

# Towards linking species traits to demography and assembly in diverse tree communities: Revisiting the importance of size and allocation

Yoshiko Iida<sup>1</sup>  | Nathan G. Swenson<sup>2</sup>

<sup>1</sup>Forestry and Forest Products Research Institute, Tsukuba, Japan

<sup>2</sup>Department of Biology, University of Maryland, Maryland

## Correspondence

Yoshiko Iida, Forestry and Forest Products Research Institute, Matsunosato 1, Tsukuba, Ibaraki 305-8687, Japan.  
Email: yyoshiko503@gmail.com

## Abstract

One of the important goals in plant ecology is to form a mechanistic link between the underlying processes driving the dynamics and structure of communities and the observed demography (i.e., growth, survival, and recruitment) and assembly (i.e., distribution of species) in a community via traits. Although the importance of traits to performance is evident, their direct links to demography and the resulting assembly in tree communities are often found to be fairly weak probably because a single “mean” trait value for a species is not enough to capture complex life histories. In this paper, we review how traits at the organ-level and at the whole plant level, demography, and assembly change with size in diverse tropical forests and summarize what we know so far. We argue the importance of trait-based life-history strategies revealing trait-environment-demography linkages across ontogenetic stages to achieve the ultimate goal of forming a mechanistic link between the underlying processes driving the dynamics and structure of communities and the observed demography and assembly.

## KEYWORDS

allometry, biomass allocation, functional trait, ontogeny, size-dependency

## 1 | INTRODUCTION

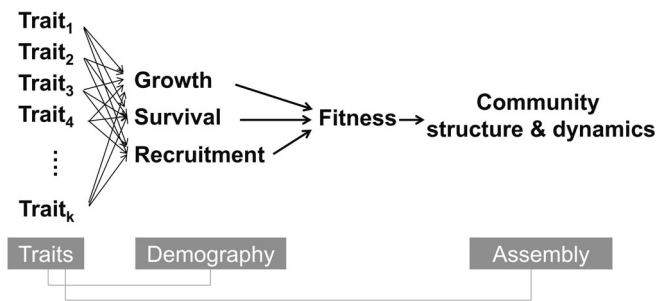
What determines the structure and dynamics of populations and how does this influence the co-existence of large numbers of species? These are fundamental questions in community ecology and represent a grand challenge in diverse biological communities such as tropical forests. The structure and dynamics of communities are the outcomes of differential demographic rates via

assembly processes at the individual and population scales (Figure 1). Thus, identifying the drivers of demographic rates will help us to understand assembly processes and the causes of community dynamics and structure. Trait-based approaches to ecology have become increasingly popular over the last two decades (e.g., McGill, Enquist, Weiher, & Westoby, 2006). While trait-based approaches have always been present in ecology, the characterization of species using a series of commonly and easily measured functional traits, that are representative of major trade-off axes in organismal form

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**FIGURE 1** A conceptual diagram of traits, demography, and assembly linkages. Traits influence demography or demographic performance (i.e., growth, survival, and recruitment), demography affects fitness and, ultimately, they determine the structure and dynamics of communities via assembly processes. This diagram is adapted from the framework of Arnold (1983) and Violle et al. (2007)

and function in plants, has generated a great deal of new interest in traits (Reich, 2014; Westoby, 1998). Likewise, studies of demography and assembly have often helped to elucidate the life-history strategies of the plant, but generalized mechanistic links between traits and demography, and traits and assembly are still unclear (e.g., Webb, Hoeting, Ames, Pyne, & Poff, 2010).

A functional trait is often defined as a morphological or physiological trait which strongly influences performance (Violle et al., 2007). For plants, several key traits in relation to the leaf-height-seed strategies scheme are examined based on their important relationships to plant performance (Westoby, 1998; Westoby, Falster, Moles, Vesk, & Wright, 2002; Westoby & Wright, 2006) and the collection of such species trait data has been rapidly accumulating worldwide (e.g., Kattge et al., 2011; Kattge et al., 2020). Despite this interest and effort, most research has focused on trait diversity in communities (e.g., Lavorel & Garnier, 2002) or trait distributions along environmental gradients (e.g., Kraft, Valencia, & Ackerly, 2008), and less work has focused on elucidating when, where and why various traits are predictive of individual demographic performance in the field (Yang, Cao, & Swenson, 2018). Such work is fundamental for elucidating the processes that link traits and demographic performance and, therefore, for continuing to develop “trait-based approaches” for studying community structure and dynamics (Figure 1).

Trait-based studies are particularly valuable in diverse communities such as tropical forests, that include many rare species, by providing a common currency for ecologists to use to compare large numbers of different species within and among local communities as well as at a global scale. During the last two decades, community-wide studies have mainly focused on the mean or

representative values of a trait and/or a demographic rate (e.g., Poorter et al., 2008; Wright et al., 2010). However, results from this work have been inconsistent with our expectations, which were previously obtained from more detailed research from physiological perspectives or from the well-known leaf economics spectrum (Wright et al., 2004). For example, at community- and global-scales, growth rates are frequently, weakly, related to leaf traits (e.g., Paine et al., 2015; Wright et al., 2010), which are indicative of photosynthesis rates and demographic trade-offs in community-wide tree species comparison (e.g., Kitajima, 1994). Thus, a major outstanding question is why the traits that are measured so frequently in ecology are not good predictors of demographic rates.

Yang et al. (2018) suggested three core issues of why trait–demographic rate relationships are generally weak in tree communities. The first issue is that the trait–demographic rate relationship varies spatially and temporally. The second issue is that a single “mean” trait value for a species is often utilized for analyses and, thus, a great deal of important information regarding intra-specific responses to the environment is masked. The third issue is that there are unmeasured traits, which are directly linked with demographic rates or unmeasured demographic responses (e.g., plastic responses) that are strongly influenced by traits. These issues arise because the whole plant life history is too complex to be summarized by one or two simple axes. To understand how traits and demography link under several different contexts, it is important to understand the mechanistic pathways to link them in a comprehensive manner. As a first step to understanding the whole of plant life history, we argue that incorporating size and allocation is essential for a robust trait-based approach. Understanding size-related variation in traits and/or demographic rates provides insights into how traits and/or demographic rates vary with respect to the three-dimensional forest structure with variable environmental conditions (first and second issues) and during life history (second issue). Biomass allocation to leaves, stems, and roots represents the strategy of species with respect to how they take up resources for future use, but the application of allocation as a functional trait in forest ecology is limited to early ontogenetic stages of seedlings and has been rarely applied in studies of later ontogenetic stages using functional traits (third issue). Thus, in this review, we will focus on the importance of size and allocation in tree communities and we argue that revisiting the importance of size and allocation helps us to identify a pathway forward for linking traits and demography and assembly to ultimately understand community structure and dynamics.

## 2 | IMPORTANCE OF SIZE, ALLOCATION AND ASSOCIATED ENVIRONMENTAL CONDITION IN FORESTS

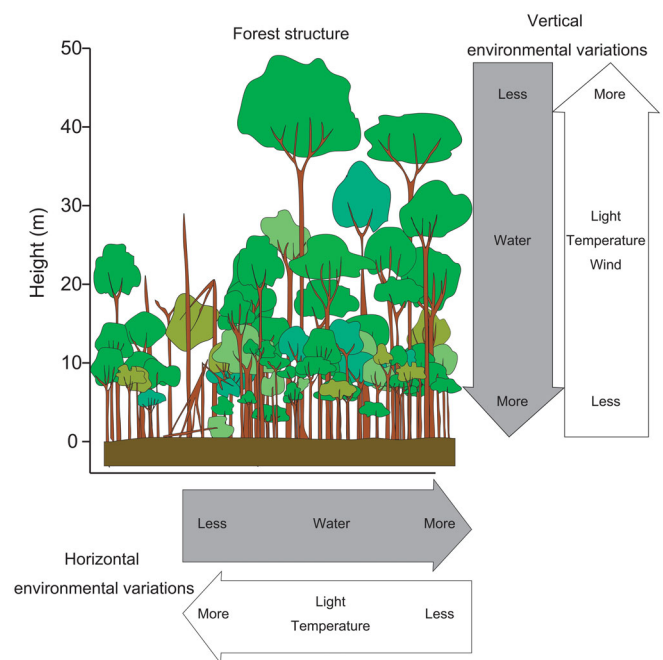
Plants are sessile and share common resources such as light, water, and nutrients, making individual size an important driver of competitive ability (or effects) and resource acquisition (Weiner, 1990). Importantly, tree height is a more suitable measurement of size in terms of asymmetric competition for light and perhaps symmetric competition for soil resources than stem diameter *per se*, but because measurements of stem diameter are more efficient, accurate and are related to overall height, crown area and rooting depth, it is generally the best measure of size available.

Long-term demographic data (growth, survival, and recruitment) collected in large permanent forest dynamics plots in the tropics for trees with more than 1 cm in stem diameter ( $D$ ), has been accumulated since the 1980s (Losos & Leigh, 2004). Compared to demographic data for trees of later ontogenetic stages such as juveniles and adults ( $D \geq 1$  cm), long-term observations for earlier ontogenetic stages such as seedlings, were not broadly examined outside of a few well-studied forest dynamics plots (e.g., Metz et al., 2008). This type of effort by many forest ecologists has led to long-term observations of dynamics not only in the tropics but worldwide. These data now allow us to estimate demographic rates of long-lived trees and to examine ontogenetic changes. It is important to note that we define ontogenetic stages based on size because trees lack well-defined ontogenetic stages after germination. Therefore, in this paper, we mainly use stem diameter at the breast height ( $D$ ) to define ontogenetic stages based on size ranges of  $D$  except for seedlings (e.g., seedlings: height < 1 m, juveniles:  $1 \leq D < 5$  cm, adult:  $D \geq 5$  or 10 cm). Please note that this simple categorization of ontogenetic stages depends on studies or authors, and does not reflect real ontogeny such as seedlings, juveniles, and adults in their life history because each species has different potential maximum stature (i.e., adult stature).

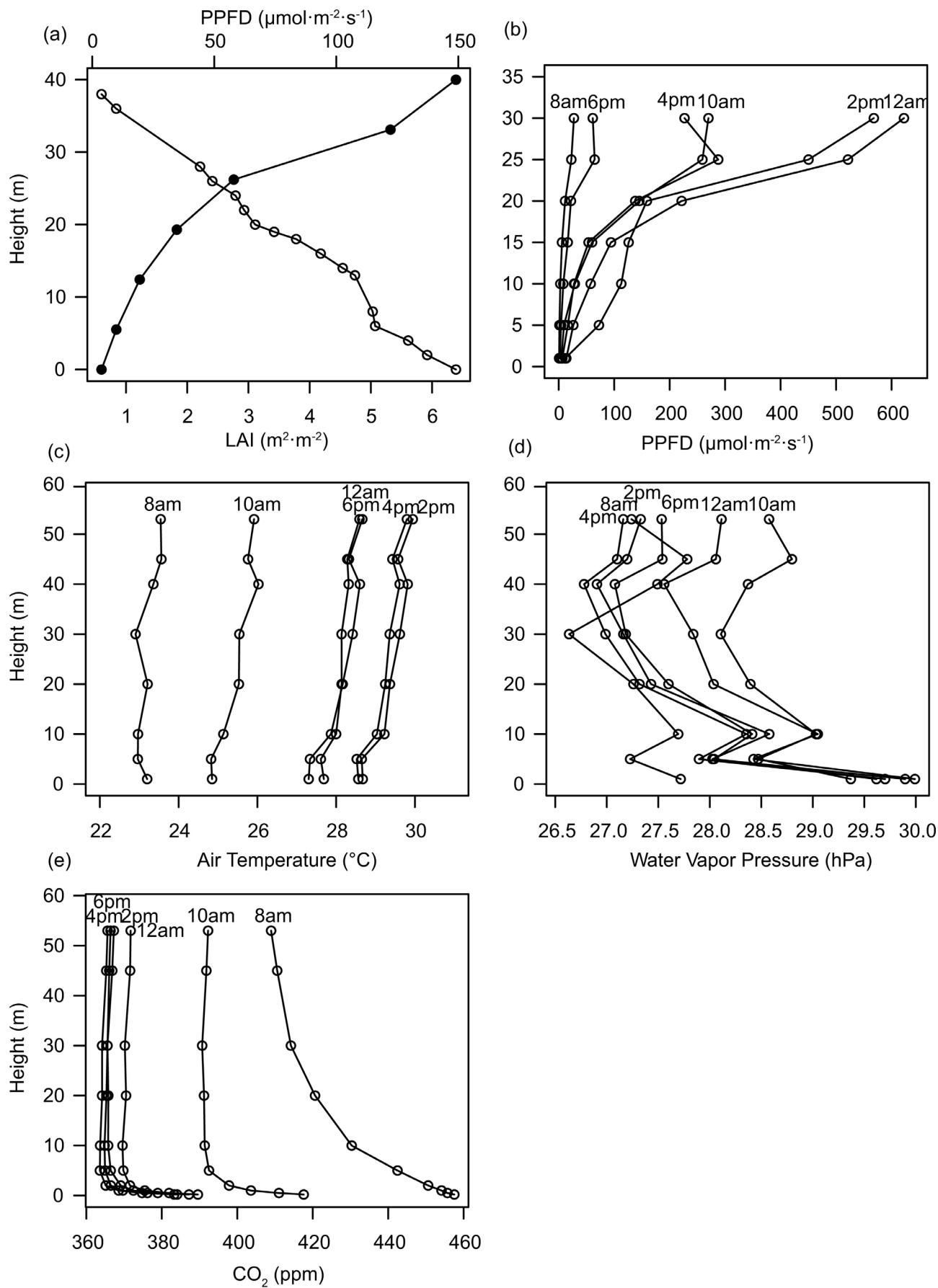
Trait-based studies of plant ecology have, generally, focused on trade-offs and correlations of traits at the plant organ-level as explained above, but plants should maximize fitness by making allocation decisions to optimize growth and survival at the whole-plant level. The relative amount of biomass allocation to a series of organs is an important measure; it is considered to be associated with the capacity for future resource acquisition and as a component of relative growth rate (Evans, 1972), hence, allocation has been studied as one of the fundamentally important concepts in plant ecology

(Poorter et al., 2012; Weiner, 2004). Due to the importance of allocation at the whole plant level in plant life-history strategies and the fact that crown area is found to be associated with demographic performance (e.g., Iida, Poorter, et al., 2014), it is important to consider traits at the organ-level and with respect to whole plant allocation and their interconnection to link to individual demographic performance (Yang et al., 2018). However, most of the trait-based studies lack information regarding the whole-plant allocation and few data exist allowing for an integration of traits at the organ-level and allocation at the individual level.

The traits of leaves and wood and whole plant allocation change with ontogeny as does the associated physiology. These changes arise from changes in the local environment with respect to the crown position (e.g., radiation, temperature, moisture, wind) via increasing plant height (Figure 2) as well as genetically controlled internal ontogenetic changes and their interactions including hydraulic constraints, senescence and allocation shifts towards reproduction (e.g., Lloyd et al., 2010; Mencuccini et al., 2005; Niinemets, 2010; Thomas, 2011). Tall and well-developed forests generate resource gradients in the vertical direction from the forest floor to the canopy, and resource variation along the horizontal direction via gaps which gradate to closed canopy



**FIGURE 2** A diagram depicting environmental variation in a well-developed rainforest. The impacts of abiotic factors (e.g., light, water, temperature, and wind) vary with a height from forest floor to canopy in the vertical direction, and with respect to gaps and closed understories in the horizontal direction [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



(Figures 2 and 3, e.g., Kosugi, Takanashi, Yokoyama, Philip, & Kamakura, 2012; Kumagai et al., 2001; Ohkubo et al., 2008; Richards, 1996; Yoda, 1974). Along vertical directions, light, temperature, and wind increase but water availability decreases from forest floor to canopy, and in horizontal directions from closed understory to gap, light and temperature increase but water availability decreases (e.g., Vitousek & Denslow, 1986). Species differ in adult stature such as emergent, canopy, subcanopy, and understory trees and this shapes light resource partitioning along vertical gradients, while species differences in light requirements such as pioneer and shade-tolerance trees shape resource partitioning along a horizontal direction, which is created by gap and canopy layers (Kitajima & Poorter, 2008; Turner, 2001) and such complex three-dimensional forest structure helps maintain species diversity (Kohyama, 1993).

The grand challenge is to link ontogenetic changes in traits with a complex three-dimensional resource environment to predict or model the demographic outcomes of individuals and populations. A failure to appreciate the importance of these ontogenetic and multi-dimensional resource gradients likely results in weaker predictions of demographic rates from traits. In the interest of advancing such research, in the following, we will review current knowledge on size-related changes in traits at the organ-level and with respect to whole plant allocation changes with sizes (Section 3), size-related changes in trait-demography relationships (Section 4), in trait-assembly relationships (Section 5), and then end by providing a concise vision for future research that integrates trait, demography, and assembly (Section 6).

### 3 | SIZE-RELATED CHANGES IN TRAITS

In this section, we review size-related changes in traits at the organ-level (leaf and wood) and at the whole plant level (architecture and allocation) and examine what kind of data should be used to address the fundamental question of how traits vary with ontogeny for traits in diverse tree communities in the tropics. At the organ-level, we focus mainly on morphological traits, which are commonly measured and highly associated with ecological strategies described by the leaf economics spectrum

(Wright et al., 2004) and the wood economics spectrum (Chave et al., 2009). This section shows how these traits change with size for understanding why a mean trait value for a species from a single ontogenetic stage may not be useful at species comparison within a tree community.

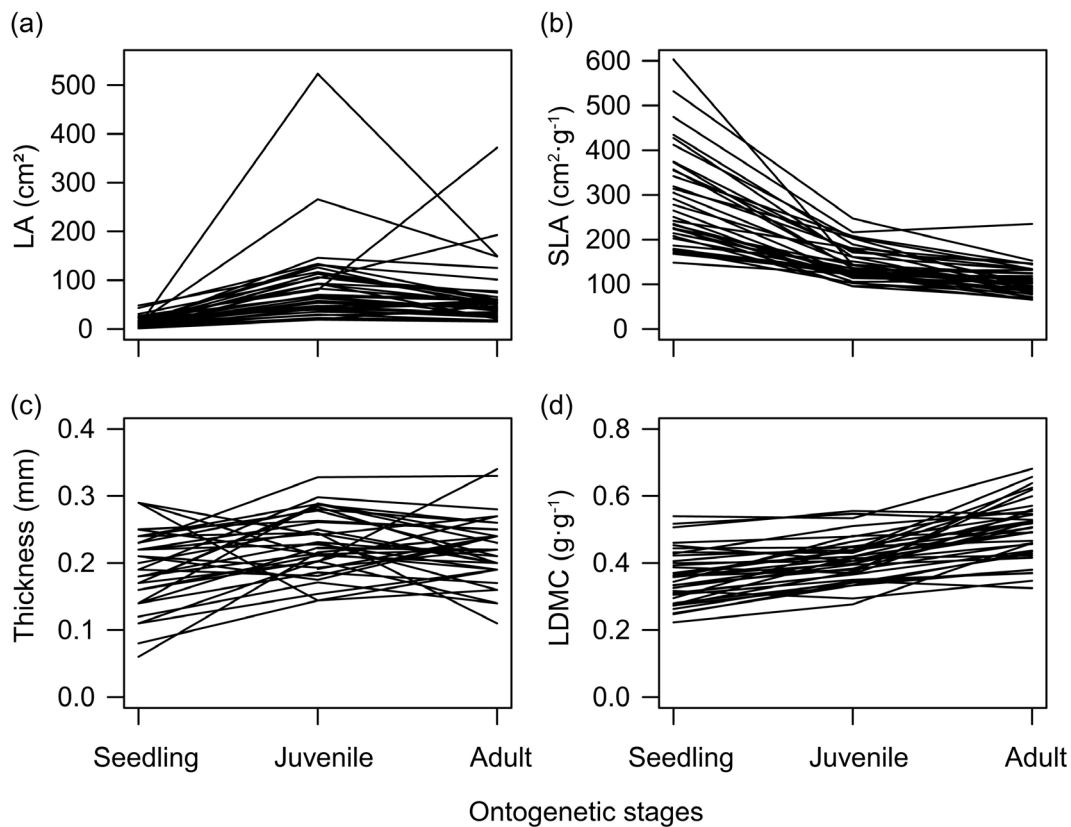
#### 3.1 | Leaf traits

Leaves are essential organs associated with photosynthesis. Species leaf traits are known to be interconnected via the leaf economic spectrum (LES) between leaves with low construction cost, high nitrogen and phosphorus concentrations, high respiration and light-saturated photosynthetic rates versus those with high construction cost, low nitrogen and phosphorus concentrations, low respiration and light-saturated photosynthetic rates (Reich, Walters, & Ellsworth, 1997; Wright et al., 2004). Leaf traits show large variations with environmental conditions (e.g., Rozendaal, Hurtado, & Poorter, 2006; Valladares, Wright, Lasso, Kitajima, & Pearcy, 2000). As trees grow and become taller, changes of the surrounding local environment of the crown in the vertical direction from the dark and wet forest floor to the well-lit and dry canopy leads to morphological and physiological changes in leaves and branches (e.g., Niinemets, 2001; Niinemets, 2002). In addition to changes in the surrounding local environments, tree height itself constrains the morphology and physiological function of leaves and branches mainly due to height-related increase in hydraulic resistance and gravity (e.g., Woodruff, Meinzer, & Lachenbruch, 2008). Thus, in terms of resource availability, light availability increases, but hydraulic challenges increase with ontogenetic changes due to an increase in tree height (Figures 2 and 3).

Specific leaf area (SLA), estimated as leaf area (LA) divided by leaf dry mass (or an inverse of leaf mass per area, LMA), a measure of leaf cost, usually declines with increasing sizes and ontogenetic changes due to environmental acclimation (especially light) and height-related hydraulic limitation (Figures 4b and 5). This trend is clear within species, across species, and even across forests in different biomes such as temperate and tropical forests (e.g., Hutchison et al., 1986; Kenzo et al., 2015; Kitajima & Poorter, 2010; Kosugi et al., 2012; Niinemets, 2002). Well-developed forest structure, where light

**FIGURE 3** Vertical gradients of abiotic factors in a lowland rainforest, Pasoh in Peninsular Malaysia. Panel (a) shows the leaf area index (LAI) (open circle) measured with the LAI-2000 and annual average photosynthetic photon flux density, PPFD (filled circle), and panel (b) shows durational variations of average PPFD at height of 1, 5, 10, 15, 20, 25 and 30 m (data were modified from Kosugi et al., 2012). Panels (c)–(e) show diurnal variation in mean values of (c) air temperature, (d) water vapor pressure, and (e) CO<sub>2</sub> at different heights (data were modified from Ohkubo et al., 2008)












**FIGURE 4** Variations in leaf traits at different ontogenetic stages across 36 species of 100 dominant species in Pasoh. Species average trait values of leaf area (LA), specific leaf area (SLA), thickness, and leaf dry matter content (LDMC) are shown at different ontogenetic stages of seedlings (height < 1 m), juvenile (1 < D < 3 cm) and adult (largest five individuals in the 50-ha plot) (Iida, Chen, Kitajima, & Wright, unpublished data)

intensity dramatically increases with increasing height from forest floor to canopy (e.g., Kosugi et al., 2012; Yoda, 1974), but these heights bring about hydraulic constraints (e.g., Kenzo et al., 2015) (Figures 2 and 3). Reported decreases in SLA at the upper canopy are due to acclimation to local environments such as higher irradiances, air temperatures and wind speeds, and height-related hydraulic limitation (e.g., Kenzo et al., 2015; Kosugi et al., 2012; Rijkers, Pons, & Bongers, 2000; Steppe, Niinemets, & Teskey, 2011).

LA, associated with the two-dimensional space where trees receive light and regulation of surface temperature, show dramatic changes over ontogeny across different layers in the canopy of individuals, as well as large variation among species (e.g., Kitajima & Poorter, 2010; Yamada & Suzuki, 1996). Under the warmer and wetter conditions of a tropical forest, the average LA is greater than for other types of forests due to the low risk of nighttime-chilling and day-overheating (Wright et al., 2017). Within a tropical rainforest, changes in LA are not straightforward as LA increases with increasing tree height during the early stages of ontogeny, but LA declines or does not change with

increasing size during the late stages of ontogeny such as after reaching the canopy (e.g., Figure 4a and 5, Yamada & Suzuki, 1996). Such species differences in LA variation during ontogeny are probably due to species differences in ontogenetic changes in relatively important factors such as thermal constraints (Givnish, 1984) and a balance of photosynthetic benefits and mechanical costs (Givnish, 1987).

Leaf thickness, density and toughness are important traits related to leaf structural resistance protecting leaves against herbivores and physical disturbance, which influences leaf lifespan, plant-herbivore interactions, litter decomposition, and nutrient cycling (Onoda et al., 2011). Reports on changes in leaf thickness, density and toughness during ontogeny are few compared to SLA. Some studies have reported that leaf thickness increases from juveniles to adults (Iida, Kohyama, et al., 2014; Palow, Nolting, & Kitajima, 2012), but others do not find the same result (Figure 4c, Kitajima & Poorter, 2010). Leaf density, estimated as fresh mass divided by volume, and leaf dry matter content (LDMC), estimated by dry mass divided by fresh mass, are highly correlated, and leaf density, LDMC, and toughness increase from saplings to

Scale	Part	Trait	Ontogenetic stages			Section	
			Seedling	Juvenile	Adult		
Organ	Leaf	SLA				2.1	
		LA					Variable
		Thickness	Variable				
		LDMC, Toughness					
		Area-based physiological/chemical traits					
Organ	Wood	WD				2.2	
		Chemical traits					Variable
Whole plant	Whole body	LMR				2.3	
		SMR					
		RMR					

**FIGURE 5** Directions of ontogenetic changes of traits. Leaf traits (LA, leaf area, thickness; LDMC, leaf dry matter content; SLA, specific leaf area, toughness, and area-based physiological or chemical traits), wood traits (WD, wood density and chemical traits), and traits at the whole plant level (LMR, leaf mass ratio; RMR, root mass ratio; SMR, stem mass ratio) were shown. Arrows show general trends of the direction of ontogenetic changes (increasing, decreasing, or variable) explained in each section. Please note that these are general trends from current citations and these trends may change when more data become available

adults (Figure 4d, Kitajima & Poorter, 2010; Palow et al., 2012) and this probably helps defense against predators or herbivores. These traits are highly interconnected: an inverse of SLA (LMA) is equal to a product of leaf density and thickness and both leaf density and thickness are correlated with leaf toughness (Kitajima & Poorter, 2010; Onoda et al., 2011). Therefore, their ontogenetic changes are not independent and co-varies with species-specific allocation strategies within a single leaf.

Leaf chemical or physiological traits related to photosynthesis such as leaf nitrogen content, stomatal conductance, dark respiration rate, photosynthetic rates mostly increase with height when they are estimated as LA based in tropical trees due to assimilation to the environment such as an increased light and height-related hydraulic stress (e.g., Figure 5, Kenzo et al., 2006; Kenzo et al., 2015; Thomas & Winner, 2002). Although other leaf traits such as leaf venation (Iida et al., 2016; Sack & Scoffoni, 2013), anatomical and physiological traits (Medeiros et al., 2019) should be important for plant performance, their ontogenetic changes are seldom reported for tropical trees and, therefore, we do not summarize trends for these additional leaf traits here.

Importantly, because leaf traits are strongly interconnected in terms of matter distribution of components

such as carbon and nitrogen and biomechanical properties in a single leaf, it is risky to synthesize ontogenetic changes in a simple way using a single trait. In addition to acclimations to surrounding local environments with an increase of height within forests, height itself affects variation in leaf traits during ontogeny. For example, stronger associations between LMA and height than between LMA and light were found in a Costa Rican tropical rain forest (Cavaleri, Oberbauer, Clark, Clark, & Ryan, 2010). In the tropics, so far, we know size-related change only for some specific traits shown above (Figure 5) or for some specific species such as large-statured species (e.g., Kenzo et al., 2006), and do not know how they co-vary with environmental conditions (not only light, but also for other variables) or by an effect of increased height during ontogeny across diverse co-occurring species at the community-level. This is simply because we do not have enough trait data from different ontogenetic stages across diverse co-occurring species with different adult statures at this point and a more focused collection of traits across sizes and their surrounding environmental conditions are needed. Further accumulation of field studies should help us understand how leaf traits co-vary with fundamental constraints in allocation within a single leaf under a given environment

and how the combination of traits involved with a particular function affects demographic difference in a given environmental context.

### 3.2 | Wood traits

The wood of trees performs important functions in terms of mechanical stability, hydraulics, defense, architecture, and carbon gain (Chave et al., 2009). In particular, wood density and anatomy are important aspects determining the mechanical strength and hydraulic conductivity for woody plants at the tissue and whole plant scale (Chave et al., 2009). The economics in wood traits are reported to be decoupled with the economics in leaf traits (e.g., Baraloto et al., 2010), contributing to the diversity of plant life strategies as one of two main independent spectra together with the leaf economics spectrum. However, because of the difficulty of sampling wood compared to leaf traits, there is still less information on how wood density changes during ontogeny, depending on local environments to link to demographic performance. This is especially true for information regarding stem wood from earlier ontogenetic stages (Gibert, Gray, Westoby, Wright, & Falster, 2016) because it requires destructive sampling of whole individual seedlings and juveniles. In the tropics, some studies have collected wood from trees with different ontogenetic stages (e.g., Martin, Thomas, & Zhao, 2013; Swenson & Enquist, 2008), but other studies estimated radial variation in woods of adult trees which reflects ontogenetic changes (Hietz, Valencia, & Wright, 2013; Osazuwa-Peters, Wright, & Zanne, 2014).

Wood density (WD) or wood specific gravity (WSG) defined as wood dry mass divided by fresh volume, is one of the major wood traits which is associated with biomechanics and drought, therefore, performance such as growth and/or mortality (Chave et al., 2009). Hietz et al. (2013) found that negative correlations between WD in the stem center and the radial WD gradient, which suggests that in species with lower inner WD (low WD at earlier ontogeny), the WD tends to become higher towards the outer wood (a relatively high increase of density during ontogeny) probably due to differences in mechanical requirement during ontogeny. Thus, changes in WD may differ across individuals with different ontogenetic stages, but most variation in WD may occur among species. For example, Osazuwa-Peters et al. (2014) showed that 88% of the variation was explained among-species differences for 20 moist tropical forest canopy species in Panama.

The amount of secondary components such as lignin and cellulose in woods are important chemical traits associated with resistance to damage from predators and pathogens (e.g., Kurokawa, Kitahashi, Koike,

Lai, & Nakashizuka, 2004) and mechanical stability (e.g., Alvarez-Clare & Kitajima, 2007). Martin et al. (2013) found that helocellulose (total cellulose and hemicellulose) concentrations in woods of seedlings were lower than that of adults for 15 of 16 Panamanian tree species, and lignin concentrations in woods of seedlings were higher than that of adults for all 16 species. This suggests that larger lignin investment at early ontogenetic stages helps seedlings to defend predators and pathogens, and mechanical constraints at the cost of investment in helocellulose. They also found no significant correlations between the chemical traits in woods in seedlings and adults. Thus, possibly chemical traits largely change with ontogeny, but there are few studies thereby preventing our ability to draw general conclusions regarding how and why chemical traits change with ontogeny across co-occurring species in tropical forests.

Anatomical traits related to xylem of wood such as vessel lumen area, vessel density, parenchyma, and fibers have important physiological functions in relation to water transport, carbohydrate storage, and strength (Baas, 1982). Such anatomical data across diverse co-occurring species is still quite limited. There are few studies on the relationships for anatomical trait data across co-occurring tropical species between different ontogenetic stages due to the difficulty of measurement. Size-related changes in wood structures should occur along with the changing requirements for the environment and ontogenetic stages (Lachenbruch, Moore, & Evans, 2011) and the size of individual trees explained a large proportion of variation in wood traits including vessel diameter across diverse species in a Panamanian forest (Hietz, Rosner, Hietz-Seifert, & Wright, 2017) and at a global scale (Olson et al., 2014). Thus, we do know that size is important for variation in anatomical traits, but there is less knowledge regarding how anatomical traits change during ontogeny among co-occurring species for tropical trees.

### 3.3 | Tree architecture and whole-plant allocation

Since plants need to allocate limited resources among competing functions such as growth, maintenance, defense, and reproduction, trade-offs are generated within a whole plant. Tree architecture and whole-plant biomass allocation have been studied as two of the fundamental features of plant life history (e.g., Halle, Oldeman, & Tomlinson, 1978; Weiner, 2004). Whole plant biomass allocation is often examined for herbaceous plants or seedlings of trees due to the necessity of destructive measurements (e.g., Poorter et al., 2012). On the other hand, for larger-sized woody plants,



aboveground dimensions (i.e., stem diameter at the breast height: DBH, tree height, crown width, and depth) of tree architecture, are often measured and those relationships are examined by using allometric functions (e.g., Iida et al., 2011; King, 1996; Kohyama, 1987; Poorter, Bongers, & Bongers, 2006).

Tree architecture is strongly associated with the height extension, light capture, and mechanical stability of trees (e.g., Iida et al., 2011; Iida et al., 2012; King, Davies, Tan, & Noor, 2006; King & Maindonald, 1999; Poorter et al., 2006) and, consequently, with demographic rates of growth and mortality (Iida, Poorter, et al., 2014; King, Davies, Tan, & Noor, 2006). Interspecific differences in tree architecture are largely associated with species adult stature and light requirements (i.e., shade-tolerance) (e.g., Iida et al., 2011; Poorter et al., 2006). Along vertical environmental gradients from forest floor to canopy (Figures 2 and 3), species with different adult statures have different tree architectures reflecting life-history strategies and the trade-off between vegetative growth to reach the exposed canopy and early reproductive output in the closed understory. That is, large-statured species tend to have slender and small crowns compared to small-statured species at small size classes and some of these trends become unclear at large size classes where small-statured species are dropped from the species comparisons. Species tree architecture also varies with species characteristics related to light requirements for regeneration to partition light in the horizontal direction between closed canopy and gap (Figure 2): species that require high levels of light for regeneration are expected to have slender stems and relatively shallow crowns at the early ontogenetic stages to realize rapid growth to exploit canopy gaps. Relatively narrow and shallow crowns are beneficial because they reduce self-shading, whereas shade-tolerant species are likely to produce wide and deep crowns to improve light capture (e.g., Givnish, 1984; Kohyama, 1987). Such interspecific differences in tree architecture associated with light requirements for regeneration change with increasing tree size (Aiba & Nakashizuka, 2009; Iida et al., 2011; Poorter et al., 2006; Xu et al., 2019) and those results are not consistent. This is probably due to different indices of light requirements and forest structure across studies. For example, several inconsistent indices of light conditions have been applied to estimate light requirement capacity such as crown exposure (Poorter, 2007), canopy openness (Davies, 1998), crowding index (Iida et al., 2011; Xu et al., 2019), and wood density (Aiba & Nakashizuka, 2009). Associations of light requirements with tree architecture were found to be quite weak in a Malaysian lowland rainforest with a tall closed canopy (Iida et al., 2011), but it was strong in a Bolivian moist

forest with relatively low, open, and semi-evergreen canopy (Poorter et al., 2006) probably due to large horizontal variation in light environments at the forest floor with a low and open canopy in this Bolivian forest.

Although estimated tree architectural relationships are often applied to estimate aboveground biomass for quantifying carbon stocks and flux (Chave et al., 2005; Feldpausch et al., 2012; Goodman, Phillips, & Baker, 2014; Ploton et al., 2016), it is less known if such differences in tree architecture are corresponding to differences in whole-plant biomass allocation across co-occurring species. Poorter et al. (2012) reviewed general size-related trends of leaf mass ratio (LMR, or called as leaf mass fraction), stem mass ratio (SMR, or called as stem mass fraction) and root mass ratio (RMR, or called as root mass fraction) expressed as ratios of total dry mass of leaves, stems or roots to whole plant biomass for woody plants. With an increase of total dry biomass, LMR declined largely, SMR increased largely and RMR declined relatively gently, suggesting that large investment shift from other parts especially leaves to stems during ontogeny to support a larger body in terms of mechanical and hydraulic stabilities (Enquist & Niklas, 2002; Savage et al., 2010).

In addition to indices of biomass allocation themselves (LMR, SMR, RMR), leaf area ratio (LAR) as the total area of leaves for an individual tree divided by total biomass and intra-crown leaf area index (LAI) as total area of leaves within crown area should be important indices for species resource capture strategies. LAR is intensively examined at early ontogenetic stages (mostly in seedlings, summarized by Gibert et al. (2016)) and often associated with relative growth rate in seedlings indicating the contribution of allocation to photosynthetic tissue to performance (e.g., Cornelissen, Diez, & Hunt, 1996) but it is not clear if this association is maintained in later ontogenetic stages. Intra-crown LAI is associated with self-shading and reported to decline with increasing size due to a decline of SLA, an increase of LA, and loss of branches in later ontogenetic stages for temperate tree species (Nock, Caspersen, & Thomas, 2008; Osada, 2005). Among five Panamanian canopy species with different successional status, later successional species exhibited larger maximum intra-crown LAI and resulting greater light extinction through a crown, which may contribute to their efficient light utilization and better competitive ability (Kitajima, Mulkey, & Wright, 2005).

In summary, it is difficult to compare species with respect to tree architecture and biomass allocation across different forests not only due to variation in environmental conditions within a forest but also due to insufficient datasets at later ontogenetic stages in allocation and

inconsistent indices to characterize species life history (i.e., light requirements for regeneration). It would be better to apply traits to quantify life history characteristics instead of indices or specific categories (e.g., pioneer, shade-tolerance, and successional status) and to examine the relationship between organ-level traits (leaf and wood) and tree architecture or biomass allocation so that species differences at the whole plant level can be compared and generalized.

### 3.4 | Life-history traits associated with reproduction (not size-related changeable)

Reproduction is directly related to fitness and there are some important life-history traits associated with reproduction (Thomas, 2011). Species differences in adult stature are often quantified using potential maximum height ( $H_{\max}$ ) or stem diameter ( $D_{\max}$ ) and this trait is strongly positively correlated with the sizes at onset of maturity, the first time trees begin to reproduce (Thomas, 1996; Wright et al., 2005). Specifically, small-statured species (i.e., shrub, treelet, understory) tend to reproduce at smaller sizes (earlier) compared to large-statured species (i.e., subcanopy, canopy, emergent). Therefore, it is believed that species with different adult stature has specific life-history strategies underlying the trade-off between early reproduction versus vegetative growth for late reproduction.

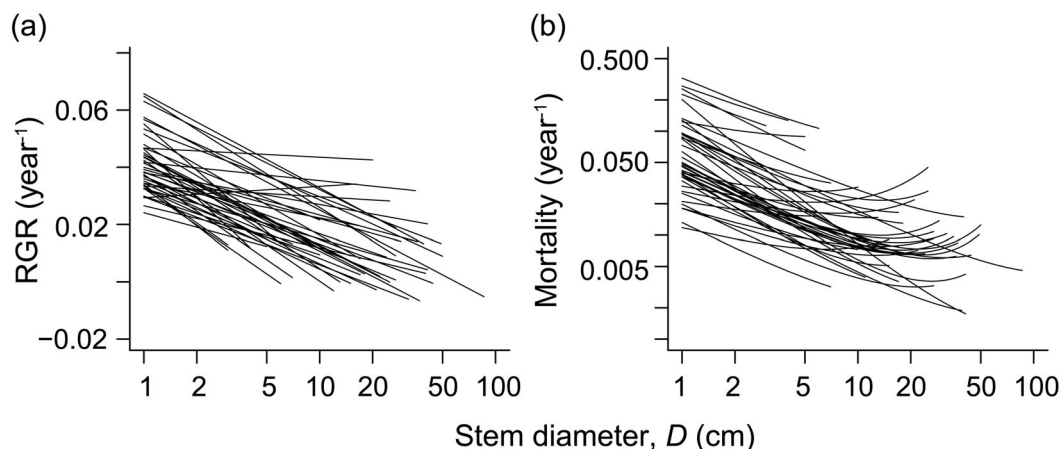
Seed size varies widely among species and seed size trades off with a number of seeds produced because a resource is limited. In theory, the tolerance-fecundity trade-off underlies the maintenance of diversity in seed size: small-seeded species have a fecundity advantage and large-seeded species are more able to tolerate stressful

environmental conditions (Muller-Landau, 2010). Small seeds tend to produce seedlings with larger LAR allowing them to have relatively fast growth by allocating to photosynthetic parts (Poorter & Rose, 2005; Turner, 2001). In a Panamanian forest, seed size, adult stature, and dispersal mode together explain interspecific variation in seed production, seed dispersal distances, and clumping of seed deposition (Muller-Landau, Wright, Calderón, Condit, & Hubbell, 2008). Thus, seed size is an important trait associated with species life-history strategies especially in terms of recruitment and reproduction.

## 4 | SIZE-RELATED CHANGES IN TRAITS-DEMOGRAPHY RELATIONSHIPS

Linking traits and demographic performance to sort out functional traits from several species traits is one of the fundamental goals to scale-up to the structure and dynamics of communities in trait-based approaches (Figure 1). Although the number of community-wide studies of traits and demography has increased, it is still quite difficult to consider size-related changes in both traits and demographic performance largely due to the difficulty of collecting data covering a wide range of sizes at a community-wide scale in a diverse tree community.

Not only species traits, but also species growth and mortality rates change with an increase of plant size. Even for relative growth rate (RGR), which is considering an effect of plant sizes such as stem diameter and biomass, it is often observed that RGR declines with an increase of plant size (Figure 6a; Iida, Kohyama, et al., 2014; Iida, Poorter, et al., 2014; Mencuccini et al., 2005; Ryan, Binkley, & Fownes, 1997). Such size-



**FIGURE 6** Size-related changes in relative growth rate (RGR) and mortality rate across 43 co-occurring species in a Taiwanese subtropical forest. Lines show changes in RGR (a) and mortality (b) with increasing stem diameter,  $D$ , by applying medians of probability distributions of RGR and mortality estimated by hierarchical Bayesian models. Figures are from Iida, Kohyama, et al. (2014)

related changes in RGR may be affected by aging, the accumulation of non-conducting wood in the stem due to an increase of cost in respiration, and allocation shift to reproduction with an increase of size. Size-related changes in mortality rates are more species-specific and have either a monotonic increase, decline, or U-shaped curves (Figure 6b; Iida, Kohyama, et al., 2014; Iida, Poorter, et al., 2014; King, Davies, & Noor, 2006; Rüger, Wirth, Wright, & Condit, 2012). Size-related increases in mortality maybe because of aging and increased respiration cost (Mencuccini et al., 2005). A decrease or U-shaped change in mortality may result from higher risks of small trees for mechanical damage by falling debris in the understory (Clark & Clark, 1991) and higher sensitivity to drought stress of small- and large-sized trees (Condit, Hubbell, & Foster, 1995; Nakagawa et al., 2000) compared to intermediate-sized trees.

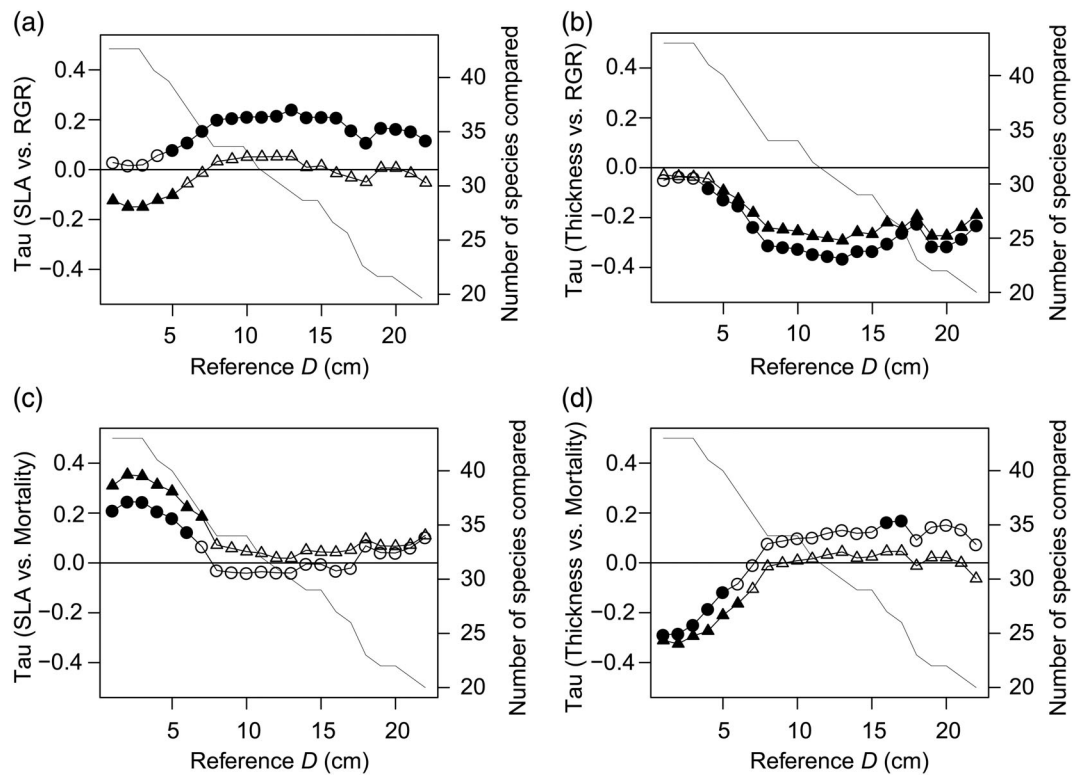
Recently, studies of size-related changes in trait-demography relationships, especially with respect to leaf traits and growth rates relationships, have been reported, albeit slowly. There are two types of approaches to studying size-related relationships between traits and demographic rates: one is to study associate species representative values of traits (i.e., species means or medians) with size-related changes in demography (e.g., Prado-Junior et al., 2016; Rüger et al., 2012; Visser et al., 2016) and another is to study size-related changes both in traits and demographic rates (e.g., Gibert et al., 2016; Iida, Kohyama, et al., 2014; Iida, Poorter, et al., 2014). The former uses species mean traits to capture a broad trend in life-history strategies, while the latter requires more challenging fieldwork, but helps to uncover the link between trait and demography at each ontogenetic stage. Both types of previous studies showed that the strength and direction of correlations differ depending on focal sizes or traits. In a Panamanian tropical forest, the importance of adult stature and seed mass in demographic rates were larger at early ontogenetic stages of seedlings but wood density became more important at stages of sapling trees (Visser et al., 2016). The significant associations of leaf trait, LMA, and demographic rates of growth and survival were not found in this forest (Rüger et al., 2012; Visser et al., 2016). However, when saplings and adults were analyzed separately in the same forest, significantly negative correlations between LMA and demographic rates were found at saplings but became non-significant or weaker at large trees ( $10 \leq D < 50$  cm) (Wright et al., 2010). Thus, LMA-demography relationships may have been missed in previous studies with species mean trait values because a representative trait value obtained from leaf samples of large trees may not be enough to catch large size-related changes in leaf traits. A meta-analysis including 103 studies showed that more than 75% of correlations between growth and traits has

been reported with data from the same stage for each trait indicating the number of observations was highly unbalanced at three ontogenetic stages of seedling, sapling, and adult depending on traits (Gibert et al., 2016).

In a Taiwanese subtropical forest, significant associations between leaf traits and demographic rates were found for 43 co-occurring species, but their strength and direction changed at different sizes (Figure 7; Iida, Kohyama, et al., 2014). For example, SLA and LA in juvenile trees were significantly negatively correlated with RGR only at small sizes and SLA and LA in adult trees were significantly positively correlated with RGR only at large sizes. For other traits such as leaf thickness, significant associations became non-significant with an increase of sizes (Figure 7d). Similarly, size-related shifts from significant to non-significant were found in associations between crown width and demographic rates in a Malaysian rainforest (Iida, Poorter, et al., 2014) and Brazilian seasonal dry forests (Prado-Junior et al., 2016). Such switches in the directionality or significance may occur due to the change in light and water conditions along a vertical profile in a forest (Figures 2 and 3). Along horizontal variations at understory, species partitions light conditions depending on their light requirement capacity, but when trees reach the exposed canopy and were released from light limitations, other factors such as water and topographic preferences affect traits-demography relationships.

Thus, there are too few studies to generalize trends, but changes in the direction and significance in correlations between traits and demography may be context-dependent and influenced by surrounding environmental conditions within the forest canopy structure. For example, species with wider crowns had higher mortality in small-sized trees in the understory in a Malaysian rainforest (Iida, Kohyama, et al., 2014), whereas it had lower mortality in Brazilian dry forests (Prado-Junior et al., 2016) probably due to differences in the relative importance of life-history strategies associated with local environmental conditions between rainforests and dry forests. These results clearly indicate that it is important to measure and accumulate data of traits from different ontogenetic stages and surrounding environmental conditions to reveal how trait-demography relationships change with size in different forest structures.

Demographic performance is influenced by the surrounding environmental conditions such as light, soil fertility, and moisture, resulting in the demographic trade-off between growth and survival in natural forests (Kobe, 1999; Kobe, Pacala, Silander, & Canham, 1995; Russo, Brown, Tan, & Davies, 2008). Although it is still not well-studied how trait-based demographic performance responds to surrounding environmental conditions in a forest (but see Iida, Abe, Tanaka, & Abe, 2019), many



**FIGURE 7** Size-related changes in correlation coefficients between leaf traits and demographic rates across 43 co-occurring species in a Taiwanese subtropical forest. Correlations between species leaf traits and demographic rates were examined for leaf traits at different life stages (juvenile; triangle or adult; circle) and for relative growth rate, RGR or mortality at different given stem diameter,  $D$  at 1 cm intervals. Each value of the correlation coefficient indicates the median of the probability distribution of Kendall's correlation coefficient, tau. In the case that 95% interval of the probability distribution of tau does not include zero, the correlation between leaf traits and mortality is significant and then the circle or triangle was filled. Forty-three species were applied for two leaf traits of specific leaf area, SLA (a, c) and thickness (b, d). The downward-sloping line shows the decline of the number of species compared. Species whose 95-percentile maximum  $D$  is less than reference  $D$  was excluded from the comparison. Figures are from Iida, Kohyama, et al. (2014)

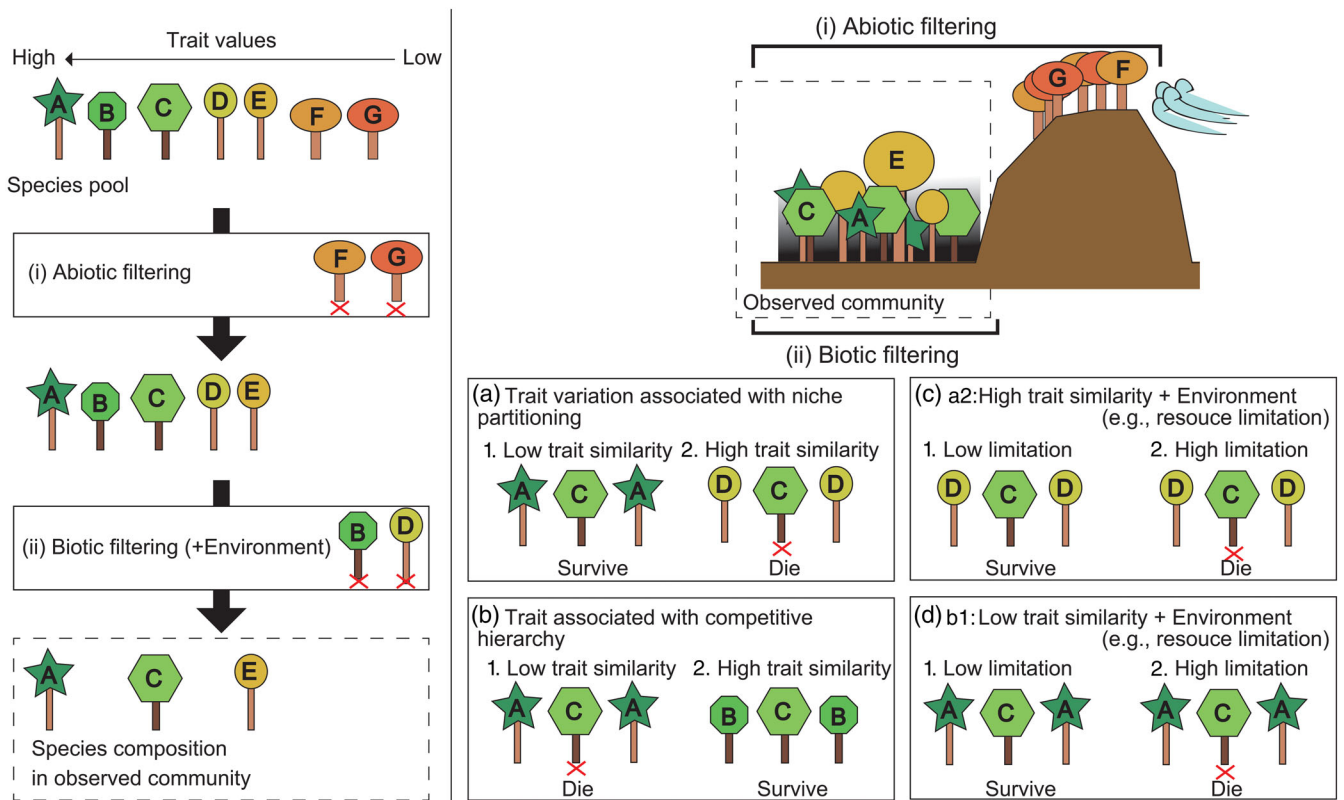
studies examined trait-assembly associations based on the assumption that target traits influence demographic performance and are, therefore, functional traits (Figure 1, see detail in next section). Not only is the demographic trade-off between growth and survival important, the demographic trade-off between adult stature and recruitment is also reported to be necessary to predict forest dynamics (Rüger et al., 2018; Rüger et al., 2020). Because of such trade-offs are ontogenetic stage-specific (e.g., Iida, Kohyama, et al., 2014; Iida, Poorter, et al., 2014), understanding trait-environment-demography linkages at different ontogenetic stages covering life history should help to reveal the underlying mechanism for predicting dynamics and structures of forests.

## 5 | SIZE-RELATED CHANGES IN TRAIT-ASSEMBLY

Understanding the processes associated with the biotic and abiotic interactions underlying the assembly of

communities is one of the main goals for community ecologists. The recent trait-based approach helps us to quantify the ecological similarity of co-occurring species to reveal the relative importance of environmental (abiotic) and biotic (e.g., niche partitioning) filters on assembly processes (Figure 8, left panel) (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Swenson, 2013; Swenson, Enquist, Thompson, & Zimmerman, 2007; Webb, Ackerly, McPeck, & Donoghue, 2002). Ecologically similar species are expected to co-occur if only a few ecological strategies (a combination of specific traits) are suitable for the given abiotic environmental context either due to strict filtering of phenotypes by the abiotic environment or the superior performance of similar phenotypes relative to others that could inhabit the area but would perform less well (Keddy, 1992). On the other hand, ecologically similar species are not expected to co-occur and ecologically dissimilar species can co-occur at a given environment (niche partitioning, for example, Silvertown, 2004). These two processes are not mutually exclusive and the





**FIGURE 8** A conceptual diagram of trait-based assembly processes. The left panel shows changes in species composition from species pool at a regional scale to an observed community at a local scale via (i) abiotic filtering and (ii) biotic filtering. Species A–G in the species pool have specific trait values and trait values decrease from species A–G. The right top panel shows an example of a community at a regional scale and an observed community at a local scale. Species G and F were filtered out from the species pool of A–G by an environmental condition related to an elevation at a regional scale because of lower trait values associated with environmental specific survival. At a local scale, species A–E were sorted by biotic filtering. The right bottom panel shows examples of trait-based biotic filtering on target species C. Species C survives if trait variation is associated with niche partitioning and neighbors have low trait similarity (a1), but dies when neighbors have high trait similarity even in the case neighbors have lower trait values than species C (a2). On the other hand, species C dies if trait variation is associated with competitive hierarchies and neighbors have higher trait values and low trait similarities (b1), but survives if neighbors have similar trait values even if those trait values are larger than species C (b2). If biotic filtering is environmental-dependent, these two processes lead to the death of species C (a2 and b1) only in the case that environmental condition is limited such as high resource limitation (c2 and d2). This diagram is adapted from the framework of Lasky, Uriarte, Boukili, and Chazdon (2014) and Chauvet, Kunstler, Roy, and Morin (2017) [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

intensity of significance may vary at different scales (Figure 8 right top), communities, and targeted ontogenetic stages.

Because physiological requirements and selective pressures may change with size, a species ecological preference may differ from earlier ontogenetic stages to the next. Thus, habitat associations between earlier and later ontogenetic stages are often inconsistent at several tree communities, because site-specific environmental conditions may be influential at different stages (e.g., Baldeck et al., 2013; Comita, Condit, & Hubbell, 2007; Green, Harms, & Connell, 2014; Paoli, 2006; Webb & Peart, 2000). Similarly, reported biotic factors such as neighborhood effects are also inconsistent across tree communities. Neighborhood effects are linked to phylogenetic similarity

at earlier ontogenetic stages (Paine et al., 2012; Webb, Gilbert, & Donoghue, 2006) and trees at later ontogenetic stages in an Ecuadorian forest (Fortunel, Valencia, Wright, Garwood, & Kraft, 2016), but not in later stages such as adult trees in Luquillo and French Alpine forests (Kunstler et al., 2012; Uriarte et al., 2010).

Recent studies have tried to understand the role of species interaction in driving community assembly as biotic filtering (Figure 8) in terms of functional traits, phylogenetic relatedness, and hierarchical competitive abilities (Fortunel et al., 2016; Kunstler et al., 2012; Lasky et al., 2015; Swenson et al., 2007). When functional traits are good predictors of tree performance and indicative of resources use and/or of defense against natural enemies, functionally similar species may fail to co-exist due to



small niche differences (Adler, Fajardo, Kleinhesselink, & Kraft, 2013) or due to the sharing of natural enemies (Connell, 1971; Janzen, 1970) than functionally dissimilar species (Figure 8a). If functional traits have phylogenetic signal, then close relatives may be expected to have smaller niche or performance differences than distant relatives. If hierarchical differences in traits relative to neighbors' trait are more important than absolute values of traits, species with superior traits are expected to competitively exclude inferior species via performance differences (Figure 8b, Kunstler et al., 2012; Mayfield & Levine, 2010). Neighborhood models incorporating such trait hierarchies often explain demographic differences better than absolute trait difference (Kunstler et al., 2012; Kunstler et al., 2016; Lasky et al., 2014), suggesting that hierarchical differences in traits relative to neighbors' trait play an important role of biotic filtering in these tree communities. The relative importance of these processes should be influenced by environmental conditions such as resource limitation and herbivore impact (Figure 8c & d, Lasky et al., 2014).

While the importance of niche versus competitive hierarchies and their relationship to traits in neighborhood models are quantified in recent studies, there are still areas of improvement necessary. For example, in most studies, the neighbors are defined as neighboring trees within a fixed radius from a target individual tree (e.g., Canham et al., 2004; Uriarte, Canham, Thompson, & Zimmerman, 2004) or within a plot of the target individual (e.g., Kunstler et al., 2012). A more biologically relevant measure of neighborhoods is to consider that neighborhoods based upon the physical overlap of crowns and/or root systems such that there is no fixed neighborhood radius (Lebrija-Trejos, Wright, Hernandez, & Reich, 2014; Zambrano et al., 2019). In the Luquillo subtropical forest in Puerto Rico, the neighborhood models using crown overlap had better support than traditional models with fixed radius, suggesting that the traditional models with the fixed radius may not have a full picture of competitive interaction (Zambrano et al., 2019). So far crown overlap is a reasonable, although imperfect, measure for neighborhood interactions in terms of light and water resource competition, and this result giving us an idea of how to incorporate whole tree allocation strategies in neighborhood models with traits.

In addition to tree architecture and allocation, dynamic crown properties such as crown plasticity are also important for demographic performance and forest dynamics (Purves, Lichstein, Strigul, & Pacala, 2008; Strigul, Pristinski, Purves, Dushoff, & Pacala, 2008). Crown plasticity, or crown displacement in response to changes in the local competitive environment helps trees to optimize the use of canopy space in mixed-species

forests (Jucker, Bouriaud, & Coomes, 2015). It is likely that remote sensing data (e.g., lidar or drones) will be used in the future for this purpose as it will permit individual-level data analysis and refined measures of crown projections. Obtaining these crown data together with microclimate datasets within a forest structure contributes to the estimation of resource acquisition efficiency and resource utilization efficiency (Onoda et al., 2014). These data help not only for empirical studies to link static trait data and observed demography and assembly, but also for novel and robust theoretical approaches to reveal underlying mechanism (e.g., Chauvet et al., 2017; Falster, Brännström, Dieckmann, & Westoby, 2011; Falster, Duursma, & FitzJohn, 2018).

Another grand challenge is confronting how we consider ontogenetic variation in traits and demography together with the surrounding environment in neighborhood models. One very simple example is dividing trees into ontogenetic stages (e.g., seedlings, juveniles, and adults). Lasky et al. (2015) examined the changes in community assembly across ontogenetic stages in a Luquillo forest (but using species representative trait value) and found that larger trees showed greater growth as the difference in species trait values among neighbors increased, suggesting that importance of trait-based niche partitioning in large size classes. Thus, trees respond differently during ontogeny. Therefore, accumulating trait data at different ontogenetic stages and associated environmental conditions also helps us to reveal assembly processes and coexistence mechanisms (Adler et al., 2013; HilleRisLambers et al., 2012).

## 6 | TOWARDS COMPREHENSIVE UNDERSTANDINGS

To achieve the ultimate goal of forming a mechanistic link between the underlying processes driving the dynamics and structure of communities and the observed demography and assembly, we argue the importance of trait-environment-demography associations covering the whole of life history. In order to consider environmental variables at different ontogenetic stages, not only the horizontal heterogeneity in resources (i.e., soil nutrient, gap versus shade) but also vertical variation is important especially in well-developed tropical forests (Figures 2 and 3). Because the relative strength of trait-demography relationships may change with ontogenetic stages (Figures 4-7), it is important to elucidate when and why trait links demographic performance and resulting assembly. To address these questions, we reviewed previous studies about size-related change in traits and associations between trait and demography/assembly in

tropical forests and showed what kinds of data and insight are missing. We found four important issues to be solved: (a) accumulated data of traits and allocation were biased at particular ontogenetic stages; (b) interconnections among traits at the organ-level and allocation at the whole-plant level are vague; (c) surrounding environmental conditions of individual trees were not measured, (d) the classical paradigm of species life history (i.e., pioneer vs. shade-tolerance, successional status) are not quantified only by the combination of traits. We believe that accumulating comprehensive field data in different forests with various forest structures leads us to elucidate important pathways for synthesizing trait-based community ecology.

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## ORCID

Yoshiko Iida  <https://orcid.org/0000-0001-6544-0101>

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