RESEARCH ARTICLE

Integrating ontogeny and ontogenetic dependency into community assembly

Advyth Ramachandran[1] | Jared D. Huxley[1] | Shane McFaul[1] | Lisa Schauer[1] | Jeff Diez[2] | Rohan Boone[3] | Tesa Madsen-Hepp[1] | Erin McCann[1] | Janet Franklin[3,4] | Danielle Logan[1] | M. Brooke Rose[3] | Marko J. Spasojevic[1]

[1]Department of Evolution, Ecology, and Organismal Biology, University of California Riverside, Riverside, California, USA

[2]Department of Biology, University of Oregon, Eugene, Oregon, USA

[3]Department of Botany and Plant Sciences, University of California Riverside, California, Riverside, USA

[4]Department of Geography, San Diego State University, San Diego, California, USA

Correspondence
Marko J. Spasojevic
Email: markos@ucr.edu

Abstract

1. Many studies of community assembly focus on a single ontogenetic stage (typically adults) when trying to infer assembly processes from patterns of biodiversity. This focus ignores the finding that assembly mechanisms may strongly differ between life-stages, and the role of ontogenetic dependency: the mechanisms by which one life stage directly affects the composition of another life stage.

2. Within a 4-ha forest dynamics plot in California USA, we explored how the relative importance of multiple assembly processes shifts across life stages and assessed ontogenetic dependency of seedlings on adults in woody plant communities. To assess variation in assembly processes across life stages, we examined how β-diversity of adult and seedling communities were each influenced by space and 13 environmental variables (soils, topography) using distance-based redundancy analysis and variation partitioning. We then assessed the ontogenetic dependency of seedlings on adults by including adult composition as a predictor in the seedling community variation partitioning.

3. We found differences between adult and seedling composition. For the adults, we found 18 species including pines, oaks and manzanitas characteristic of this mid-elevation forest. For seedlings, we found 11 species, and that oaks made up 75% of all seedlings while only making up 45% of all adults. Adult β-diversity was primarily explained by space (44.0%) with environment only explaining 18.6% and 37.4% unexplained. In contrast, most of the explained variation in seedling β-diversity was due to ontogenetic dependency alone (13.6% explained by adult composition) with 1.6% explained by space and the environment jointly, and 62.8% unexplained.

4. *Synthesis*: Here, we describe a conceptual framework for integrating ontogeny more explicitly into community assembly research and demonstrate how different assembly processes structured adult and seedling β-diversity in a temperate dry forest. While adult β-diversity was largely driven by spatial processes, seedling β-diversity was largely unexplained, with ontogenetic dependency comprising most of the explained variation. These patterns suggest that future assembly

research should consider how assembly processes and their underlying mechanisms may shift with ontogeny, and that interactions between ontogenetic stages (ontogenetic dependency) are critical to consider when assessing variation in assembly processes.

1 | INTRODUCTION

Understanding what drives spatial variation in community assembly processes is a key goal in ecology (Myers et al., 2013; Weiher et al., 2011), with important implications for understanding the impact of anthropogenic climate change on biodiversity (Lavergne et al., 2010; Mokany & Ferrier, 2011) and informing ecosystem management (Wainwright et al., 2018). Recently, there has been a growing recognition that a community is the result of the differential growth and survival of organisms throughout their lifetimes (ontogeny; Larson & Funk, 2016; Máliš et al., 2016), and that therefore each ontogenetic stage is a pathway by which assembly processes may interact to influence overall community structure (Larson et al., 2021; Lasky et al., 2015). Despite decades of research on the role of ontogenetic variation in influencing forest diversity (Clark & Clark, 1984; Connell et al., 1984; Grubb, 1977), and advances in identifying relevant regeneration traits and filters (Larson & Funk, 2016), ontogeny has not been explicitly integrated into modern community assembly frameworks (e.g. Spasojevic & Suding, 2012; Weiher et al., 2011). Moreover, few community assembly studies have explicitly considered that ontogenetic stages can interact; one ontogenetic stage can influence assembly at a different stage within ecological communities. Here, we expand upon the concept of "demographic dependency" developed by Heiland et al. (2022) to develop the concept of "ontogenetic dependency", which refers to all mechanisms by which the community at one life stage (e.g. adult trees) can affect the abundance and composition of a community at another life stage (e.g. seedlings) during community assembly.

In general, spatial variation in community composition (β-diversity) arises through four interacting higher-order processes of community assembly: speciation (the formation of new species), dispersal (the movement of species through space), ecological drift (changes in species relative abundances that are random with respect to species identity), and niche selection (changes in species relative abundances resulting from deterministic fitness differences between species; Vellend, 2010, 2016). While speciation occurs at time scales longer than those considered in most community assembly research (Mittelbach & Schemske, 2015), the relative influences of dispersal, ecological drift, and niche selection can be inferred from patterns of β-diversity (Myers & LaManna, 2016), can differ among ontogenetic stages (Parrish & Bazzaz, 1985; Spasojevic et al., 2014), and may exhibit ontogenetic dependency. First, dispersal can play a

strong role in determining β-diversity patterns (Leibold et al., 2004). Specifically, the factors that determine the timing and amount of offspring production in reproductive adults directly impact composition of juvenile communities (Davis, Synes, et al., 2019; Pearse et al., 2017). As only reproductively mature life stages produce offspring that can disperse (Wang & Smith, 2002), dispersal is a key driver of ontogenetic dependency (Figure 1—dashed arrow).

Second, the relative importance of niche selection and ecological drift can also change with ontogeny (Figure 1; Comita et al., 2007; Green et al., 2014), though in more complex ways which may vary among ecosystems. First, the strength of the mechanisms underlying niche selection can vary with life stage because traits, and therefore functional strategies, often shift with ontogeny (Garbowski et al., 2021). For example, seedlings often tolerate a narrower range of environmental conditions than adults (Grubb, 1977; Poorter, 2007), often have high mortality rates compared to adults (Eriksson & Ehrlén, 2008; Green & Harms, 2018), may rely on a more resource-acquisitive functional strategy (Dayrell et al., 2018; Spasojevic et al., 2014) and/or employ different strategies to respond to drought (Cavender-Bares & Bazzaz, 2000) as compared to adults. As a result of such ontogenetic trait variation, the response of organisms to biotic and abiotic filters may be different at each life stage (Larson & Funk, 2016), which can result in divergent spatial distributions (Bell et al., 2014; Lenoir et al., 2009). Finally, the relative importance of ecological drift can vary with life stage in two ways. First, drift may be stronger at life stages at which cohort sizes are smaller leading to greater demographic stochasticity (Orrock & Watling, 2010). For example, low recruitment of juveniles or high mortality of adults can reduce population sizes leading to an increase in the strength of ecological drift (Fox & Kendall, 2002). Second, the chance of non-random mortality can be different among life stages (Green & Harms, 2018). For example, Green et al. (2014) found that mortality was nearly random for large size-classes in tropical forest trees, while non-random mortality was strong for small size-classes, suggesting that ecological drift was relatively more important at the adult life stage in that system.

Importantly, ontogenetic dependency between life stages can arise from niche selection and ecological drift. First, ontogenetic dependency necessarily arises because early life stages determine the composition of later life stages (Figure 1, rightward-facing arrows), generally over long timescales. High turnover (high mortality and replacement) in earlier life stages can cause the effects of
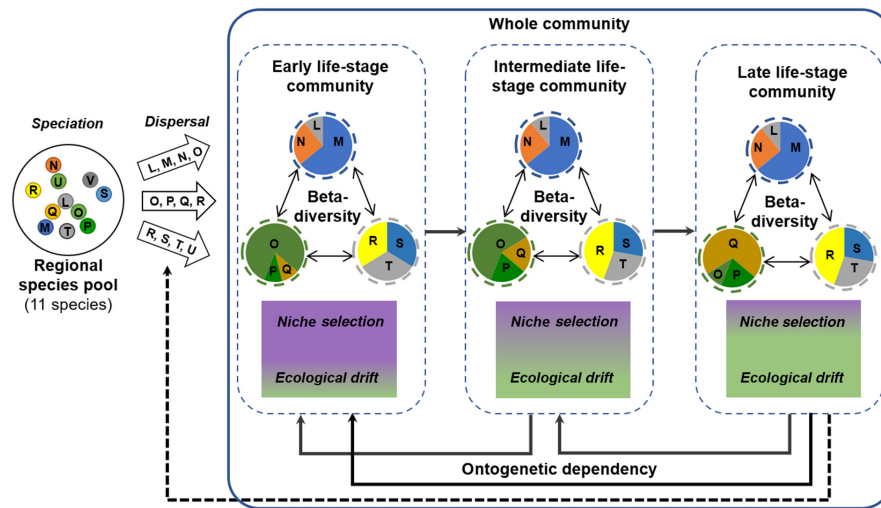
FIGURE 1 A general conceptual framework that describes how community assembly processes may shift with ontogeny (life stage) and can exhibit ontogenetic dependency (dashed and solid arrows) across three hypothetical life stages. Membership of species in the regional species pool (small coloured circles where letters represent different species, and different colours represent different traits) is determined by speciation (and immigration). White arrows represent the subset of four species that disperse to each of the local communities, and each local community (larger pie circles) is composed of three species from the regional pool able to establish post-dispersal, with the relative abundance of each species shown by the size of the pie wedge. The dashed coloured circles around each local community represent environmental conditions, where species that best match the environment have colours that match the dashed circle (i.e., species sorting). Here, the whole community (within the solid blue line) is divided into three ontogenetic stages (e.g., seedlings, sapling, adults for woody plants) that are differentially influenced by niche selection (purple) and ecological drift (green) resulting in relative abundances that differ among local communities within and among life stages. In this hypothetical example, niche selection is stronger at the early life stage resulting in stronger species sorting—better matching between dominant species in each community (larger pie wedge) and the environmental conditions (colored dashed circle) in most communities. As ecological drift becomes more important at later life stages, some communities exhibit less species sorting as the dominant species no longer matches the dashed circle in two of the communities. Due to these ontogenetic differences in assembly processes, in most communities the composition changes from one ontogenetic stage to another. In this example the composition of the O, P, Q community shows ontogenetic shifts in composition at each stage where the community composition (wedge size) changes at each life stage; the R, S, T community shows ontogenetic shifts in composition at only one life stage; and the L, M, N community does not show no change in composition with ontogeny. Ontogenetic dependency is first exhibited via dispersal (dashed arrow) where assembly mechanisms that determine the timing and amount of offspring production in reproductive adults directly impact the composition of early life stage communities. Ontogenetic dependency necessarily arises from the survival and transition of earlier life stages to later life stages (solid right-facing arrows). Ontogenetic dependency can also arise if the late life stage alters niche selection and/or ecological drift (solid left-facing arrows). In both directions, processes that directly impact one life stage have cascading impacts on another life stages. In the present study, we only assessed two ontogenetic stages and only investigated pathways of ontogenetic dependency corresponding to the effects of adults on seedlings through dispersal and niche selection.

niche selection to accrue to later life stages (Green & Harms, 2018). For example, high juvenile mortality at niche margins can cause adult distributions to be narrower than juvenile distributions because adult occurrence is dependent upon juvenile occurrence (Heiland et al., 2022). At smaller spatial scales, seedlings may occupy a wider range of microhabitats than adults within a given site (Comita et al., 2007; Webb & Peart, 2000) as adults are restricted to the subset of sites that are suitable for individuals to survive and successfully transition to larger size-classes over time and over multiple cycles of recruitment (Beyns et al., 2021; Comita et al., 2007). Similarly, the outcomes of ecological drift in early life stages should also accrue to partially determine the composition of later life stages. Second, ontogenetic dependency can result when later life stages influence the composition of earlier life stages (Figure 1, leftward-facing arrows) by modifying abiotic or biotic filters (i.e. niche selection). The most classic example in trees is seedling shade/light tolerance, where a combination of drift and selection determine canopy structure and

light availability (Peterson & Reich, 2008) which in turn influence seedling success (Comita & Hubbell, 2009; Walters & Reich, 1996). For example, Song et al. (2018) found that canopy damage of adults from snow increased seedling community size and species richness by altering light availability. In such cases, the process affecting the adult life stage also determines seedling successes; its effects are not limited to a single life stage (Figure 1—solid arrows). Crucially, such processes would be obscured by a focus on a single ontogenetic stage and thus considering interactions between ontogenetic stages is important for understanding community assembly.

Here, we aimed to understand: (1) the relative importance of assembly processes that influence β-diversity of woody plant communities in a temperate dry forest, (2) how the relative importance of such processes may shift with ontogeny, and (3) the degree of ontogenetic dependency in these processes. Forests exemplify ontogenetic shifts with large differences between adults and juveniles due to significant ontogenetic trait variation

in trees (Spasojevic et al., 2014; Williams-Linera & Manrique-Ascencio, 2020) and thus, forests are excellent study systems to investigate how assembly may vary with ontogeny. Using data from a 4-ha forest dynamics plot where every stem larger than 1 cm DBH has been mapped, identified, tagged, and measured, in conjunction with 256 1-m^2 seedling plots where every stem shorter than 1 m tall was mapped, identified, tagged, and measured, we asked the following questions. (1) Does community composition differ between the adult and seedling communities (Figure 1 differences between "early life-stage community" and "late life-stage community") and do these differences result in differences in β-diversity across ontogenetic stages? (2) Is β-diversity in adult and seedling communities associated with different assembly processes (Figure 1 differences in niche selection and drift between "early life-stage community" and "late life-stage community")? To answer this question, we first compare observed patterns of β-diversity to deviations from a null model of random assembly to assess the role of ecological drift, and then used variation partitioning to assess the amount of variation in β-diversity explained by the environment (both spatially structured and unstructured; inferred to be the effect of niche selection), and space (inferred to be the effect of dispersal). (3) What is the effect of adults on seedling composition via ontogenetic dependency (Figure 1 solid black arrow from "late life-stage community" to "early life-stage community")? To answer this question, we repeated the variation partitioning analysis of seedling β-diversity and included adult composition as an explanatory variable to infer ontogenetic dependency.

2 | MATERIALS AND METHODS

2.1 | Study site

Our study was conducted in the Hall Canyon Research Natural Area within the San Bernardino National Forest (Forest Service, United States Department of Agriculture). The site is adjacent to the University of California, Riverside's James San Jacinto Mountains Natural Reserve (33.81115 N, −116.7707 W; mean annual temperature 11.7°C; mean annual precipitation 665 mm; ~1650 m a.s.l.). The Hall Canyon Research Natural Area is found on the western (windward) slope of Mt. San Jacinto at the lower elevational distribution of Southern California montane mixed-conifer forest which is characterized by pines, firs, and cedars; and the upper elevational distribution of Southern California montane hardwood forest which is characterized by oaks and montane chaparral. This forest type is sometimes termed mixed-evergreen forest or montane hardwood-conifer forest (Barbour et al., 2007; North et al., 2016). The area has been relatively undisturbed for over 100 years, with the last recorded logging sometime in the 1800s (records are unreliable) and the last large fire in 1885 (Keeler-Wolf, 1989). The forest now exhibits the hallmarks of fire-suppression, including high stand density and leaf litter accumulation (Savage, 1994). Additionally, this forest

has experienced sustained drought for the last several decades (Williams et al., 2020). The bedrock is entirely late Cretaceous granitics from the San Jacinto Pluton (Keeler-Wolf, 1989) and soils are classified as lithic Xerorthents, which are shallow, coarse, well drained, with a low water holding capacity, and contain a large volume of rock fragments and outcrops (Sheppard & Lassoie, 1998).

2.2 | Forest composition

Our study was conducted in the San Jacinto Forest Dynamics Plot (SJFDP), a 4 ha (200×200 m, subdivided into 100 20×20 quadrats) stem-mapped forest dynamics plot (Figure 2), that follows the protocols of the Smithsonian Institution Center for Tropical Forest Science (CTFS) Forest Global Earth Observatory (ForestGEO) network. The SJFDP includes strong edaphic and topographic gradients characteristic of the area: elevation in the SJFDP ranges from 1746 to 1808 m (mean = 1774 m) and slope ranges from 6.43 to 38.10° (mean = 13.8°) at the 20×20 m scale. As of 2019, all free-standing stems of woody species greater than 1 cm diameter at breast height (DBH) have been tagged, identified, measured and mapped following CTFS-ForestGEO protocols (Condit, 1998).

To quantify woody species seedling composition across the SJFDP, we surveyed the central 64 20×20 m quadrats (out of 100 total quadrats) in 2021, leaving a 20-m buffer between seedling plots and the edge of the SJFDP. The purpose of the buffer was to ensure that adult composition is quantified for all of the 8 quadrats surrounding every quadrat in which seedling composition was quantified so that we can more accurately assess the influence of adult composition on seedling composition. To estimate seedling composition within each of the central 64 quadrats, we established four 1 m^2 subplots ($n = 256$ subplots). Each subplot was positioned 7 m from the corner of each quadrat and aligned on a 45-degree angle relative to the x-y axes of the SJFDP grid (65°, 155°, 245°, 335°; Figure 2). Subplot locations were moved to the nearest suitable location if the initial subplot location was completely occupied by a log or rock. In each subplot, we identified all seedlings (defined as individuals under 1 m tall following the CTFS-ForestGEO protocol; Condit, 1998) to species, mapped their locations in a 100-cell grid, measured their height, and added an identification tag unique to each individual. As we only sampled seedlings in one year and seedling recruitment can fluctuate interannually in similar forests (Davis et al., 2016), we acknowledge that our study may not fully capture long-term seedling composition.

2.3 | Environmental heterogeneity

To quantify environmental variation among quadrats we measured 8 soil variables and 6 topographic variables. In the centre of each 20×20 m quadrat, we collected a sample of ~500 g of soil (0- to 10-cm depth) excluding the top organic horizon and analyzed organic matter (OM, by loss on ignition), phosphorus (P, Weak Bray
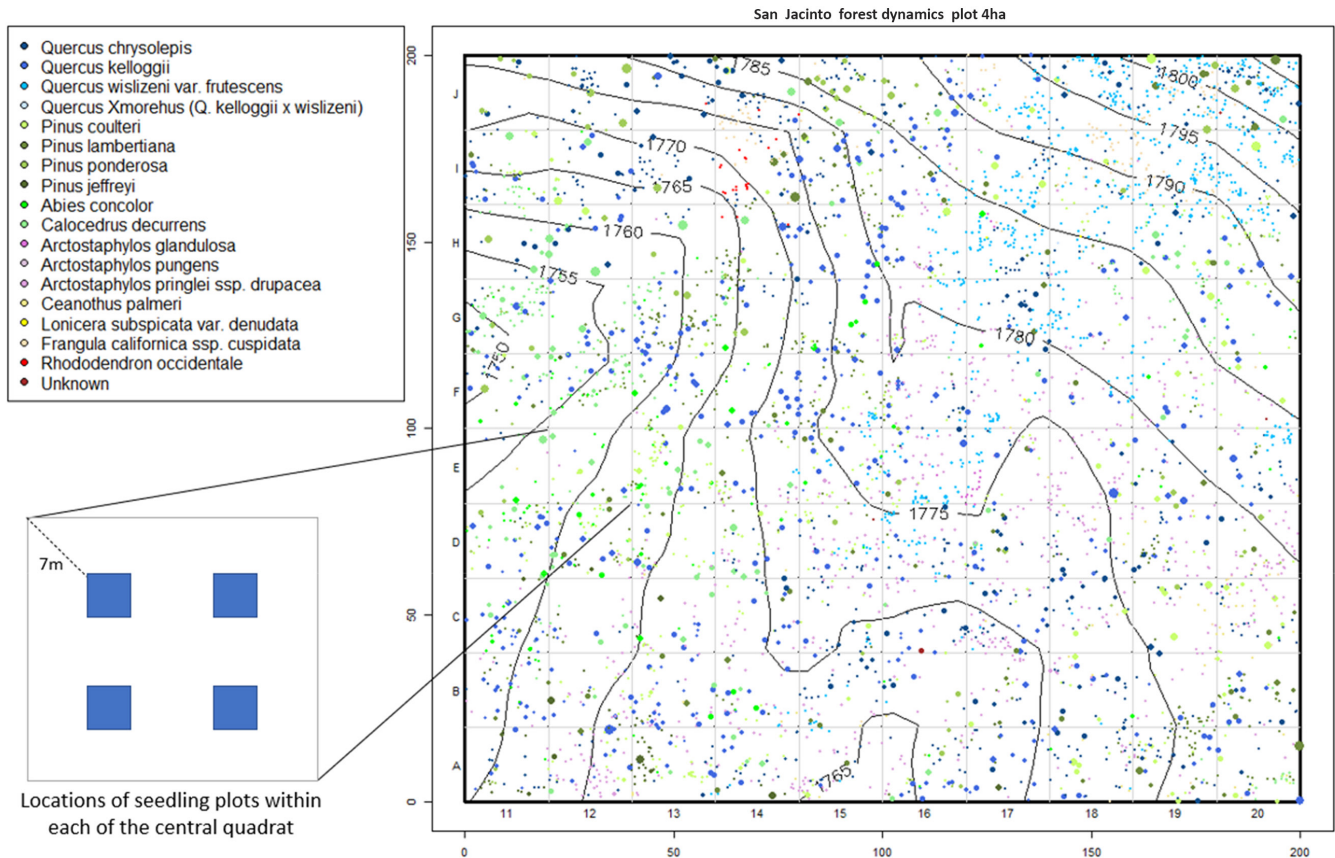
FIGURE 2 Stem map of the 4 ha San Jacinto Forest dynamics plot. Each colored point represents a main stem greater than 1 cm diameter at breast height (secondary stems are not shown). Grey lines indicate 20×20 m quadrats ($n=100$, with inset letters and numbers delimitating quadrat identities). X and Y axis values represent distance in meters from the bottom left corner. Inset quadrat shows location of four 1 m² seedling plots (blue squares) within each of the central 64 quadrats, 7 m from the corner (black circle) of each quadrat.

and Sodium Bicarbonate), potassium (K), magnesium (Mg), calcium (Ca), sodium (Na) and cation exchange capacity (CEC, cations and CEC by ammonium acetate method) and pH (analysis was done by A & L Western Laboratories). For each 20×20 m quadrat, we additionally calculated 6 topographic variables: mean elevation, slope, convexity, aspect, topographic position index, topographic ruggedness index, and flow direction. Mean elevation above sea level was quantified as the mean elevation of the four corners of each quadrat. The slope was quantified using the slope tool in ArcGIS 10.1. To quantify the remaining terrain characteristics, we used a 1-m digital elevation model (DEM) from the USGS 3D Elevation Program (3DEP) and the RASTER package in R (Hijmans et al., 2013). Because aspect is a circular variable, we used cosine(aspect) in our analyses (Legendre et al., 2009). South aspect was measured as cos(aspect)*sin(slope), where higher values correspond to south-facing slopes that are associated with warmer and/or drier site conditions (Ackerly et al., 2020). Finally, we calculated the topographic position index (TPI) as the difference between the elevation of a quadrat and the mean elevation of the eight surrounding quadrats, topographic ruggedness index (TRI) as the mean absolute difference between the elevation of a quadrat and the elevation of the eight surrounding quadrats, and flow direction (flowdir) as the direction of the greatest drop in elevation for a given quadrat.

2.4 | Statistical analyses

For all analyses, we refer to stems larger than 1 cm DBH as "adults" even though this size definition includes saplings that are not yet reproductive. Adult composition was quantified for all 100 20×20 m quadrats. To quantify seedling composition per quadrat, we summed all seedlings across each of the four subplots contained within a quadrat.

To explore the difference between seedling and adult composition (Question 1; Figure 1 differences between "early life-stage community" and "late life-stage community"), we first visualized differences in community composition among life-stages using a non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity among quadrats in R (R Core Team, 2019). Bray–Curtis dissimilarity is a semi-metric measure of dissimilarity used for continuous numerical data and does not group samples by shared zeros in the dataset. We gauged the fit of our NMDS analysis using stress, a measure of departure from monotonicity in the relationship between the dissimilarity in the original n-dimensional space and distance in 2-dimensional ordination space. In general, stress values <0.1 correspond to a good indication of the similarities between samples, whereas stress values >0.2 indicate a poor relationship (Clarke, 1993). Stress values

do not affect analyses conducted on dissimilarity matrices, only how well the dissimilarity among sites is represented in a two-dimensional figure (Clarke, 1993). We then used permutational analysis of variance (PERMANOVA: Anderson, 2001) in the ᴠᴇɢᴀɴ package (Oksanen et al., 2013) in R to test for differences in community composition among seedlings and adults. Permutational analysis of variance is very similar to an ANOVA but allows for the analysis of differences in species composition rather than species numbers (Anderson, 2001). We then calculated β-diversity as the dissimilarity (distance to centroid) in species composition for each community (Anderson et al., 2006) and tested for differences in β-diversity between adult and seedling communities using a permutation-based test of multivariate homogeneity of group dispersions (Anderson, 2006). We also examined if observed β-diversity differed from stochastic assembly (ecological drift) by comparing our observed β-diversity for both seedlings and adults to the distribution of β-diversity based on 1000 iterations of a null model. To construct this null model, we randomized our site by species matrix, effectively removing any effect of niche selection, while maintaining richness and abundance distributions within each community (Mori et al., 2015). We then evaluated departures of observed taxonomic β-diversity from the null expectation by calculating a standardized effect size (SES):

$$\frac{\beta_{OBS} - \beta_{NULL}}{\beta_{SDnull}}$$

where β_{OBS} is the observed β-diversity, β_{NULL} is the mean of the null distribution, and β_{SDnull} is the standard deviation of the null β-diversity distribution. Lastly, we used indicator species analysis (Dufrene & Legendre, 1997) which assesses the strength and statistical significance of the relationship between species occurrence/abundance and groups of sites to ask which species are driving significant differences in community composition, using the ɪɴᴅɪᴄꜱᴘᴇᴄɪᴇꜱ package in R (Cáceres & Legendre, 2009).

To explore the relative importance of different assembly processes (niche selection and dispersal) within the adult community and within the seedling community, (Question 2), we compared the extent to which observed β-diversity was explained by environmental variables (described above) and spatial variables using distance-based redundancy analysis (dbRDA; Legendre et al., 2009; Peres-Neto et al., 2006). Spatial variables included spatial eigenvectors obtained from Moran's Eigenvalue Mapping (MEM) which represent a spectral decomposition of the spatial relationships among the study quadrats which are represented by sine waves roughly ordered from broad-scale (low values) to fine-scale (high values) within our study design (Dray et al., 2006). Following Blanchet et al. (2008), we used dbRDA to partition variation in β-diversity for adults and seedlings into individual fractions explained by pure (spatially unstructured) environmental variables (E), spatially structured environmental variables (E+S), and spatial variables (S). We then performed forward model selection using the 'Forward.sel' function in the

R ᴘᴀᴄᴋꜰᴏʀ package (Dray et al., 2007). Environmental and spatial variables retained after forward model selection were used to partition variation in taxonomic β-diversity into the individual fractions listed above.

Finally, to evaluate the role of ontogenetic dependency in driving seedling composition (Question 3), we reran the dbRDA to partition variation in β-diversity for seedlings into the same E, E+S, and S fractions described above, while adding fractions explained by adult composition (A), adult composition that is spatially structured (A+S), adult composition that is structured by spatially unstructured environment variables (A+E), and adult composition that is structured by spatially structured environmental variables (A+S+E). Adult composition for all of the 100 quadrats was used to analyze the effect of adult composition on seedling composition to more fully capture the adult community on all sides of each seedling plot. We then performed forward model selection using the 'Forward.sel' function in the R ᴘᴀᴄᴋꜰᴏʀ package (Dray et al., 2007). Environmental and spatial variables and the adult species retained after forward model selection were used to partition variation in taxonomic β-diversity into the individual fractions listed above. We did not examine the influence of the seedling stage on the adult stage as this process occurs over long timescales encompassing many cycles of recruitment and transition of seedlings to later life stages, and our one-time survey dataset is not appropriate to answer this question.

3 | RESULTS

3.1 | Forest composition

Across the 4 ha SJFD we measured 4,684 main stems (stem number ranges from 11 to 95 per quadrat with a mean of 44) and a total of 18 species (Figure 2). Species richness varied from 3 to 11 species (mean = 6.72) per quadrat. Within the 256 seedling subplots, we found a total of 576 seedlings of 11 species. Overall, we found that the composition of the adult and seedling communities significantly differed ($F_{1,162} = 34.85$, $p = 0.001$; Figure 3a, Stress = 0.19), while β-diversity only modestly differed (adults = 0.44, seedlings = 0.40; $F_{1,162} = 5.14$, $p = 0.022$). For both the adults and seedlings, β-diversity was significantly lower than the null expectation (adult SES = −12.4; seedling SES = −25.9) suggesting that β-diversity is lower than would be expected based on an assembly model of ecological drift. Our indicator species analysis found that the difference in composition between adult and seedling communities was primarily driven by differences in the abundance of *Pinus lambertiana*, *Pinus coulteri*, *Pinus ponderosa*, *Pinus jeffreyi*, *Quercus wislizeni*, and *Arctostaphylos pringlei*, which were abundant in the adult community but were relatively absent in the seedling community (Figure 3b). Finally, *Quercus kelloggii*, *Quercus chrysolepis*, and *Calocedrus decurrens* were the dominant species in the seedling class, while there were few seedlings of *Pinus* and *Arctostaphylos* species.

3.2 | Shifts in assembly with ontogeny

For the adult community, we found that that environment alone explained 0% of the variation in β-diversity, spatially structured environmental variables explained 18.6%, and spatial processes explained 44.0%, while 37.4% remained unexplained (Adults Figure 4, Table 1). For the seedling community, we found that environment alone explained 0% of the variation in β-diversity, spatially structured environmental variables explained 5.7%, and spatial processes

explained 21.9% while 72.4% remained unexplained (Seedlings$_1$ Figure 4, Table 1).

3.3 | Ontogenetic dependency

After including adult composition as a predictor in our analysis of seedling composition, we found that the environmental fraction remained unchanged at 0%, while the spatially structured
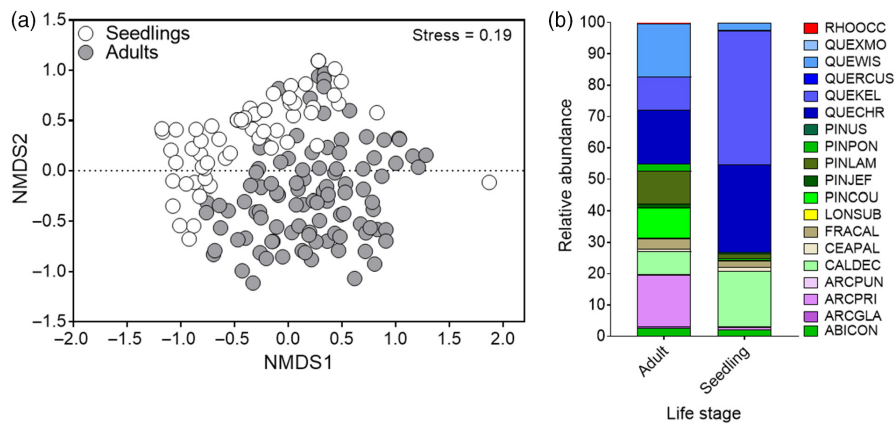

FIGURE 3 Mismatch between seedling and adult composition in the SJFDP. (a) ordination plot (nonmetric multi-dimensional scaling) of differences in community composition between adult quadrats (grey points) and seedling plots (white points). (b) Relative abundance of species separated by life stage (adults on the left, seedling on the right). Species codes: ABICON: *Abies concolor*; ARCGLA: *Arctostaphylos glandulosa*; ARCPRI: *Arctostaphylos pringlei* ssp. *drupacea*; ARCPUN: *Arctostaphylos pungens*; CALDEC: *Calocedrus decurrens*; CEAPAL: *Ceanothus palmeri*; FRACAL: *Frangula californica* ssp. *cuspidata*; LONSUB: *Lonicera subspicata var. denudata*; PINCOU: *Pinus coulteri*; PINJEF: *Pinus jeffreyi*; PINLAM: *Pinus lambertiana*; PINLON: *Pinus ponderosa*; QUECHR: *Quercus chrysolepis*; QUEKEL: *Quercus kelloggii*; QUEWIS: *Quercus wislizeni* var. *frutescens*; QUEXMO: *Quercus Xmorehus* (*Q. kelloggii x wislizeni*); RHOOCC: *Rhododendron occidentale*.
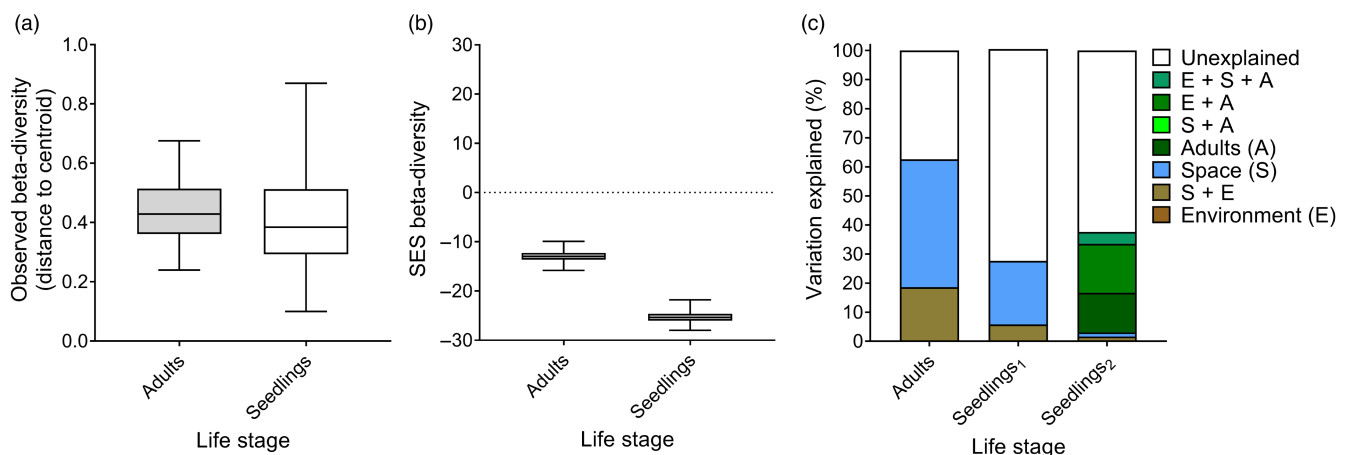

FIGURE 4 Differences in β-diversity among adults and seedlings. (a) Differences in observed β-diversity between adult and seedling communities measured as the distance to centroid of dissimilarity in species composition for each ontogenetic stage. (b) Differences in the Standardized Effect Size (SES) of β-diversity between adult and seedling communities based on 1000 iterations of a null model which effectively removed any effect of niche selection, while maintaining richness and abundance distributions within each community. Values below zero indicate that β-diversity is lower than expected based on an assembly model of ecological drift. (c) Percent variation of observed β-diversity explained by environmental and spatial variables used in the distance-based redundancy analyses. Seedling$_1$ represents analysis with only spatial and environmental variables. Seedling$_2$ represents analysis with spatial, environmental, and adult composition variables where the adult fraction represents ontogenetic dependency. The partitions show the adjusted R^2 values for all combinations of environmental variables, spatial variables, and adult composition, based on distance-based redundancy analysis. Specific variables for all fractions are listed in Table 1.

TABLE 1 Model selection results. Significance of environmental and spatial variables used in the distance-based redundancy analyses of β-diversity. Seedling$_1$ represents analysis with only spatial and environmental fractions. Seedling$_2$ represents analysis with spatial, environmental, and adult composition fractions. An "X" indicates explanatory variables that were retained after forward model selection for observed β-diversity at each site. Number of PCNM eigenfunctions represents the number of significant eigenfunctions retained in each analysis. Species codes (see Figure 3 legend for definitions) represent the significant adult species that were retained in the seedling analysis.

	Observed β-diversity		
Explanatory variable	**Adults**	**Seedlings$_1$**	**Seedlings$_2$**
Environment: soil			
Organic Matter			
Phosphorus			
pH			
Magnesium	X	X	X
Potassium	X		
Calcium			
Environment: topography			
South aspect	X		
Elevation	X		
Slope			
Convexity			
Topographic Position Index			
Topographic Roughness Index			
Flow direction			
Space			
Number of MEM eigenvectors	17	8	8
Adult composition			
Species code			CALDEC, CEAPAL, QUECHR, QUEWIS

environmental variables decreased from 5.7% to 1.6%, and spatial processes decreased from 21.9% to 1.5% (Seedlings$_2$ Figure 4, Table 1). The pure adult fraction explained 13.6% of the variation, spatially structured adult composition explained 0% of the variation in seedling β-diversity, and adult-structured environment explained 16.8%. Lastly, 4.1% of the variation was explained by the joint influence of adults, space and the environment, while 62.4% of the variation remained unexplained (Seedlings$_2$ Figure 4, Table 1).

4 | DISCUSSION

There is a growing recognition of the importance of ontogeny in community assembly (Larson & Funk, 2016; Lasky et al., 2015; Máliš

et al., 2016) and in forest systems the spatial relationship between adult and juvenile trees has long been studied (Clark & Clark, 1984; Grubb, 1977; Nicotra et al., 1999). However, ontogeny has not been well integrated into community assembly frameworks (Spasojevic et al., 2018; Spasojevic & Suding, 2012; Weiher et al., 2011) and few assembly studies have explicitly considered the role of ontogenetic dependency. We found patterns suggesting that the relative importance of assembly processes shift from the seedling to adult life stage in forest tree communities—where the processes explaining adult β-diversity (spatial processes) did not explain seedling β-diversity. We also found evidence for ontogenetic dependency where the adult community (Figure 4: A, A+E, A+S, and A+E+S fractions) explained most of the explained variation in seedling composition across space. Overall, our results are consistent with the hypothesis that dispersal and niche selection shift with ontogeny and highlight the importance of considering ontogenetic dependency, where the community at one life stage can affect another. Taken together, our results suggest that approaches to predict vegetation dynamics under global change should more explicitly consider the role of ontogeny.

4.1 | Forest composition

We found a significant difference between the adult and seedling species composition (Question 1; Figure 3a) with *Pinus* species underrepresented and *Quercus* seedlings overrepresented in the seedling class compared to proportions in the adult community (Figure 3b). There are several possible drivers of this mismatch ranging from short timescale interannual variations in the seedling pool to long-term patterns of recruitment. First, our study only measured species composition over a brief time window while seedling recruitment can be episodic in association with precipitation in western North American forests (Davis et al., 2016; Littlefield et al., 2020). It is possible that 2021, a drought year, simply favored oak recruitment over pine recruitment, resulting in the patterns we observed. Additionally, both the pine species (Fryer, 2018; Gucker, 2007) and oak species (Tollefson, 2008) are known to exhibit masting cycles. However, the demographics we observed are consistent with other studies in similar mixed-conifer forests (Dolanc et al., 2014; Fettig et al., 2019; Minnich et al., 1995) and a 1994 age-class study conducted at the same site, which also found a strikingly low abundance of *Pinus ponderosa*, *Pinus jeffreyi*, and *Pinus coulteri* seedlings and an over-representation of *Quercus chrysolepis* and *Quercus kelloggii* seedlings relative to adults (Savage, 1994), suggesting the patterns we observed may be reflective of long-term trends. It is important to note that differences in survival rates between species (i.e. high pine seedling survival and low oak seedling survival) could prevent changes in canopy species composition, and thus the seedling-adult mismatch we observed is not necessarily indicative of a long-term shift in forest composition. For example, *Quercus kelloggii* is known to exhibit very high seedling density relative to adult densities, as well

as high seedling mortality (Fites-Kaufman et al., 2007), suggesting that high seedling abundance is not necessarily indicative of increasing canopy dominance in this species.

If the mismatch reflects long-term community dynamics, it could result from environmental effects on seed production (i.e. a lack of pinecone production), germination, and survival across demographic stages. Critically, fire suppression in this forest may be driving much of the variation in these demographic processes as fire plays a central role in this dry forest system (Minnich, 2007). Some of the species in the SJFDP (e.g. *Pinus coulteri* and *Arctostaphylos* spp.) require fire for germination (Keeley & Syphard, 2018) while others such as *Pinus ponderosa* benefit from surface fire, which promotes both germination and seedling persistence (Fryer, 2018). Thus, the lack of fire in this system could be promoting oak seedling recruitment which can occur under low-light conditions (Tollefson, 2008), and inhibiting pine recruitment which requires the open canopy conditions produced by periodic fire (Fryer, 2018). The abundance of *Abies concolor* and *Calocedrus decurrens* (both shade-tolerant species) further suggests that fire suppression is a key driver of composition, and is consistent with the demographics of similar fire-suppressed forests (Dolanc et al., 2014; Minnich et al., 1995).

In addition to fire suppression, increased summer water deficit due to climatic warming could be causing differential seedling survival between species (Moran et al., 2019) and thus, the over-representation of oaks in the seedling class could reflect increasing oak dominance in the SJFDP. The dominance of oaks over pines is expected with climate change (McIntyre et al., 2015) as pine and oak species may have different tolerances to drought (Fettig et al., 2019). For example, *Quercus chrysolepis* is found in more arid habitats (Pavlik, 1991) than the pine species (Minnich & Everett, 2001) in the SJFDP. While further research is needed to disentangle the role of fire suppression versus climatic warming in driving the observed patterns, our results suggest a high potential for change in this forest. With extremely low numbers of seedlings in the *Pinus* and *Arctostaphylos* species, demographic stochasticity could lead to profound shifts in composition.

4.2 | Ontogenetic shifts in assembly processes

Differences in β-diversity patterns between seedlings and adults suggest that the compositional differences are due to assembly mechanisms shifting with ontogeny in this forest (Question 2). We found that contemporary adult composition is largely driven by space, but that elevation, aspect, magnesium, and potassium (Table 1) may be important abiotic mechanisms underlying niche selection for adults. In contrast, seedling composition is largely unexplained, with a modest amount of variation explained by space, and magnesium being the only predictive abiotic factor (Table 1). It is possible that the spatial component driving adult and seedling composition is the result of unquantified environmental factors such as microsites formed by hydrologic processes (McLaughlin et al., 2017) or topography (Dobrowski, 2011; Serra-Diaz et al., 2016). Additionally, for

seedlings, the spatial component may reflect recruitment in canopy gaps resulting from treefall as older trees perish from drought—similar patterns have been found after disturbance in tropical forests (Franklin & Rey, 2016).

More of the β-diversity was unexplained for seedlings than for adults, which could result from unmeasured environmental variables that are not spatially structured at the scale of our $20 \times 20\,\text{m}$ quadrats (e.g. light levels, which are likely associated with fine-scale tree canopy structure) or ecological drift (Vellend et al., 2014) which may be more important for seedlings than for adults (Cui & Zheng, 2016; but see Green et al., 2014). However, our null modelling found that seedlings had lower β-diversity than expected from the null expectation of random assembly than the adults (adult SES $= -12.4$; seedling SES $= -25.9$) suggesting slower than expected distance-decay for seedlings (Siefert et al., 2013). This indicates that seedling composition is more homogenous across space, exhibiting slower species turnover with increasing geographic distance than adults. Importantly, higher magnitude and negative SES is indicative of deterministically lower turnover than expected by chance (less non-random spatial aggregation of seedlings) suggesting that dispersal may drive spatial variation in seedling communities through processes such as mass effects (Leibold et al., 2004). Lastly, the increased explanatory power of the E and E+S fractions for adults suggests that niche selection may be more important for adults than for seedlings for the topoedaphic variables we measured, a result consistent with other studies (Comita et al., 2007; Yang et al., 2016; Sellan et al., 2019; but see Asefa et al., 2020; Qiao et al., 2015).

Finally, it is important to acknowledge the limitations of our approach, which inferred community assembly processes from patterns of β-diversity. First, it is possible that lower-level mechanisms rather than higher-level processes shift in importance from the seedling to adult life stage, and that we simply did not measure the specific environmental variables that are important for seedlings. For example, variation in light availability is a known driver of seedlings in this system generally (Moghaddas et al., 2008), but we lacked plot scale measurements. Second, environmental filters may have changed temporally, such that seedlings of the present are responding to a different set of filters than contemporary adult trees experienced in the past as seedlings, resulting in divergent distributions compared to mature trees (Lenoir et al., 2009; Serra-Diaz et al., 2016). Many adult trees in the SJFDP recruited decades ago (Savage, 1994) when environmental conditions and anthropogenic influences were distinct from those of the present. Thus it is possible that sites formerly suitable for seedling establishment are now unsuitable (Comita et al., 2007), possibly due to climatic changes (Petrie et al., 2017) or forest densification due to fire suppression (Minnich et al., 1995). Specifically, the low explanatory power of environmental variables for seedlings (weak influence of niche selection) we observed could be the result of certain species expanding their distributions into sites in which they were formerly competitively inferior (i.e. range shifts; Serra-Diaz et al., 2016). This case represents a temporal shift in the environment causing a shift in composition, not a fixed difference in niche selection among ontogenetic stages.

4.3 | Ontogenetic dependency

Finally, we found evidence for ontogenetic dependency in this temperate dry forest (Question 3). Adult composition was predictive of variation in seedling composition and explained more of the variation in β-diversity than space or the environment alone. While dispersal, niche selection, and drift all have the potential to cause ontogenetic dependency, the specific mechanisms underlying the pattern we observed cannot be discerned fully from our observational approach. Seedlings only grow where propagules can disperse from mature adults, ensuring some degree of ontogenetically dependent dispersal in any community. However, the A + S (adult and space) fraction explained 0% of seedling composition suggesting that dispersal may be playing a role at a scale larger than the spatial scale of our plot, or at a timeframe not captured by our sampling (e.g. masting). The largest fraction was the environmentally-structured adult composition fraction (E + A), which explained 16.8% of seedling composition. Importantly, this fraction suggests that adults may be modifying the environment in a way that directly impacts seedlings—a case of ontogenetic dependency arising from altered niche selection. Only 4.1% of the variation in the seedling community was explained by the joint influence of adults, space, and the environment (the adults creating spatial variation in the environment), suggesting that the environmental impact of adults has little spatial structure at the scale being considered. Finally, the pure adult fraction explained 13.6% of the variation in seedling composition, suggesting that the adult community has an impact on seedlings that is not associated with the environmental variables we measured or the spatial structure of adults at the scale in consideration. For example, this pattern could result from adult modification of the environment through alterations in microclimate (Davis, Dobrowski, et al., 2019), the light environment (Caldeira et al., 2014), litter environment (Callaway, 2007), or through biotic interactions such as mycorrhizae associated with adult trees facilitating conspecific seedlings (Bingham & Simard, 2012), all of which we did not measure or plant–soil feedbacks (van der Putten et al., 2013) associated with soil variables we did not measure. Taken together, these results suggest some level of ontogenetic dependence of the seedling community on the adult community that is not primarily linked to seed dispersal, but rather through altered abiotic conditions. Further research—experiments that quantify seedling performance under varying degrees of conspecific and heterospecific adult cover—could determine specific mechanisms underlying the pure adult fraction which cannot be determined from our observational approach.

5 | CONCLUSIONS

We found patterns suggesting that higher-level community assembly processes (drift, dispersal and selection inferred from patterns of β-diversity) shift in relative importance from the seedling to adult stage in a temperate dry forest. Specifically, niche selection may be more important in shaping adult rather than seedling composition in this forest, while ontogenetic dependency unrelated to seed dispersal explains more of the variation in seedling composition than any of the environmental or spatial factors measured in our 4-ha plot. Overall, our results suggest that research focused on understanding biodiversity responses to environmental change would benefit from an explicit consideration of ontogenetic shifts in assembly mechanisms and ontogenetic dependency. First, recognizing that the contributions of assembly processes and the underlying filters themselves can differ with life stage (Larson & Funk, 2016) is critical to identifying key mechanisms preventing life stage transitions that filter out species and therefore cause vegetation shifts (Davis et al., 2018). Second, the common assumption that divergent regional distributions between life stages are the result of temporal range shifts may need to be reconsidered, as seedlings may be more widely distributed because they occupy sites that are unsuitable for transition into larger size classes (saplings or adults; Heiland et al., 2022; Máliš et al., 2016). Third, ontogenetic dependency describes the multiple effects of adult communities on seedling communities: not just by controlling seed input (dispersal) but also through altering the probability of ecological drift and shaping selective pressures (niche selection). While most studied in forests, the ontogenetic dependency concept can describe interactions between life stages in all communities and is not limited to forest systems. Critically, we posit that integrating ontogeny and ontogenetic dependency into the community assembly framework will help elucidate the processes that drive regeneration, which is central to predicting community dynamics.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14132.

DATA AVAILABILITY STATEMENT

All data used for this work are available at Dryad: https://doi.org/10.6086/D1267D (Spasojevic, 2023).

ORCID

Jared D. Huxley https://orcid.org/0000-0001-8921-6235
Tesa Madsen-Hepp https://orcid.org/0000-0002-3288-8943
Marko J. Spasojevic https://orcid.org/0000-0003-1808-0048

REFERENCES

Ackerly, D. D., Kling, M. M., Clark, M. L., Papper, P., Oldfather, M. F., Flint, A. L., & Flint, L. E. (2020). Topoclimates, refugia, and biotic responses to climate change. *Frontiers in Ecology and the Environment*, *18*(5), 288–297. https://doi.org/10.1002/fee.2204

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*(1), 32–46.

Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, *62*(1), 245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x

Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, *9*(6), 683–693.

Asefa, M., Wen, H.-D., Cao, M., & Hu, Y.-H. (2020). Key community assembly processes switch between scales in shaping beta diversity in two primary forests, Southwest China. *Forests*, *11*(10), Article 10. https://doi.org/10.3390/f11101106

Barbour, M., Keeler-Wolf, T., & Schoenherr, A. A. (2007). *Terrestrial vegetation of California*. University of California Press.

Bell, D. M., Bradford, J. B., & Lauenroth, W. K. (2014). Early indicators of change: Divergent climate envelopes between tree life stages imply range shifts in the western u nited s tates. *Global Ecology and Biogeography*, *23*(2), 168–180.

Beyns, R., Bauman, D., & Drouet, T. (2021). Fine-scale tree spatial patterns are shaped by dispersal limitation which correlates with functional traits in a natural temperate forest. *Journal of Vegetation Science*, *32*(4), e13070. https://doi.org/10.1111/jvs.13070

Bingham, M. A., & Simard, S. (2012). Ectomycorrhizal networks of *Pseudotsuga menziesii* var. glauca trees facilitate establishment of conspecific seedlings under drought. *Ecosystems*, *15*(2), 188–199. https://doi.org/10.1007/s10021-011-9502-2

Blanchet, F. G., Legendre, P., & Borcard, D. (2008). Forward selection of explanatory variables. *Ecology*, *89*(9), 2623–2632. https://doi.org/10.1890/07-0986.1

Cáceres, M. D., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, *90*(12), 3566–3574. https://doi.org/10.1890/08-1823.1

Caldeira, M. C., Ibáñez, I., Nogueira, C., Bugalho, M. N., Lecomte, X., Moreira, A., & Pereira, J. S. (2014). Direct and indirect effects of tree canopy facilitation in the recruitment of Mediterranean oaks. *Journal of Applied Ecology*, *51*(2), 349–358. https://doi.org/10.1111/1365-2664.12189

Callaway, R. M. (2007). Direct mechanisms for facilitation. In *Positive interactions and interdependence in plant communities* (pp. 15–116). Springer.

Cavender-Bares, J., & Bazzaz, F. A. (2000). Changes in drought response strategies with ontogeny in *Quercus rubra*: Implications for scaling from seedlings to mature trees. *Oecologia*, *124*(1), 8–18. https://doi.org/10.1007/PL00008865

Clark, D. A., & Clark, D. B. (1984). Spacing dynamics of a tropical rain forest tree: Evaluation of the Janzen-Connell model. *The American Naturalist*, *124*(6), 769–788.

Clarke, K. R. (1993). Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*(1), 117–143.

Comita, L. S., Condit, R., & Hubbell, S. P. (2007). Developmental changes in habitat associations of tropical trees. *Journal of Ecology*, *95*(3), 482–492. https://doi.org/10.1111/J.1365-2745.2007.01229.X

Comita, L. S., & Hubbell, S. P. (2009). Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology*, *90*(2), 328–334.

Condit, R. (1998). *Tropical forest census plots: Methods and results from Barro Colorado Island, Panama and a Comparison with Other Plots*. Springer-Verlag Berlin Heidelberg and R.G. Landes Company.

Connell, J. H., Tracey, J. G., & Webb, L. J. (1984). Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecological Monographs*, *54*(2), 141–164. https://doi.org/10.2307/1942659

Cui, W., & Zheng, X.-X. (2016). Partitioning tree species diversity and developmental changes in habitat associations in a subtropical evergreen broadleaf secondary forest in Southern China. *Forests*, *7*(10), Article 10. https://doi.org/10.3390/f7100228

Davis, F. W., Sweet, L. C., Serra-Diaz, J. M., Franklin, J., McCullough, I., Flint, A., Flint, L., Dingman, J. R., Regan, H. M., Syphard, A. D., Hannah, L., Redmond, K., & Moritz, M. A. (2016). Shrinking windows of opportunity for oak seedling establishment in southern California mountains. *Ecosphere*, *7*(11), e01573. https://doi.org/10.1002/ecs2.1573

Davis, F. W., Synes, N. W., Fricker, G. A., McCullough, I. M., Serra-Diaz, J. M., Franklin, J., & Flint, A. L. (2019). LiDAR-derived topography and forest structure predict fine-scale variation in daily surface temperatures in oak savanna and conifer forest landscapes. *Agricultural and Forest Meteorology*, *269–270*, 192–202. https://doi.org/10.1016/j.agrformet.2019.02.015

Davis, K. T., Dobrowski, S. Z., Higuera, P. E., Holden, Z. A., Veblen, T. T., Rother, M. T., Parks, S. A., Sala, A., & Maneta, M. P. (2019). Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(13), 6193–6198.

Davis, K. T., Higuera, P. E., & Sala, A. (2018). Anticipating fire-mediated impacts of climate change using a demographic framework. *Functional Ecology*, *32*(7), 1729–1745.

Dayrell, R. L. C., Arruda, A. J., Pierce, S., Negreiros, D., Meyer, P. B., Lambers, H., & Silveira, F. A. O. (2018). Ontogenetic shifts in plant ecological strategies. *Functional Ecology*, *32*(12), 2730–2741. https://doi.org/10.1111/1365-2435.13221/SUPPINFO

Dobrowski, S. Z. (2011). A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology*, *17*(2), 1022–1035.

Dolanc, C. R., Safford, H. D., Dobrowski, S. Z., & Thorne, J. H. (2014). Twentieth century shifts in abundance and composition of vegetation types of the Sierra Nevada, CA, US. *Applied Vegetation Science*, *17*(3), 442–455. https://doi.org/10.1111/avsc.12079

Dray, S., Legendre, P., & Blanchet, F. G. (2007). *Packfor: Forward selection with permutation*, R package version 0.0–7.

Dray, S., Legendre, P., & Peres-Neto, P. R. (2006). Spatial modelling: A comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling*, *196*(3–4), 483–493. https://doi.org/10.1016/j.ecolmodel.2006.02.015

Dufrene, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, *67*, 345–366.

Eriksson, O., & Ehrlén, J. (2008). Seedling recruitment and population ecology. In M. A. Leck, R. L. Simpson, & V. T. Parker (Eds.), *Seedling ecology and evolution* (pp. 239–254). Cambridge University Press. https://doi.org/10.1017/CBO9780511815133.013

Fettig, C. J., Mortenson, L. A., Bulaon, B. M., & Foulk, P. B. (2019). Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. *Forest Ecology and Management*, *432*, 164–178. https://doi.org/10.1016/j.foreco.2018.09.006

Fites-Kaufman, J. A., Rundel, P., Stephenson, N., & Weixelman, D. (2007). Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. In M. Barbour, T. Keeler-Wolf, & A. A. Schoenherr (Eds.), *Terrestrial vegetation of California* (pp. 456–501). Berkeley, CA: University of California Press.

Fox, G. A., & Kendall, B. E. (2002). Demographic stochasticity and the variance reduction effect. *Ecology*, *83*(7), 1928–1934.

Franklin, J., & Rey, S. J. (2016). Heterogeneous tree recruitment following disturbance in insular tropical forest, Kingdom of Tonga. *Journal of Tropical Ecology*, *32*(6), 536–542. https://doi.org/10.1017/S0266467416000456

Fryer, J. L. (2018). *Pinus ponderosa* var. Benthamiana, P. p. Var. Ponderosa: Ponderosa pine. In *Fire effects information system*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory. https://www.fs.usda.gov/database/feis/plants/tree/pinponp/all.html

Garbowski, M., Johnston, D. B., & Brown, C. S. (2021). Leaf and root traits, but not relationships among traits, vary with ontogeny in seedlings. *Plant and Soil*, *460*(1), 247–261. https://doi.org/10.1007/s11104-020-04790-z

Green, P. T., & Harms, K. E. (2018). The causes of disproportionate non-random mortality among life-cycle stages. *Ecology*, *99*(1), 36–46. https://doi.org/10.1002/ecy.2039

Green, P. T., Harms, K. E., & Connell, J. H. (2014). Nonrandom, diversifying processes are disproportionately strong in the smallest size classes of a tropical forest. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(52), 18649–18654.

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biological Reviews*, *52*(1), 107–145. https://doi.org/10.1111/J.1469-185X.1977.TB01347.X

Gucker, C. L. (2007). *Pinus jeffreyi*. In *Fire effects information system*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. https://www.fs.fed.us/database/feis/plants/tree/pinjef/all.html

Heiland, L., Kunstler, G., Ruiz-Benito, P., Buras, A., Dahlgren, J., & Hülsmann, L. (2022). Divergent occurrences of juvenile and adult trees are explained by both environmental change and ontogenetic effects. *Ecography*, *2022*(3), e06042. https://doi.org/10.1111/ecog.06042

Hijmans, R. J., Van Etten, J., Mattiuzzi, M., Sumner, M., Greenberg, J. A., Lamigueiro, O. P., Bevan, A., Racine, E. B., & Shortridge, A. (2013). Raster package in R. Version. https://MirroRs.Sjtug.Sjtu.Edu.Cn/Cran/Web/PackaGes/Raster/Raster.Pdf

Keeler-Wolf, T. (1989). Establishment record for Hall Canyon Research Natural Area within San Bernardino National Forest, Riverside County, California. (Unpublished Report on File).

Keeley, J. E., & Syphard, A. D. (2018). Chapter seventeen. South Coast Bioregion. In *Fire in California's ecosystems* (pp. 319–352). University of California Press.

Larson, J. E., Ebinger, K. R., & Suding, K. N. (2021). Water the odds? Spring rainfall and emergence-related seed traits drive plant recruitment. *Oikos*, *130*(10), 1665–1678. https://doi.org/10.1111/oik.08638

Larson, J. E., & Funk, J. L. (2016). Regeneration: An overlooked aspect of trait-based plant community assembly models. *Journal of Ecology*, *104*(5), 1284–1298. https://doi.org/10.1111/1365-2745.12613

Lasky, J. R., Bachelot, B., Muscarella, R., Schwartz, N., Forero-Montaña, J., Nytch, C. J., Swenson, N. G., Thompson, J., Zimmerman, J. K., & Uriarte, M. (2015). Ontogenetic shifts in trait-mediated mechanisms of plant community assembly. *Ecology*, *96*(8), 2157–2169. https://doi.org/10.1890/14-1809.1

Lavergne, S., Mouquet, N., Thuiller, W., & Ronce, O. (2010). Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics*, *41*, 321–350.

Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I.-F., & He, F. (2009). Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology*, *90*(3), 663–674. https://doi.org/10.1890/07-1880.1

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, *7*(7), 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lenoir, J., Gégout, J. C., Pierrat, J. C., Bontemps, J. D., & Dhôte, J. F. (2009). Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). *Ecography*, *32*(5), 765–777. https://doi.org/10.1111/j.1600-0587.2009.05791.x

Littlefield, C. E., Dobrowski, S. Z., Abatzoglou, J. T., Parks, D. S. A., & Davis, K. T. (2020). *A climatic dipole drives short-and long-term patterns of postfire forest recovery in the western United States*. https://doi.org/10.1073/pnas.2007434117/-/DCSupplemental

Máliš, F., Kopecký, M., Petřík, P., Vladovič, J., Merganič, J., & Vida, T. (2016). Life stage, not climate change, explains observed tree range shifts. *Global Change Biology*, *22*(5), 1904–1914. https://doi.org/10.1111/gcb.13210

McIntyre, P. J., Thorne, J. H., Dolanc, C. R., Flint, A. L., Flint, L. E., Kelly, M., & Ackerly, D. D. (2015). Twentieth-century shifts in forest structure in California: Denser forests, smaller trees, and increased dominance of oaks. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(5), 1458–1463.

McLaughlin, B. C., Ackerly, D. D., Klos, P. Z., Natali, J., Dawson, T. E., & Thompson, S. E. (2017). Hydrologic refugia, plants, and climate change. *Global Change Biology*, *23*(8), 2941–2961. https://doi.org/10.1111/gcb.13629

Minnich, R. A. (2007). Southern California coniferous forest. In M. Barbour, T. Keeler-Wolf, & A. A. Schoenherr (Eds.), *Terrestrial vegetation of California* (pp. 339–336). Berkeley, CA: University of California Press.

Minnich, R. A., Barbour, M. G., Burk, J. H., & Fernau, R. F. (1995). Sixty years of change in Californian conifer forests of the San Bernardino mountains. *Conservation Biology*, *9*(4), 902–914. https://doi.org/10.1046/j.1523-1739.1995.09040902.x

Minnich, R. A., & Everett, R. G. (2001). Conifer tree distributions in Southern California. *Madrono*, *48*(3), 177–197.

Mittelbach, G. G., & Schemske, D. W. (2015). Ecological and evolutionary perspectives on community assembly. *Trends in Ecology & Evolution*, *30*(5), 241–247. https://doi.org/10.1016/j.tree.2015.02.008

Moghaddas, J. J., York, R. A., & Stephens, S. L. (2008). Initial response of conifer and California black oak seedlings following fuel reduction activities in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management*, *255*(8), 3141–3150. https://doi.org/10.1016/j.foreco.2007.11.009

Mokany, K., & Ferrier, S. (2011). Predicting impacts of climate change on biodiversity: A role for semi-mechanistic community-level modelling. *Diversity and Distributions*, *17*(2), 374–380.

Moran, E. V., Das, A. J., Keeley, J. E., & Stephenson, N. L. (2019). Negative impacts of summer heat on Sierra Nevada tree

seedlings. *Ecosphere*, *10*(6), e02776. https://doi.org/10.1002/ecs2.2776

Mori, A. S., Fujii, S., Kitagawa, R., & Koide, D. (2015). Null model approaches to evaluating the relative role of different assembly processes in shaping ecological communities. *Oecologia*, *178*(1), 261–273. https://doi.org/10.1007/s00442-014-3170-9

Myers, J. A., Chase, J. M., Jimenez, I., Jorgensen, P. M., Araujo-Murakami, A., Paniagua-Zambrana, N., & Seidel, R. (2013). Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecology Letters*, *16*(2), 151–157. https://doi.org/10.1111/ele.12021

Myers, J. A., & LaManna, J. A. (2016). The promise and pitfalls of β-diversity in ecology and conservation. *Journal of Vegetation Science*, *27*(6), 1081–1083. https://doi.org/10.1111/jvs.12482

Nicotra, A. B., Chazdon, R. L., & Iriarte, S. V. B. (1999). Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology*, *80*(6), 1908–1926. https://doi.org/10.1890/0012-9658(1999)080[1908:SHOLAW]2.0.CO;2

North, M., Collins, B. M., Safford, H., & Stephenson, N. L. (2016). Montane forests. In H. Mooney & E. Zavaleta (Eds.), *Ecosystems of California* (pp. 553–577). University of California Press. Chapter 27.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., & Wagner, H. (2013). Vegan: Community ecology package. R package version 2.6-4.

Orrock, J. L., & Watling, J. I. (2010). Local community size mediates ecological drift and competition in metacommunities. *Proceedings of the Royal Society B-Biological Sciences*, *277*(1691), 2185–2191. https://doi.org/10.1098/rspb.2009.2344

Parrish, J. A. D., & Bazzaz, F. A. (1985). Ontogenetic niche shifts in old-field annuals. *Ecology*, *66*(4), 1296–1302. https://doi.org/10.2307/1939182

Pavlik, B. M. (1991). *Oaks of California*. Cachuma Press.

Pearse, I. S., LaMontagne, J. M., & Koenig, W. D. (2017). Inter-annual variation in seed production has increased over time (1900–2014). *Proceedings of the Royal Society B: Biological Sciences*, *284*(1868), 20171666. https://doi.org/10.1098/rspb.2017.1666

Peres-Neto, P. R., Legendre, P., Dray, S., & Borcard, D. (2006). Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology*, *87*(10), 2614–2625. https://doi.org/10.1890/0012-9658(2006)87[2614:vposdm]2.0.co;2

Peterson, D. W., & Reich, P. B. (2008). Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. *Plant Ecology*, *194*(1), 5–16.

Petrie, M. D., Bradford, J. B., Hubbard, R. M., Lauenroth, W. K., Andrews, C. M., & Schlaepfer, D. R. (2017). Climate change may restrict dryland forest regeneration in the 21st century. *Ecology*, *98*(6), 1548–1559. https://doi.org/10.1002/ECY.1791

Poorter, L. (2007). Are species adapted to their regeneration niche, adult niche, or both? *The American Naturalist*, *169*(4), 433–442. https://doi.org/10.1086/512045

Qiao, X., Li, Q., Jiang, Q., Lu, J., Franklin, S., Tang, Z., Wang, Q., Zhang, J., Lu, Z., Bao, D., Guo, Y., Liu, H., Xu, Y., & Jiang, M. (2015). Beta diversity determinants in Badagongshan, a subtropical forest in central China. *Scientific Reports*, *5*(1), Article 1. https://doi.org/10.1038/srep17043

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Savage, M. (1994). Anthropogenic and natural disturbance and patterns of mortality in a mixed conifer forest in California. *Canadian Journal of Forest Research*, *24*(6), 1149–1159. https://doi.org/10.1139/x94-152

Sellan, G., Thompson, J., Majalap, N., & Brearley, F. Q. (2019). Soil characteristics influence species composition and forest structure differentially among tree size classes in a Bornean heath forest. *Plant and Soil*, *438*(1), 173–185. https://doi.org/10.1007/s11104-019-04000-5

Serra-Diaz, J. M., Franklin, J., Dillon, W. W., Syphard, A. D., Davis, F. W., & Meentemeyer, R. K. (2016). California forests show early indications of both range shifts and local persistence under climate change. *Global Ecology and Biogeography*, *25*(2), 164–175.

Sheppard, P. R., & Lassoie, J. P. (1998). Fire regime of the lodgepole pine forest of Mt. San Jacinto, California. *Madroño*, *1*, 47–56.

Siefert, A., Ravenscroft, C., Weiser, M. D., & Swenson, N. G. (2013). Functional beta-diversity patterns reveal deterministic community assembly processes in eastern North American trees. *Global Ecology and Biogeography*, *22*(6), 682–691. https://doi.org/10.1111/geb.12030

Song, X., Hogan, J. A., Lin, L., Wen, H., Cao, M., & Yang, J. (2018). Canopy openness and topographic habitat drive tree seedling recruitment after snow damage in an old-growth subtropical forest. *Forest Ecology and Management*, *429*, 493–502. https://doi.org/10.1016/j.foreco.2018.07.038

Spasojevic, M. J. (2023). Data from: San Jacinto forest dynamics plots seedling, adult, and environmental data. Dryad https://doi.org/10.6086/D1267D

Spasojevic, M. J., Catano, C. P., LaManna, J. A., & Myers, J. A. (2018). Integrating species traits into species pools. *Ecology*, *99*(6), 1265–1276. https://doi.org/10.1002/ecy.2220

Spasojevic, M. J., & Suding, K. N. (2012). Inferring community assembly mechanisms from functional diversity patterns: The importance of multiple assembly processes. *Journal of Ecology*, *100*(3), 652–661.

Spasojevic, M. J., Yablon, E. A., Oberle, B., & Myers, J. A. (2014). Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere*, *5*(10), art129. https://doi.org/10.1890/ES14-000159.1

Tollefson, J. E. (2008). *Quercus chrysolepis*. In *Fire effects information system*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. https://www.fs.fed.us/database/feis/plants/tree/quechr/all.html

van der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., Kardol, P., Klironomos, J. N., Kulmatiski, A., Schweitzer, J. A., Suding, K. N., Van de Voorde, T. F. J., & Wardle, D. A. (2013). Plant–soil feedbacks: The past, the present and future challenges. *Journal of Ecology*, *101*(2), 265–276. https://doi.org/10.1111/1365-2745.12054

Vellend, M. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, *85*(2), 183–206. https://doi.org/10.1086/652373

Vellend, M. (2016). *The theory of ecological communities*. Princeton University Press.

Vellend, M., Srivastava, D. S., Anderson, K. M., Brown, C. D., Jankowski, J. E., Kleynhans, E. J., Kraft, N. J. B., Letaw, A. D., Macdonald, A. A. M., Maclean, J. E., Myers-Smith, I. H., Norris, A. R., & Xue, X. (2014). Assessing the relative importance of neutral stochasticity in ecological communities. *Oikos*, *123*(12), 1420–1430. https://doi.org/10.1111/oik.01493

Wainwright, C. E., Staples, T. L., Charles, L. S., Flanagan, T. C., Lai, H. R., Loy, X., Reynolds, V. A., & Mayfield, M. M. (2018). Links between community ecology theory and ecological restoration are on the rise. *Journal of Applied Ecology*, *55*(2), 570–581. https://doi.org/10.1111/1365-2664.12975

Walters, M. B., & Reich, P. B. (1996). Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology*, *77*(3), 841–853.

Wang, B. C., & Smith, T. B. (2002). Closing the seed dispersal loop. *Trends in Ecology & Evolution*, *17*(8), 379–386.

Webb, C. O., & Peart, D. R. (2000). Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology*, *88*(3), 464–478. https://doi.org/10.1046/J.1365-2745.2000.00462.X

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., & Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *366*(1576), 2403–2413. https://doi.org/10.1098/rstb.2011.0056

Williams, A. P., Cook, E. R., Smerdon, J. E., Cook, B. I., Abatzoglou, J. T., Bolles, K., Baek, S. H., Badger, A. M., & Livneh, B. (2020). Large contribution from anthropogenic warming to an emerging North American megadrought. *Science*, *368*(6488), 314–318.

Williams-Linera, G., & Manrique-Ascencio, A. (2020). Functional traits of tree saplings and adults in a tropical cloud forest restoration context. *Botanical Sciences*, *98*(1), 76–85.

Yang, Q.-S., Shen, G.-C., Liu, H.-M., Wang, Z.-H., Ma, Z.-P., Fang, X.-F., Zhang, J., & Wang, X.-H. (2016). Detangling the effects of environmental filtering and dispersal limitation on aggregated distributions of tree and shrub species: Life stage matters. *PLoS ONE*, *11*(5), e0156326. https://doi.org/10.1371/journal.pone.0156326