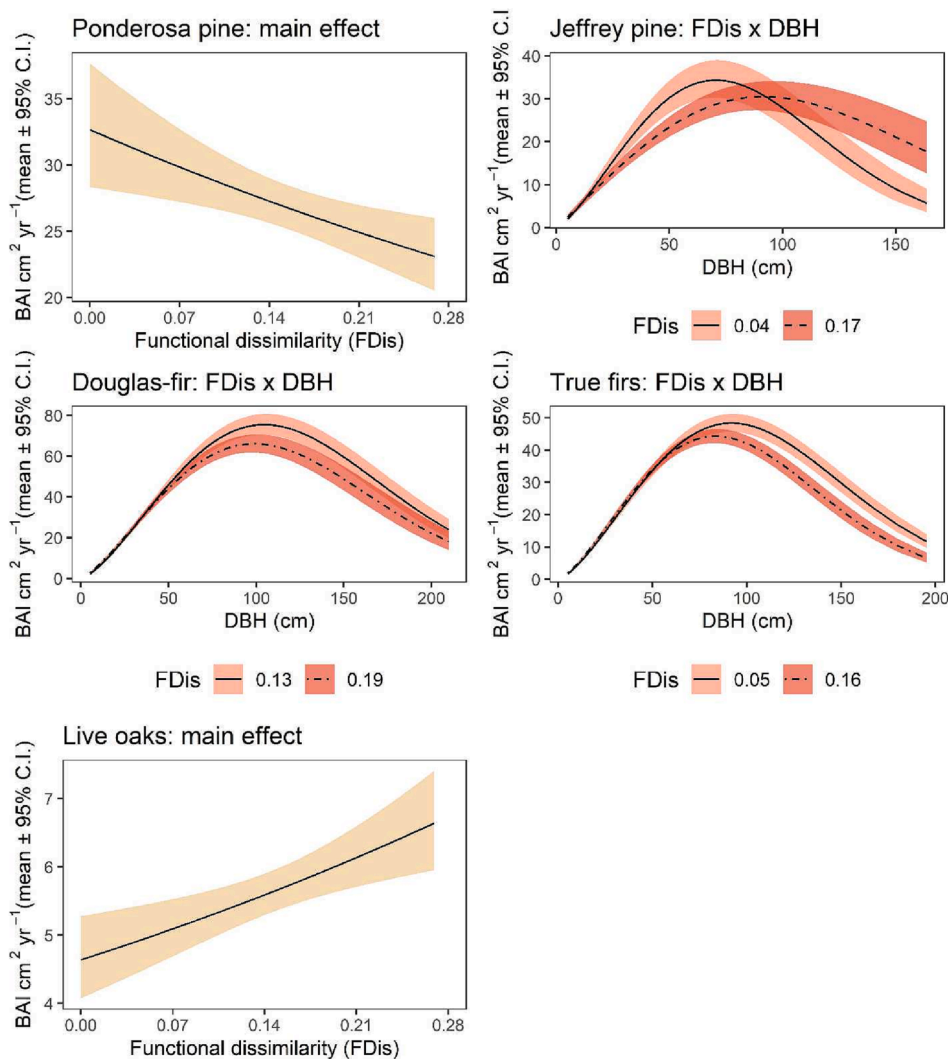
Fig. 3. Predicted value of modeled individual tree periodic basal area increment (BAI) over the 10-yr observation period, based on the best-supported model for each species group. For ponderosa pine and the live oaks, FDis is plotted on the x-axis. For Jeffrey pine, Douglas-fir, and the true firs, DBH is plotted on the X-axis to illustrate important thresholds in these complex curvilinear relationships. Moderator values are presented as the 25th and 75th percentile values of covariates. Abbreviations are as follows: DBH = diameter at breast height.

We found no support for mediating roles of site characteristics on BAI-FDis relationships. These results contrast with Bertness and Callaway's (1994) prediction of positive species-mixture effects under higher abiotic stress, as well as evidence that mixture effects generally become more positive with increasing water availability (Belluau et al., 2021; Jactel et al., 2018) and under poorer soil fertility (Toïgo et al., 2015). It is important to note that we examined long-term climatic averages rather than the drought conditions seen by trees in this remeasurement interval. While short-term climatic fluctuations can also alter species interactions (Pretzsch et al., 2013), they are difficult to account for given FIA's rolling ten-year remeasurement framework and temporal lags in BAI effects.

Because LCR, which was included as a predictor in BAI models, was in turn often influenced by FDis, the detection of distinct BAI-FDis relationships in many species may point to a driving role of additional processes not mediated by LCR. For example, variation in traits related to water use efficiency or nutrient demand and cycling (Forrester and Bauhus, 2016) among the species in this study may account for LCR not fully mediating FDis effects in some species (e.g., ponderosa pine), while accounting for the simultaneous lack or presence of an LCR-FDis relationship in others (e.g., Douglas-fir and incense-cedar). Lower insect and pathogen activity in mixed stands may also benefit BAI, independent of competition reduction or facilitation mechanisms. That LCR does not fully mediate functional diversity effects on BAI has potential implications for forest growth and yield modeling. Previous research found that

for structurally complex stands (as opposed to compositional diversity), including LCR can help account for variability in within-stand growing conditions in models such as the Forest Vegetation Simulator (Dickinson et al., 2019). Future research should investigate the extent to which assessing LCR during stand inventories can improve growth and yield model predictions in functionally diverse stands.

4.3. Tree mortality

We found evidence that functional diversity altered the individual-tree mortality odds of the true firs group. We found evidence that low FDis was associated with elevated mortality in both small and large fir trees. This patten is characteristic of many species subject to self-thinning mortality in small trees and senescence in large trees (Yang et al., 2003). In contrast, the mortality-DBH relationship was more consistent across the diameter range under high FDis. In California, recent outbreaks of fir engraver (*Scolytus ventralis*) have resulted in substantial fir mortality (Fettig et al., 2019), but are unlikely to help explain the relationship between FDis and mortality of large firs as fir engraver colonizes firs of all sizes (Fettig, 2016). Functional diversity effects are unlikely to have altered the relationship between fir size and fir engraver host selection preferences.

We also found evidence that competition, as represented by our SDIL index, mediated the functional diversity effect on true fir mortality odds. Ferrell et al. (1994) found that fir engraver tended to colonize shorter

Table 6

Summary of model comparison results for mortality models for seven species groups.

Resp	Species group	Hyp.	Model terms*	LogLik	ΔAICc	R2
Mort	Ponderosa pine	0	$DBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT$	−705.0	0.0	0.53
Mort	Jeffrey pine	0	$DBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT$	−317.1	0.0	0.59
Mort.	Douglas-fir	0	$DBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT$	−1288.7	0.0	0.39
Mort	True firs	2	$DBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT + FDis + FDis*DBH + FDis*DBH^2$	−1303.2	0.0	0.40
Mort	True firs	3	$DBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT + FDis + FDis*SDIL$	−3063.2	3.8	0.40
Mort	True firs	0	$DBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT$	−3089.8	47.1	0.40
Mort	Incense-cedar	0	$DBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT$	−502.9	0.0	0.53
Mort	Live oaks	0	$DBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT$	−901.5	0.0	0.51
Mort	Deciduous oaks	0	$DBH + DBH^2 + SDIL + LCR_1 + siteclcd + lMAP + MAT$	−552.1	0.0	0.51

Note: Only plausible models are displayed in this table. Please see Table S4 and Fig. S3 for additional model results. Abbreviations: Hyp. = hypothesis model, LogLik = log-likelihood, AICc = corrected Akaike's information criterion, R2 = coefficient of determination. See Table 2 for model term abbreviations and Table 3 for the list of hypotheses.

dominant and codominant trees, consistent with trees subject to low SDIL (and thus more dominant social positions) in our study. There are several plausible explanations for the relationship between FDis and mortality of firs under low competition. Under some conditions, low stand density may exacerbate drought stress through a combination of large overstory tree size, high individual-tree leaf area, and lack of developed root systems in regeneration (Clark et al., 2016). Diverse stands can also increase evapotranspiration and lower water use efficiency (Ammer, 2019), a conceivable situation in cases where firs were growing in association with more drought-tolerant pine and hardwood species. Alternatively, it is important to note that recent studies in the Sierra Nevada have found that thinning increases resistance of white fir to fir engraver (Bernal et al., 2023). Finally, low competition may be indicative prolonged tree mortality events, such as root disease, which continued to contribute to elevated mortality over the observation period.

Common agents of tree mortality are diverse among the tree response groups represented in our study. In general, mixed-species forests have been shown to be more resilient to specialized insect herbivores, small mammalian herbivores, soil-borne fungal diseases, wildfires, and windthrow (Jactel et al., 2017). The lack of evidence for widespread mortality-FDis relationships in our study was unexpected, but may

reflect several factors. LCR is an important predictor of tree mortality risk and commonly used in silvicultural prescriptions as criteria for tree retention or removal (Zarnoch et al., 2004). Including LCR, which was often responsive to FDis, in our mortality models likely dampened functional diversity effects. Of note, mortality decreased with increasing LCR in all species. Another possible contributor is that higher productivity in functionally diverse stands could have accelerated stand development, including self-thinning in small trees and faster recruitment of large trees. Given that we investigated only LCR as an indicator of tree vigor, future studies should confirm whether indicators such as crown class, foliage transparency, or crown volume (Zarnoch et al., 2004) produce similar results.

In recent years, wildfires and outbreaks of bark beetles incited by droughts have caused unprecedented levels of tree mortality in California. While droughts have had an important influence on this region for millennia, an exceptional drought occurred in 2012–2015, (resampling dates for FIA plots used in our study ranged from 2010 to 2019) that in some areas was the most severe in 1,200 years (Griffin and Anchukaitis, 2014). This resulted in progressive canopy water stress in at least 888 million trees and severe canopy water stress in at least 58 million trees (Asner et al., 2016). In ponderosa pine and California mixed-conifer forests in the central and southern Sierra Nevada (e.g., on the Eldorado, Stanislaus, Sierra and Sequoia National Forests), where tree mortality was most severe, ~49% of trees died (Fettig et al., 2019). Such abrupt and severe levels of tree mortality likely compromised detection of subtle mortality-FDis relationships in our study.

Modeling mortality is also inherently challenging compared to other components of forest change. For example, recent efforts to predict levels of tree mortality in the western U.S. using FIA data and a plant hydraulic model explained only a small amount of variation (R^2 median = 0.10, Venturas et al., 2020). Although limited by our desire to use a multiple regression framework to adjust for other covariates and examine interactions, other analysis approaches, such as random forests, may offer greater statistical power with these data.

5. Conclusions

We found evidence that functional diversity commonly altered the vigor and growth of major California tree species. We found comparatively few species where a simple main effect adequately reflected functional diversity effects on tree responses. Instead, functional diversity effects were commonly contingent on tree, stand, and site factors. Furthermore, functional diversity effects on LCR and/or BAI ranged from positive to antagonistic for a given species group, depending on the value of these factors. We found that tree size was a common modifier of functional diversity effects on LCR and BAI for most conifers, along with weaker evidence that tree competition modulated functional diversity effects on true fir LCR. We found that site factors (climate or site quality) modulated FDis effects on LCR for Jeffrey pine, live oak, and deciduous oaks. Functional diversity affected only true fir mortality, with the effect contingent on tree size and competition.

Our study had several limitations suggesting directions for further research. First, dropping the 6% of trees with non-positive growth would have inflated our BAI results, with the effect likely most acute in overstocked stands on poor sites. Second, our choice of competition index was inherently size asymmetric and discounted the influence of trees smaller than a given subject tree (Larocque et al., 2012). Examining competition symmetry may help illuminate the mechanisms driving tree performance-diversity relationships. Third, by discounting the influence of small trees, our competition index may have confounded FDis confounded with unmeasured total stand density. However, a simple model of FDis as a function of stand-level SDI, MAP, MAP and site class did not reveal evidence of a confounded FDis-SDI relationship ($F = 0.04$, $p = 0.84$). Fourth, our model building and comparison process was conservative in not including three-way interactions, excluding multiple two-way interactions, and by fitting models separately by species. Not
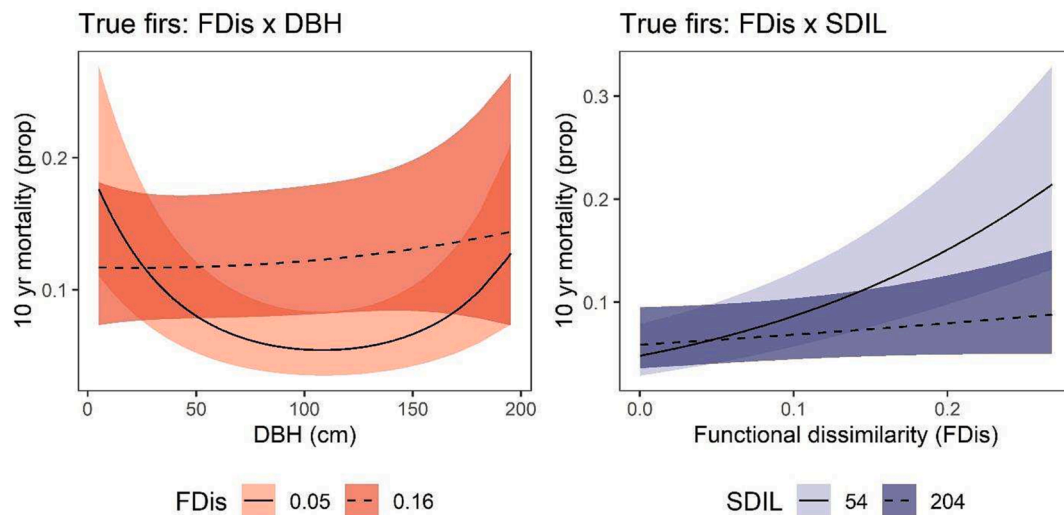
Fig. 4. Predicted value of modeled individual tree mortality odds over the 10-yr observation period, based on the best-supported model for each species group. For the DBH × FDis interaction (left panel), diameter at breast height (DBH) is plotted on the X-axis to illustrate important thresholds in this complex curvilinear relationship. All moderator values are presented as the 25th and 75th percentile values of covariates. Abbreviations are as follows: DBH = diameter at breast height; SDIL = competition index based on stand density index of subplot neighbors larger than a given tree.

fitting all-species models prohibited direct comparisons across species, while not examining three-way interactions may have missed potentially interesting tree-site-functional diversity relationships (e.g., Madrigal-González et al., 2016). Fifth, our study investigates tree-level responses, which cannot be confidently extended to the stand level to establish the presence of over or under-yielding (Forrester and Pretzsch, 2015). Our study provides a broad reconnaissance of functional diversity effects in California Mediterranean climate forest ecosystems, and in-depth investigations of specific study systems, modulating factors, or stand-level responses could provide fruitful topics for future studies.

Our investigation into California forest functional diversity effects examined a region widely impacted by dramatic shifts in historical stand structure and species composition primarily associated with historical fire suppression. Mixed-species management for climate change adaptation would need to balance restoration and fire risk reduction objectives. Our results suggest that forest restoration treatments could be most effective when tailoring both stand density and functional diversity to benefit key management objectives. Our findings generally offer support for treatments designed to favor fire-resistant species such as ponderosa and Jeffrey pine by reducing stand densities overall and particularly among functionally dissimilar species including firs and/or oaks. Where objectives include promoting growth of oaks, thinning can be beneficial, although thinning that selectively reduces functional diversity seems less important in the case of deciduous oaks and may even have some detrimental effects, in the case of live oaks. Lastly, live crown ratio appeared to effectively mediate functional diversity effects on tree mortality. Measuring this variable in routine stand inventories might support more accurate forest modeling during silvicultural planning.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121135.

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