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An extensive suite of functional traits distinguishes Hawaiian wet and dry forests and enables prediction of species vital rates

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Abstract

1. The application of functional traits to predict and explain plant species' distributions and vital rates has been a major direction in functional ecology for decades, yet numerous physiological traits have not yet been incorporated into the approach.
2. Using commonly measured traits such as leaf mass per area (LMA) and wood density (WD), and additional traits related to water transport, gas exchange and resource economics, including leaf vein, stomatal and wilting traits, we tested hypotheses for Hawaiian wet montane and lowland dry forests (MWF and LDF, respectively): (1) Forests would differ in a wide range of traits as expected from contrasting adaptation; (2) trait values would be more convergent among dry than wet forest species due to the stronger environmental filtering; (3) traits would be intercorrelated within "modules" supporting given functions; (4) relative growth rate (RGR) and mortality rate (*m*) would correlate with a number of specific traits; with (5) stronger relationships when stratifying by tree size; and (6) RGR and *m* can be strongly explained from trait-based models.
3. The MWF species' traits were associated with adaptation to high soil moisture and nutrient supply and greater shade tolerance, whereas the LDF species' traits were associated with drought tolerance. Thus, on average, MWF species achieved higher maximum heights than LDF species and had leaves with larger epidermal cells, higher maximum stomatal conductance and CO_2 assimilation rate, lower vein lengths per area, higher saturated water content and greater shrinkage when dry, lower dry matter content, higher phosphorus concentration, lower nitrogen to phosphorus ratio, high chlorophyll to nitrogen ratio, high carbon isotope discrimination, high stomatal conductance to nitrogen ratio, less negative turgor loss point and lower WD. Functional traits were more variable in the MWF than LDF, were

correlated within modules, and predicted species' RGR and *m* across forests, with stronger relationships when stratifying by tree size. Models based on multiple traits predicted vital rates across forests ($R^2 = 0.70–0.72$; $p < 0.01$).

4. Our findings are consistent with a powerful role of broad suites of functional traits in contributing to forest species' distributions, integrated plant design and vital rates.

KEYWORDS
drought tolerance, endemic species, forest tree demography, growth analysis

1 | INTRODUCTION

Functional traits influence plant growth, reproduction and survival and thereby fitness (Lavorel & Garnier, 2002; Violle et al., 2007) and thus can be used to predict vital rates (Adler et al., 2014; Poorter et al., 2008; Uriarte, Lasky, Boukili, Chazdon, & Merow, 2016), habitat preferences (Shipley et al., 2017) and spatial distributions (Stahl, Reu, & Wirth, 2014). For decades, most studies have focused on relatively few commonly measured functional traits, with some justification given that overall trait variation can be simplified statistically into a few fundamental dimensions (Diaz et al., 2016; Messier et al., 2017). However, several have argued that more extensive suites of traits would enable strong predictive and explanatory power (Greenwood et al., 2017; Paine et al., 2015; Reich, 2014; Yang, Cao, & Swenson, 2018a), and this argument has conceptual support because mechanistic models of growth and survival are sensitive to a broad set of traits as inputs (Marks & Leichowicz, 2006; Osborne & Sack, 2012; Sterck, Markesteijn, Schieving, & Poorter, 2011). The traits measured in this study include well-studied functional traits within the leaf and wood "economics spectra" (LES and WES, respectively), which describe trade-offs in plant carbon balance with given traits contributing to either fast growth and resource turnover, or slow growth and longer tissue life spans and stress tolerance (Chave et al., 2009; Wright et al., 2004). In addition, we included a wider set of traits recognized to have proximal physiological influence on water transport, gas exchange and resource economics. The aim of this study was to assess six key hypotheses derived from first principles in trait physiology and ecology (Table 1), utilizing 45 traits expected to show contrasting adaptation across forests, and/or to influence relative growth rate (RGR_{dbh} and RGR_{biom}) and mortality (*m*) (Table 2). We pursued this aim while recognizing that many more traits than those we included play important roles and that species differ in the traits with most important influence on vital rates.

First, we tested the ability of an extensive suite of traits to resolve variation between Hawaiian wet and dry forest species given their contrasting adaptation. We assessed traits which, based on the previous literature, would have specific mechanistic influences on resource acquisition, growth and stress tolerance (Table 1, with detailed reasoning in Supporting Information Table S10). In particular, we expected that relative to the dry forest, the wet forest species would have shifted their traits values in the direction beneficial to their adaptation to greater availability of water and soil nutrients. Such trait shifts would include greater mean and maximum plant height (King, Davies, & Noor, 2006; Koch, Sillett, Jennings, & Davis, 2004); lower wood density (WD; Chave et al., 2009; Gleason et al., 2016; Hacke, Sperry, Pockman, Davis, & McCulloh, 2001) and seed mass (Gross, 1984; Khurana & Singh, 2004); higher overall rates of photosynthesis, and rates of electron transport and carboxylation (all per unit leaf area and/or dry mass), and higher values for the ratio of internal to ambient CO_2 (c_i:c_a), related to higher values of carbon isotope discrimination (Δ_{leaf}; Farquhar, Ehleringer, & Hubick, 1989; Franks & Beerling, 2009; Donovan & Ehleringer, 1994; Wang et al., 2017); larger and denser stomata and higher stomatal conductance (Beaulieu, Leitch, Patel, Pendharkar, & Knight, 2008; Franks & Beerling, 2009; Franks & Farquhar, 2007; Hetherington & Woodward, 2003; Sack & Buckley, 2016; Wang et al., 2015); higher densities of leaf major and minor veins and free ending veins (Brodribb, Feild, & Jordan, 2007; Iida et al., 2016; Sack & Frole, 2006; Sack & Scoffoni, 2013; Scoffoni et al., 2016); thinner and larger leaves of higher saturated water content and lower dry mass density, lower water mass and dry mass per area and lower dry matter content with lesser shrinkage in area under dehydration (Bartlett, Scoffoni, & Sack, 2012b; Diaz et al., 2016; Evans, 1973; Niinemets, 2001; Ogburn & Edwards, 2012; Sack & Scoffoni, 2013; Scoffoni, Vuong, Diep, Cochard, & Sack, 2014; Vendramini et al., 2002; Westoby & Wright, 2006; Wright et al., 2004); high foliar concentrations of nitrogen (N), phosphorus (P) and chlorophyll (*Chl*), and lower concentration of carbon (Chatuverdi, Raghubanshi, & Singh, 2011; Lambers & Poorter, 2004; Wright et al., 2004); lower N:P (Elser et al., 2000); and greater stomatal opening relative to maximum aperture, and relative to N (Franks & Beerling, 2009; Wright, Reich, & Westoby, 2001). Given that species of the wet forest are adapted to lower understorey irradiance also led to the expectation of lower rates of photosynthesis and greater Δ_{leaf} (Donovan & Ehleringer, 1994; Evans, 2013; Farquhar et al., 1989; Franks & Beerling, 2009), larger leaf area (Chatuverdi et al., 2011; Niinemets, 2001), lower LMA (Sack, Grubb, & Marañón, 2003b; Walters & Reich, 1999), lower N and P and higher C and *Chl* concentrations (Givnish, 1988; Niinemets, 2001; Lusk & Warton, 2007; Poorter, Niinemets, Poorter, Wright, & Villar, 2009; Chatuverdi et al., 2011); higher *Chl* to N ratio

TABLE 1 Framework of hypotheses derived from first principles of trait-based physiology and ecology to test the application of an extensive suite of traits to resolve variation among forests and to enable prediction of vital rates across species

Hypothesis	Explanation based on first principles	References	Test	Support?
1. Wet and dry forest species would differ in numerous traits as expected from contrasting adaptation	Adaptation to contrasting climate and soil would lead to variation among species in numerous functional traits important in plant performance	Schimper (1903), Marks and Leichowicz (2006), Lohbeck et al. (2015) and Levine, Bascompte, Adler, and Allesina (2017)	Nested ANOVAs for individual-level traits and *t* tests for species-level traits	Yes
2. Trait values would be more convergent among dry than wet forest species due to the selective pressure imposed by low-resource availability	Environmental filtering is expected to reduce functional diversity by constraining the range of possible trait states across habitats	Cornwell et al. (2006), Mayfield, Boni, and Ackerly (2009), Lebrija-Trejos et al. (2010), Kraft et al. (2014), Nathan et al. (2016) and Asefa et al. (2017)	*t* test on the coefficient of variation in traits from MWF and LDF; *F* tests on the variance of each trait between MWF and LDF	Yes
3. Traits would be intercorrelated within functional “modules”	Selection on multiple traits across environments would lead to trait–trait correlations within organs and functional "modules" due to common developmental pathway, function, or benefit in given environments	Sack et al. (2003a,b), Givnish et al. (2005), Poorter, Lambers, and Evans (2014) and Li et al. (2015b)	Pearson's correlations between traits within functional “modules”	Yes
4. RGR and *m* would correlate with specific traits	Traits contribute mechanistically directly to RGRs and *m* in given habitats	Kitajima (1994), Grime (2001), Sack et al. (2013), Marks and Leichowicz (2006) and Wright et al. (2010)	Pearson's correlations between specific traits and vital rates	Yes
5. RGR and *m* would correlate with traits more frequently when stratifying by tree size	Ontogenetic- and size-related trends in traits and vital rates mean that trait–vital rate correlations would be reduced given comparison of species mean values when species vary in size distributions; stratifying by size should therefore strengthen trait–vital rate relationships	Iida et al. (2014), Iida et al. (2016) and Prado-Junior et al. (2016)	Bayesian model to estimate vital rates at given plant sizes followed by Kendall's correlations between traits and vital rates at each size	Yes
6. RGR and *m* can be predicted based on trait-based models	Given relationships of vital rates with given traits, combinations of traits should be strongly predictive	Poorter et al. (2008), Uriarte et al. (2016) and Thomas and Vesk (2017)	Linear regression	Yes

TABLE 2 Study traits relating to stomatal morphology, leaf venation, leaf and wood economics and structure, leaf composition, and estimated photosynthesis and plant size, and the vital rates measured for species from a montane wet forest (W) and a lowland dry forest (D) in Hawai'i. For the traits, we provide symbols; units; hypotheses for given traits for differences between forests and results from statistical tests; and hypotheses for correlations with vital rates (relative growth rate and mortality) and results from Pearson's correlation tests (when one result is presented this represents species from both forests together, and when two results are presented these represent species in the wet and dry forests separately); and references supporting the hypotheses. ns indicates no significant difference at $p < 0.05$. "W" represents the expectation that, all else being equal, given the specific hypothesis, the wet forest would have a higher trait value than the dry forest on average; "D" that the dry forest would have the higher trait value on average; and "either" denotes the existence of multiple published hypotheses whereby either MWF or LDF could be expected to have the higher trait value (Supporting Information Table S10). Positive signs (+) indicate the expectation or finding of a positive correlation with relative growth rate and mortality rate; negative signs (−) indicate the opposite. For detailed reasoning behind each hypothesis and references, see Supporting Information Table S10. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$

Trait/vital rate	Symbol	Unit	Hypotheses: W or D higher?	W or D higher?	Hypotheses: trait–vital rate correlation	Direction of trait–vital rate correlation	Reference
Stomatal morphology							
Stomatal density	d	stomata/mm^2	either	ns	+	+**	1–5
Stomatal differentiation rate (or index)	i	-	either	W*	+	+**	2–6
Stomatal area	s	μm^2	W	W*	+	ns	1, 5, 7
Guard cell length	GC_L	μm	W	W*			1, 5, 7
Guard cell width	GC_W	μm	W	W**			1, 5, 7
Pore length	SP_L	μm	W	W*			1, 5, 7
Epidermal pavement cell area	e	μm^2	W	W*			8
Maximum stomatal conductance	g_{max}	mol m^{-2} s^{-1}	either	W*	+	+*	2–5, 9–10
Leaf venation							
Major vein density	VLA_{major}	mm per mm^2	either	D***	+	ns	2–4, 11–15
Minor vein density	VLA_{minor}	mm per mm^2	either	D***	+	ns	2–4, 11–15
Total vein density	VLA_{total}	mm per mm^2	either	D***	+	ns	2–4, 11–15
Free ending vein density	FEV	# per mm^2	either	D**			2–4, 11–15
Leaf and wood economics and structure							
Leaf area	LA	cm^2	W	ns	+	W ns; D −*	16–18
Leaf mass per area	LMA	g/m^2	either	ns	−	W +*; D −*	12, 18–23
Leaf thickness	LT	mm	either	ns	−	−*	12, 18–23
Leaf density	LD	g/cm^3	either	ns	−	W +*; D −*	12, 18–23
Leaf dry matter content	LDMC	g/g	D	D*	−	ns	18, 24
Saturated water content	SWC	g/g	either	W**			25–27
Water mass per area	WMA	g/m^2	D	ns			25–27
Percentage loss area (dry)	PLA_{dry}	%	W	W**			28, 29
Wood density	WD	g/cm^3	either	D***	−	ns	5, 30–32

(Continues)

TABLE 2 (Continued)

Trait/vital rate	Symbol	Unit	Hypotheses: W or D higher?	W or D higher?	Hypotheses: trait–vital rate correlation	Direction of trait–vital rate correlation	Reference
Leaf composition							
Nitrogen concentration per leaf area	N_{area}	g/m^2	either	ns	+	W +*; D −*	2–5, 20
Nitrogen concentration per leaf mass	N_{mass}	mg/g	either	ns	+	+*	2–5, 20
Phosphorus concentration per leaf area	P_{area}	g/m^2	either	ns	+	W +*; D −*	2–5, 20
Phosphorus concentration per leaf mass	P_{mass}	mg/g	either	W**	+	+*	2–5, 20
Chlorophyll concentration	Chl_{area}	SPAD	either	ns			2–4, 33
Chlorophyll per mass	Chl_{mass}	SPAD g^{-1} m^2	either	ns			2–4, 33
Carbon concentration per leaf mass	C_{mass}	mg/g	W	ns			34–35
Nitrogen/phosphorus ratio	N:P	–	either	D**	–	ns	35
Chlorophyll/nitrogen per area ratio	Chl_{area}:N_{area}	SPAD g^{-1} m^2	W	ns			5
Carbon isotope discrimination	Δ_{leaf}	‰	W	W***			36–39
|Turgor loss point|	$\|\pi_{tlp}\|$	MPa	D	D***			28
Estimated photosynthesis							
Electron transport rate per area	$Jmax_{area}$	μmol m^{-2} s^{-1}	either	ns	+	W +*; D −*	2–4, 36–38
Electron transport rate per mass	$Jmax_{mass}$	nmol g^{-1} s^{-1}	either	ns	+	+*	2–4, 36–38
Maximum rate of carboxylation per area	$Vcmax_{area}$	μmol m^{-2} s^{-1}	either	ns	+	W +*; D −*	2–4, 36–38
Maximum rate of carboxylation per mass	$Vcmax_{mass}$	nmol g^{-1} s^{-1}	either	ns	+	+*	2–4, 36–38
Ratio of intercellular to ambient CO_2 concentrations	c_i:c_a	–	either	W***	+	ns	36–38
Time integrated leaf CO_2 assimilation rate per area	$\bar{A}_{area}$	μmol m^{-2} s^{-1}	either	ns	+	W +*; D −*	9
Time integrated leaf CO_2 assimilation rate per mass	$\bar{A}_{mass}$	nmol g^{-1} s^{-1}	either	W***	+	+*	9
Time integrated stomatal conductance	$\bar{g}_{cleaf}$	mmol m^{-2} s^{-1}	either	W**	+	W +*; D −*	9
Time integrated/maximum stomatal conductance ratio	$\bar{g}_{cleaf}$: g_{max}	–	either	ns			2–4, 9
Maximum stomatal conductance/nitrogen per area ratio	g_{max}:N_{area}	mol g^{-1} s^{-1}	W	W**			40
Plant size							
Mean height	H	m	W	ns			46–47
Maximum height	H_{max}	m	W	W*			46–47
Seed mass	SM	mg	D	ns			48–49

(Continues)

TABLE 2 (Continued)

Trait/vital rate	Symbol	Unit	Hypotheses: W or D higher?	W or D higher?	Hypotheses: trait–vital rate correlation	Direction of trait–vital rate correlation	Reference
Vital rates							
Relative growth rate (diameter increment)	RGR_{dbh}	$cm\ cm^{-1}\ year^{-1}$	either	ns			5, 20, 41
Relative growth rate (biomass increment)	RGR_{biom}	$kg\ kg^{-1}\ year^{-1}$	either	ns			5, 20, 41
Mortality rate	*m*	% per year	either	D**			42–45

References: 1. Hetherington and Woodward (2003); 2. Maximov (1931); 3. Grubb (1998); 4. Scoffoni et al. (2011); 5. Givnish (1988); 6. Sack and Buckley (2016); 7. Franks and Farquhar (2007); 8. Beaulieu et al. (2008); 9. Franks and Beerling (2009); 10. Wang et al. (2015); 11. Sack and Frole (2006); 12. Brodribb et al. (2007); 13. Sack and Scoffoni (2013); 14. Iida et al. (2016); 15. Scoffoni et al. (2016); 16. Sack et al. (2012); 17. Wright et al. (2017); 18. Niinemets (2001); 19. Evans (1973); 20. Wright et al. (2004); 21. Westoby and Wright (2006); 22. Lusk and Warton (2007); 23. Poorter et al. (2009); 24. Diaz et al. (2016); 25. Vendramini et al. (2002); 26. Sack, Tyree and Holbrook (2005); 27. Ogburn and Edwards (2012); 28. Bartlett et al. (2012a,b); 29. Scoffoni et al. (2014); 30. Hacke et al. (2001); 31. Chave et al. (2009); 32. Gleason et al. (2016); 33. Chatuverdi et al. (2011); 34. Lambers and Poorter (2004); 35. Elser et al. (2000); 36. Farquhar et al. (1989); 37. Donovan and Ehleringer (1994); 38. Evans (2013); 39. Wang et al. (2017); 40. Wright et al. (2001); 41. Gibert et al. (2016); 42. Wright et al. (2010); 43. McDowell et al. (2008); 44. McDowell et al. (2018); 45. Kobe and Coates (1997); 46. Koch et al. (2004); 47. King et al. (2006); 48. Gross (1984); 49. Khurana and Singh (2004).

(Givnish, 1988); and lower stomatal and vein densities (Givnish, 1988; Sack & Scoffoni, 2013; Sack et al., 2012). The literature also supports contrasting hypotheses in which dry forest species gain drought tolerance by achieving higher photosynthetic activity when water is available, linked with smaller and more numerous stomata and epidermal pavement cells (Grubb, 1998; Maximov, 1931; Scoffoni, Rawls, McKown, Cochard, & Sack, 2011; Wang et al., 2017), higher vein densities (Sack & Scoffoni, 2013) and high N and P per mass (Wright et al., 2001). We also expected the dry forest species to have more negative turgor loss point (Bartlett et al., 2012b), thick and small leaves (Sack et al., 2012; Wright et al., 2017) and high WD (Chave et al., 2009; Gleason et al., 2016; Hacke et al., 2001), and traits associated with high water use efficiency, reflected in low c_i:c_a and carbon isotope discrimination (Donovan & Ehleringer, 1994; Farquhar et al., 1989).

Second, we tested the hypothesis that on average, species of the dry forest would have narrower ranges in trait values than the wet forest (Nathan, Osem, Shachak, Meron, & Salguero-Gómez, 2016). Two main processes of community assembly affect functional diversity at local scale: environmental (or habitat) filtering and biotic interactions (Asefa et al., 2017; Chesson, 2000; Cornwell, Schwilk, & Ackerly, 2006). In low-resource habitats, environmental filtering is expected to more strongly constrain trait diversity, as would the reduction of biotic interactions which would promote greater niche overlap (Lebrija-Trejos, Meave, Poorter, Pérez-García, & Bongers, 2010; Nathan et al., 2016; Weiher & Keddy, 1995).

Third, we tested the hypothesis that traits would be intercorrelated in “modules” due to their contributions to given functions (Li et al., 2015b; Sack, Cowan, Jaikumar, & Holbrook, 2003a) or “strategies” (Westoby, Falster, Moles, Vesk, & Wright, 2002). Modules are defined as clusters of traits that show co-variation among themselves, due to selection, but are relatively independent of other clusters (Armbruster, Pelabon, Bolstad, & Hansen, 2014; Wagner & Altenberg, 1996). Such co-selection has been a main explanation for why plant phenotypes are organized into dimensions (or axes), such as the leaf and wood economic spectra (Chave et al., 2009; Wright et al., 2004). Several of the newly added traits are expected to be mechanistically related to traits from the LES and WES and are therefore grouped within the same trait modules (Table 2).

Fourth, we hypothesized that across species, RGR and *m* would be positively correlated due to life-history trade-offs, and parallel associations with given traits (Kitajima, 1994; Philipson et al., 2014; Russo et al., 2010; Visser et al., 2016; Wright et al., 2010). Further, we hypothesized that RGR and *m* would relate positively to photosynthetic rate (Donovan & Ehleringer, 1994; Franks & Beerling, 2009); leaf area (Iida et al., 2016), N and P concentrations (Iida et al., 2016; Osone, Ishida, & Tateno, 2008); the sizes and numbers of stomata (Hetherington & Woodward, 2003; Wang et al., 2015); maximum stomatal conductance and vein densities (Hetherington & Woodward, 2003; Iida et al., 2016), and negatively to LMA (Iida et al., 2016; Osone et al., 2008; Wright et al., 2010); leaf thickness, density and dry matter content (Iida et al., 2016; Niinemets, 2001); N:P (Elser et al., 2000); and WD (Philipson et al., 2014; Visser et al., 2016; Wright et al., 2010). We also tested whether trait relationships with vital rates differed between forests (Kobe & Coates, 1997; Lusk, Reich, Montgomery, Ackerly, & Cavender-Bares, 2008).

Fifth, we expected to uncover more relationships of traits with vital rates when accounting for tree size (Iida et al., 2014, 2016; Prado-Junior et al., 2016).

Finally, based on the expectations of strong trait–vital rate associations, we hypothesized that RGR and m can be predicted based on trait-based models.

Our study focused on Hawaiian forests with low species diversity located across highly contrasting environments (Table 3; Price & Clague, 2002; Ostertag, Inman-Narahari, Cordell, Giardina, & Sack, 2014). By testing our framework of hypotheses, we more generally addressed the question of whether considering an extensive suite of mechanistic traits has value for trait-based ecological theory and applications.

2 | MATERIALS AND METHODS

For additional details for each methods section, see correspondingly named section in Supporting Information Methods, Appendix S1.

2.1 | Study sites

The study was based in forest dynamics plots (FDPs) on Hawai'i Island within montane wet forest (MWF) and within lowland dry forest (LDF), part of the Hawai'i Permanent Plot Network established in 2008–09 (HIPPNET; Figure 1; Supporting Information Methods; Ostertag et al., 2014). The MWF and LDF plots contrast strongly in climate and soil composition: The substrate in the MWF is formed from weathered volcanic material and is old, deep and moderately well drained, while LDF has younger, shallow and highly organic substrate (websoilsurvey.nrcs.usda.gov). The forests also have distinct species, with only *Metrosideros polymorpha* common to both, being the canopy co-dominant in the MWF and limited to a few individuals in the LDF.

Both FDPs were established using the standard methodology of the Center for Tropical Forest Science global FDP network (Condit, 1998). From 2008 to 2009, all live, native woody plants ≥1 cm diameter at breast height (DBH, at 130 cm), were tagged and mapped relative to 5 m × 5 m grids installed throughout the plots and measured for DBH (Ostertag et al., 2014).

Some of our study questions were addressed by comparing these single forests that were selected to be highly representative of their forest type, an approach previously used in many ecophysiological comparisons of forests (e.g., Baltzer, Davies, Bunyavejchewin, & Noor, 2008; Blackman, Brodribb, & Jordan, 2012; Falcão et al., 2015; Markesteijn, Iraipi, Bongers, & Poorter, 2010; Zhu, Song, Li, & Ye, 2013). Notably, statistical differences between forests are not necessarily generalizable, but enable refined hypotheses for testing in future studies of replicate forests of each type. However, when predicting species' vital rates from traits, statistical significance is expected to reflect a higher generality, as each species represents a replicate data point (Sokal & Rohlf, 2012).

2.2 | Measurement of relative growth rate and mortality

A total of 21,805 individual trees of 29 species from both forest plots were measured for DBH in the first census, 2008, and the 18,745 of those trees that were alive were remeasured in the second census in 2013. From individual plant DBH in both censuses, we used the function "*AGB.tree*" available in the "*CTFS R Package*" (ctfs.si.edu/Public/CTFSRPackage/) to calculate above-ground biomass using allometric equations specific for "wet" and "dry" forests that use DBH and wood density as species-specific inputs (Chave et al., 2005). We then calculated relative growth rates in DBH and above-ground biomass ($\mathrm{RGR}_{\mathrm{dbh}}$ and $\mathrm{RGR}_{\mathrm{biom}}$, respectively) as $\frac{\ln(x_{t1})-\ln(x_{t0})}{\Delta t}$, where x is DBH or above-ground biomass and Δt is the time between measurements (in years). $\mathrm{RGR}_{\mathrm{dbh}}$ is the most commonly used in the literature, but $\mathrm{RGR}_{\mathrm{biom}}$ is arguably most relevant for relating mechanistically to traits on one hand and to forest scale processes on the other (Gil-Pelegrín, Peguero-Pina, & Sancho-Knapik, 2017). Annual mortality rate (m) was calculated for each of the same 29 species using survival data from both censuses as $m=[1-(N_1/N_0)^{(1/\Delta t)}]\times 100$, where N_1 is the number of live individuals at census 2, N_0 is the number of live individuals at census 1, and Δt is the time between measurements (in years; Sheil, Burslem, & Alder, 1995). Due to the potential for demographic stochasticity in small populations to affect vital rate estimates, species with <15 individuals were excluded from analyses of RGR and m (Fiske, Bruna, & Bolker, 2008); for $\mathrm{RGR}_{\mathrm{dbh},}$ the mean coefficient of variation was fivefold higher for species with $n < 15$ than those with $n > 15$ individuals (80% and 16% respectively).

2.3 | Seed mass and maximum height

Species' mean height (H) was calculated across all individuals in the plot, estimated from allometries (Ostertag et al., 2014), and maximum height (H_{max}) was calculated as the 95th percentile height of each species. Seed dry mass values were compiled from seed banks across Hawai'i (L. Sack & A. Yoshinaga, unpublished data).

2.4 | Sampling for leaf and wood trait measurements

We sampled all native woody species from both FDPs, that is, 20 species in the MWF and 15 species in the LDF (Table 3; Ostertag et al., 2014). Data were collected for five randomly selected individuals per species, given availability in the plot, but stomatal and venation traits were measured for only three randomly selected individuals; for this study, those three individuals per species were used for all trait analyses. For each individual, we used pole pruners to collect the most

TABLE 3 List of all species from the montane wet forest (MWF) and lowland dry forest (LDF) sites in Hawai'i with family, species code, growth form, leaf habit (evergreen, E; or deciduous, D) and type (simple, S; compound, C; or phyllode, P) and forest stratum. Nomenclature follows Wagner, Herbst and Sommer (1999) with updates from The Plant List (2013) and Lu and Morden (2014)

Species	Family	Code	Growth form	Leaf habit and type	Forest stratum
Montane Wet Forest (MWF)					
Acacia koa A. Gray	Fabaceae	ACAKOA	Tree	E, P	Canopy
Broussaisia arguta Gaudich.	Hydrangeaceae	BROARG	Shrub	E, S	Understorey
Cheirodendron trigynum (Gaudich.) A. Heller	Araliaceae	CHETRI	Tree	E, C	Canopy
Cibotium chamissoi Kaulf.	Cibotiaceae	CIBCHA	Tree fern	E, C	Understorey
Cibotium glaucum (Sm.) Hook. & Arn.	Cibotiaceae	CIBGLA	Tree fern	E, C	Understorey
Cibotium menziesii Hook.	Cibotiaceae	CIBMEN	Tree fern	E, C	Understorey
Clermontia parviflora Gaudich. ex A. Gray	Campanulaceae	CLEPAR	Shrub	E, C	Understorey
Coprosma rhynchocarpa A. Gray	Rubiaceae	COPRHY	Tree	E, S	Sub-canopy
Ilex anomala Hook. & Arn.	Aquifoliaceae	ILEANO	Tree	E, S	Sub-canopy
Kadua axillaris (Wawra) W.L.Wagner & Lorence	Rubiaceae	KADAXI	Shrub/Small tree	E, S	Understorey
Leptecophylla tameiameiae (Cham. & Schltdl.) C.M. Weiller	Ericaceae	LEPTAM	Shrub	E, S	Understorey
Melicope clusiifolia (A. Gray) T.G. Hartley & B.C. Stone	Rutaceae	MELCLU	Shrub/Small tree	E, S	Understorey
Metrosideros polymorpha Gaudich.	Myrtaceae	METPOL_W	Shrub/Tall tree	E, S	Canopy
Myrsine lessertiana A. DC.	Primulaceae	MYRLES	Tree	E, S	Sub-canopy
Myrsine sandwicensis A. DC.	Primulaceae	MYRSAN	Shrub/Small tree	E, S	Understorey
Perrottetia sandwicensis A. Gray	Dipentodontaceae	PERSAN	Shrub/Small tree	E, S	Understorey
Pipturus albidus (Hook. & Arn.) A. Gray	Urticaceae	PIPALB	Shrub	E, S	Understorey
Psychotria hawaiiensis (A. Gray) Fosberg	Rubiaceae	PSYHAW	Tree	E, S	Sub-canopy
Trematolobelia grandifolia (Rock) O. Deg.	Campanulaceae	TREGRA	Shrub	E, S	Understorey
Vaccinium calycinum Sm.	Ericaceae	VACCAL	Shrub	E, S	Understorey
Lowland dry forest (LDF)					
Euphorbia multiformis Gaudich. ex Hook. & Arn.	Euphorbiaceae	EUPMUL	Shrub	D, S	Understorey
Chrysodracon hawaiiensis (O. Degener & I. Degener) P.-L. Lu & Morden	Asparagaceae	CHRHAW	Tree	E, S	Sub-canopy
Diospyros sandwicensis (A. DC.) Fosberg	Ebenaceae	DIOSAN	Tree	E, S	Canopy
Dodonaea viscosa Jacq.	Sapindaceae	DODVIS	Shrub	E, S	Understorey
Erythrina sandwicensis O. Deg.	Fabaceae	ERYSAN	Tree	D, C	Canopy
Metrosideros polymorpha Gaudich.	Myrtaceae	METPOL_D	Shrub/Tall tree	E, S	Canopy
Myoporum sandwicense A. Gray	Scrophulariaceae	MYOSAN	Shrub/Small tree	D, S	Understorey
Osteomeles anthyllidifolia (Sm.) Lindl.	Rosaceae	OSTANT	Shrub	E, C	Understorey
Pittosporum terminalioides Planch. ex A.Gray	Pittosporaceae	PITTER	Tree	E, S	Understorey
Psydrax odorata (G. Forst.) A.C. Sm. & S.P. Darwin	Rubiaceae	PSYODO	Shrub/Small tree	E, S	Understorey
Santalum paniculatum Hook. & Arn.	Santalaceae	SANPAN	Shrub/Tree	E, S	Canopy
Senna gaudichaudii (Hook. & Arn.) H.S. Irwin & Barneby	Fabaceae	SENGAU	Shrub	D, C	Understorey
Sophora chrysophylla (Salisb.) Seem.	Fabaceae	SOPCHR	Shrub/Tree	D, C	Canopy
Sida fallax Walp.	Malvaceae	SIDFAL	Shrub	E, S	Understorey
Wikstroemia sandwicensis Meisn.	Thymelaeaceae	WIKSAN	Shrub/Tree	E, S	Understorey

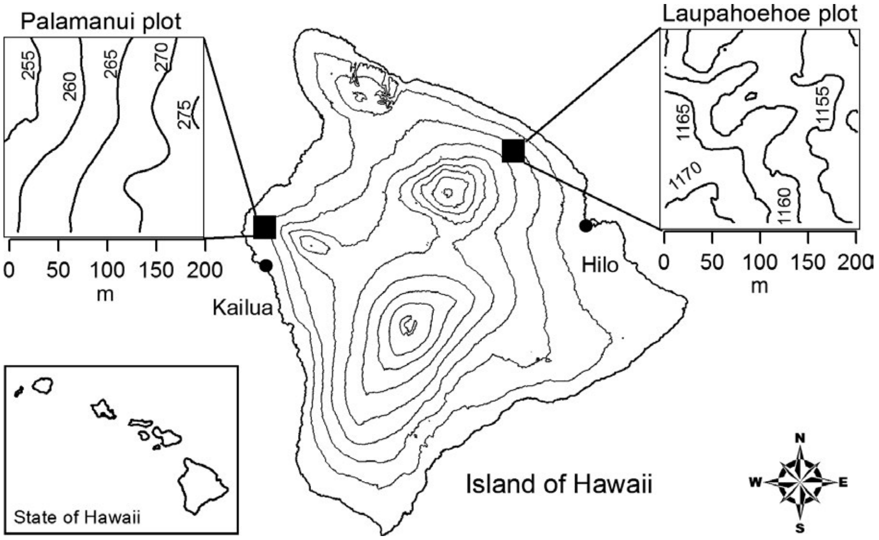

FIGURE 1 Contour map of the Pālamanui (LDF) and Laupāhoehoe (MWF) 4-ha plots on Hawai'i Island

exposed mature branch grown in the current year, with no signs of damage and herbivory. Branches were carried to the laboratory in plastic with moist paper and rehydrated overnight under plastic before harvesting stem sections and fully expanded leaves and stems for all subsequent analyses. For compound-leafed species (Table 3), leaflets were used; for *Acacia koa*, phyllodes were used.

2.5 | Leaf stomatal and venation traits

We measured stomatal and venation traits on one leaf from each of three individuals per species. Stomatal measurements were obtained from microscopy images taken from nail varnish impressions of both leaf surfaces. We measured stomatal density (*d*) and stomatal index (i.e., differentiation rate, the number of stomata per numbers of stomata plus epidermal pavement cells, *i*), stomatal pore length (SP_L), guard cell length and width (GC_L, GC_W), stomatal area (*s*) and epidermal pavement cell area (*e*) (Sack, Melcher, Liu, Middleton, & Pardee, 2006) and calculated the maximum theoretical stomatal conductance (g_{max}; Franks & Farquhar, 2007; Sack & Buckley, 2016).

For the venation traits, fixed leaves were cleared, stained and scanned for major vein density (VLA_{major}) and the top, middle and bottom of each leaf were imaged under light microscope for measurements of minor and free ending vein densities (VLA_{minor} and FEV) (Scoffoni et al., 2011). *Euphorbia multiformis* var. *microphylla* (EUPMUL; Table 3), the single C_4 species in the study (Yang, Morden, Sporck-Koehler, Sack, & Berry, 2018b), was removed from analyses of across-species correlations of vein traits with vital rates; C_4 species are known to differ from C_3 species in the relationship of photosynthetic rate to vein density and thus would be expected to differ in their relationships of vital rates to vein traits (Ogle, 2003).

2.6 | Leaf and wood economics and structure, and leaf composition

Leaf structure and composition traits were measured in three leaves per studied individual. Leaf saturated mass was measured using an analytical balance (0.01 mg; XS205; Mettler-Toledo, OH, USA) and leaf thickness (LT) using digital callipers (0.01 mm; Fowler, Chicago, IL, USA). The leaf area (LA) was measured using a flatbed scanner and analysed using the software ImageJ (http://imagej.nih.gov/ij/). After scanning, leaves were oven-dried at 70° for 72 hr and their dry mass and area were measured again. Leaf mass per area (LMA) was calculated as lamina dry mass divided by saturated area; leaf density (LD) as LMA divided by LT; saturated water content (SWC) as (saturated mass minus dry mass) divided by dry mass; water mass per area (WMA) as the (saturated mass minus dry mass) divided by saturated area; leaf dry matter content (LDMC) as dry mass divided by saturated mass; and percentage loss in area after drying (PLA_{dry}) as the per cent decline in area from saturated to dry leaves (Ogburn & Edwards, 2012; Pérez-Harguindeguy et al., 2013; Witkowski & Lamont, 1991).

We measured wood density (WD) from one 5-cm-branch segment of each of the studied individuals after bark removal by water-displacement (Pérez-Harguindeguy et al., 2013).

The concentration of leaf nitrogen, phosphorus, carbon per mass (N_{mass}, P_{mass} and C_{mass}) and carbon isotope ratio ($\delta^{13}C$) were determined using oven-dried leaves of three individuals per species by the University of Hawaii at Hilo Analytical Laboratory facility (Fry et al., 1996; Pérez-Harguindeguy et al., 2013). N_{mass} and P_{mass} were converted into N_{area} and P_{area} by multiplying by LMA. The carbon isotope discrimination (Δ_{leaf}; in parts per thousand, ‰) was calculated following (Farquhar & Richards, 1984). The chlorophyll concentration per area (*Chl*) was measured using a SPAD meter (Monje & Bugbee, 1992; SPAD-502, Konica Minolta, Japan), and the chlorophyll concentration per mass was determined by dividing by LMA.

Turgor loss point (π_{tlp}) was measured in three leaves per studied individual. We used a vapour-pressure osmometer (Vapro 5520, Wescor, USA) to obtain the osmotic concentration (π_o) of the leaves and used calibration equations to estimate π_{tlp} (Bartlett et al., 2012a).

2.7 | Estimating photosynthetic traits

We estimated maximum rate of carboxylation per mass ($Vcmax_{mass}$) and electron transport rate ($Jmax_{mass}$) from leaf N and P concentrations per mass (Domingues et al., 2010). The ratio of intercellular CO_2 concentration (c_i) to ambient CO_2 concentration (c_a) was estimated from Δ_{leaf} (Farquhar, O'Leary, & Berry, 1982; Franks et al., 2014). Estimates of leaf lifetime integrated CO_2 assimilation rate ($\bar{A}_{mass}$) and stomatal conductance to CO_2 ($\bar{g}_{cleaf}$) were derived from Vcmax_{mass}, Jmax_{mass} and isotope composition data using the Farquhar, von Caemmerer and Berry model (Franks, Drake, & Beerling, 2009). To convert Vcmax_{mass}, Jmax_{mass} and $\bar{A}_{mass}$ to an area basis, we multiplied the trait values by LMA. We also calculated the ratio between $\bar{g}_{cleaf}$ and g_{max}, an index of the degree that stomata are open on average relative to their anatomical maximum aperture (McElwain, Yiotis, & Lawson, 2016), and the ratio between g_{max} and N_{area}; a lower value would indicate that at full stomatal opening, the species has more conservative water use for a given investment in photosynthetic machinery (Wright et al., 2001).

2.8 | Statistical analyses

Differences in traits between MWF and LDF species were determined using nested ANOVAs with species nested within forest type, followed by a Tukey test at 5% probability when differences were detected (Sokal & Rohlf, 2012). Differences between forests in traits established as species means (RGRs, m, H, H_{max} and SM) were tested using t tests. Traits that did not fulfil the normality and homoscedasticity assumptions were log-transformed prior to analyses. To test whether trait variation differed between forests, we (a) performed F tests to compare the variances in each trait (Minitab Release 17; State College, PA, USA) and (b) calculated the coefficient of variation (CV; %) for each trait in each forest as $\mathrm{CV}_{forest} = \frac{\sigma_{forest}}{\bar{x}_{forest}} \times 100$ and applied a paired t test across all traits.

Functional traits were grouped into six "modules" according to their contributions to given functions or "strategies": The "stomatal morphology" module included traits such as d and s; the "leaf venation" module included traits such as VLA_{minor} and FEVs; the "leaf and wood economics and structure" module included traits such as LMA and WD; the "leaf composition" module included leaf nutrient concentrations and $|\pi_{tlp}|$; the "estimated photosynthesis" module included traits such as $\bar{A}_{mass}$ and Vc_{max}; and the "plant size" module included traits such as H_{max} and SM (Table 2).

To investigate trait–trait and trait–vital rate relationships within and across modules, we calculated Pearson's correlations for untransformed and log-transformed data, to test for either approximately linear or nonlinear (i.e., approximate power-law) relationships, respectively, and the higher correlation value is reported in the text. These analyses were applied to all species from both forests (Supporting Information Table S4; described in the main text) and to species of each forest separately (Supporting Information Tables S5 and S6).

We focus on frequentist statistical approaches, following the bulk of previous studies on trait–vital rate relationships. However, in the case of analysing size-dependent changes in the relationships between vital rates (RGR_{dbh} and m) and functional traits, we utilized a hierarchical Bayesian approach following (Iida et al., 2014), the most sophisticated previous approach for resolving such an influence. Detailed description of parameters, priors and MCMC settings are provided in the Supporting Information Methods (see Appendix S1), and model code is available on GitHub (https://github.com/camilamedeiros/Medeiros_et_al_2018).

RGR_{dbh} for each individual ith tree of species j (RGRdbh_{ij}) was modelled as a linear function of the natural logarithm of the initial diameter, $\mathrm{DBH1}_{ij}$, based on two parameters estimated for species j (α_{kj}; k = 1, 2) and given the input of the initial stem diameter ($\mathrm{DBH1}_i$), the final stem diameter ($\mathrm{DBH2}_i$) and the census interval of the ith tree (Δt_i).

$$\mathrm{RGRdbh}_{ij} = \alpha_{1j} + \alpha_{2j} \times \ln(\mathrm{DBH1}_i) \tag{1}$$

$$\ln(\mathrm{DBH2}_i) = \ln(\mathrm{DBH1}_i) + \mathrm{RGRdbh}_{ij} \times \Delta t_i \tag{2}$$

To estimate m for each individual ith tree belonging to species j (m_{ij}), we first calculated the probability of survival of the ith individual tree (p_i) from observations of whether the tree survived the census period (S_i = 1) or not (S_i = 0). We assumed that S_i followed a Bernoulli distribution of the probability of survival (p_i).

$$S_i \sim \mathrm{Bernoulli}(p_i) \tag{3}$$

The p_i of the ith tree was calculated from the per capita annual mortality rate, m_{ij}, adjusted to the census interval (Δt_i), which was a function of three species-specific parameters β_{kj} (k = 1, 2, 3).

$$p_i = \exp(-m_{ij} \times \Delta t_i) \tag{4}$$

$$\ln(m_{ij}) = \beta_{1j} + \beta_{2j} \times \ln(\mathrm{DBH1}_i) + \beta_{3j} \times \mathrm{DBH1}_i \tag{5}$$

Posteriors were estimated via Markov chain Monte Carlo implemented in JAGS (Just Another Gibbs Sampler; Plummer, 2003) from R, using the package "*R2Jags*." These analyses were carried out including all species from both forests.

To analyse trait–demographic rate relationships for given plant size classes, we first calculated RGR_{dbh} and m using Equations 1 and 5, respectively, by using the posterior distribution of species-specific parameters α_1 and α_2 for RGR_{dbh} (Supporting Information Table S7) and β_{1j}, β_{2j} and β_{3j} for m (Supporting Information Table S7) and substituting the DBH1 term for a reference diameter at 1-cm DBH classes (Iida et al., 2014). When the DBH of a size class exceeded a given species' actual maximum DBH (calculated as the 95th percentile of the species' individuals in the plots), that species was dropped from the analysis in larger size classes. We then calculated the Kendall correlation coefficient (τ) between the RGR_{dbh} and m (calculated for each species in each 1-cm DBH class) and species' mean values for functional traits. We decided to use Kendall correlation following (Iida et al., 2014) because of the typical non-normality of the size class stratified vital rates (Prado-Junior et al., 2016). The maximum DBH class included in our analysis was 10 cm because analysis of correlations lost power with lower species numbers available to test at larger plant sizes ($n < 9$). To reduce the rate of false positive discoveries, the correlations were considered significant only when 99% of the probability distribution (used as credible interval) of τ did not include zero, rather than 95% as in previous studies (Iida et al., 2014).

Finally, to test the ability of traits to predict plant $\mathrm{RGR_{dbh}}$, $\mathrm{RGR_{biom}}$ and m, we built multiple regression models that included as independent variables functional traits and a term for forest membership (site; coded as 0 for MWF species and 1 for LDF species). We selected seven traits to include in the models, based on consideration of the 26 traits hypothesized a priori to mechanistically influence $\mathrm{RGR_{dbh}}$, $\mathrm{RGR_{biom}}$ and m. To avoid collinearity, we did not choose traits that were partially redundant, that is, correlated, and calculated in part from the same measurements and involved within similar physiological processes and within the same trait category (e.g., we considered LMA and not leaf thickness, given that LMA equals leaf thickness × density; Table 2). We selected the trait most strongly correlated with vital rates from each trait module in Table 2, except for the "Leaf and wood economics and structure" module, from which we selected one leaf- and one wood-related trait.

To compare model performance, we included only species that had complete observations for all traits (final sample size = 16 species; Supporting Information Table S8). To select the trait-based models that best predicted $\mathrm{RGR_{dbh,}}$ $\mathrm{RGR_{biom}}$ and m, we used forward, backward and bidirectional procedures of variable selection and compared models using Akaike criterion (AIC) using the "*stepAIC*" function in the "*MASS*" package (Supporting Information Table S9) and calculated the AIC corrected for small sample sizes (AICc) (Hastie & Pregibon, 1992; Hurvich & Tsai, 1989; Venables & Ripley, 2002). To find the percentage contribution of each variable to the prediction of $\mathrm{RGR_{dbh}}$, $\mathrm{RGR_{biom}}$ and m, we performed a hierarchical partitioning analysis using the "*hier.part*" package (Chevan & Sutherland, 1991).

All statistical analyses and plots were performed using R software (R Core Team, 2016) and packages available from the CRAN platform.

3 | RESULTS

3.1 | Variation in vital rates and functional traits between forests types

On average, m was 39% higher in species from LDF than in species from MWF. Although several MWF species had higher growth rates than those of LDF, species means for $\mathrm{RGR_{dbh}}$ and $\mathrm{RGR_{biom}}$ were statistically similar in the MWF and LDF (Figure 2).

Traits varied strongly between and within forests. On average across the measured traits, 16% of the total variation was accounted for by forest type, 73% by species differences within forests and 11% by individuals within species (nested ANOVAs; Supporting Information Table S1). The MWF showed stronger trait variation than the LDF; the variance was higher in the MWF for 20 traits, in the LDF for six traits and not different between forests on the remaining 19 traits (F tests; Supporting Information Table S3), and on average across all traits, the coefficient of variation (CV) was 13.5 ± 0.8% in the MWF and 10.1 ± 0.6% in the LDF (paired t test; $p < 0.001$).

Species from MWF and LDF differed in 24 of the 45 functional traits (53%) used to test hypotheses (Table 2, Supporting Information Tables S1 and S2; Figure 2). MWF species had higher values on average for stomatal index (i) and area (s), dimensions of guard cells ($\mathrm{GC_L}$, $\mathrm{GC_W}$ and $\mathrm{SP_L}$) and epidermal pavement cells (e), and had on average a 70% higher g_{max} (Figure 2; Table 2, Supporting Information Table S1). Additionally, SWC and $\mathrm{PLA_{dry}}$ were 47-49% higher in the MWF than in the LDF species, and $\bar{A}_{\mathrm{mass}}$, $\bar{g}_{\mathrm{cleaf}}$ and c_{i}:c_{a} ratio were 28%–33% higher for the MWF than the LDF species (Figure 2; Table 2, Supporting Information Table S1). $\mathrm{P_{mass}}$, g_{max}:$\mathrm{N_{area}}$ and $\mathrm{H_{max}}$ were 49%, 17% and 82% higher in the MWF species than in the LDF species, respectively (Table 2, Supporting Information Tables S1 and S2; Figure 2).

Conversely, species from the LDF had values 46%–70% higher on average than species from the MWF for $\mathrm{VLA_{major}}$, $\mathrm{VLA_{minor}}$, $\mathrm{VLA_{total}}$ and FEVs, and values 22%-42% higher on average for LDMC, WD and N:P (Figure 2; Table 2, Supporting Information Table S1). The LDF species also had a π_{tlp} more negative by 0.6 MPa on average, and 25% lower Δ_{leaf} than MWF species (Figure 2; Table 2, Supporting Information Table S1).

3.2 | Associations among vital rates

Across forests, the two measures of relative growth rates ($\mathrm{RGR_{dbh}}$ and $\mathrm{RGR_{biom}}$) were strongly intercorrelated ($r = 0.97$; $p < 0.001$), and both were correlated with m ($r = 0.55$ and 0.57, respectively; $p < 0.05$; Figure 3a,b). Within the LDF, but not the MWF, m was positively correlated with $\mathrm{RGR_{dbh}}$ and $\mathrm{RGR_{biom}}$ ($r = 0.76$ and 0.93, respectively; $p < 0.05$; Supporting Information Tables S5 and S6).

When using the Bayesian approach to account for plant sizes, we found positive correlations across species between m and both $\mathrm{RGR_{dbh}}$ and $\mathrm{RGR_{biom}}$ in all size classes ($\tau > 0$; Figure 3c,d).

3.3 | Trait–trait coordination

Traits were highly intercorrelated within functional modules (i.e., stomatal morphology traits, venation traits, leaf and wood economics and structure traits, and compositional traits) when considering species from both forests together, and in the MWF and LDF separately (Supplementary Results, "*Trait-trait coordination*"; Supporting Information Tables S4–S6).

3.4 | Trait relationships with plant vital rates

Overall, eight traits were correlated with $\mathrm{RGR_{dbh}}$ and/or $\mathrm{RGR_{biom}}$ and seven were correlated with m (Supporting Information Table S4). Of the 26 traits hypothesized to correlate with vital rates, three traits were correlated with $\mathrm{RGR_{dbh}}$,

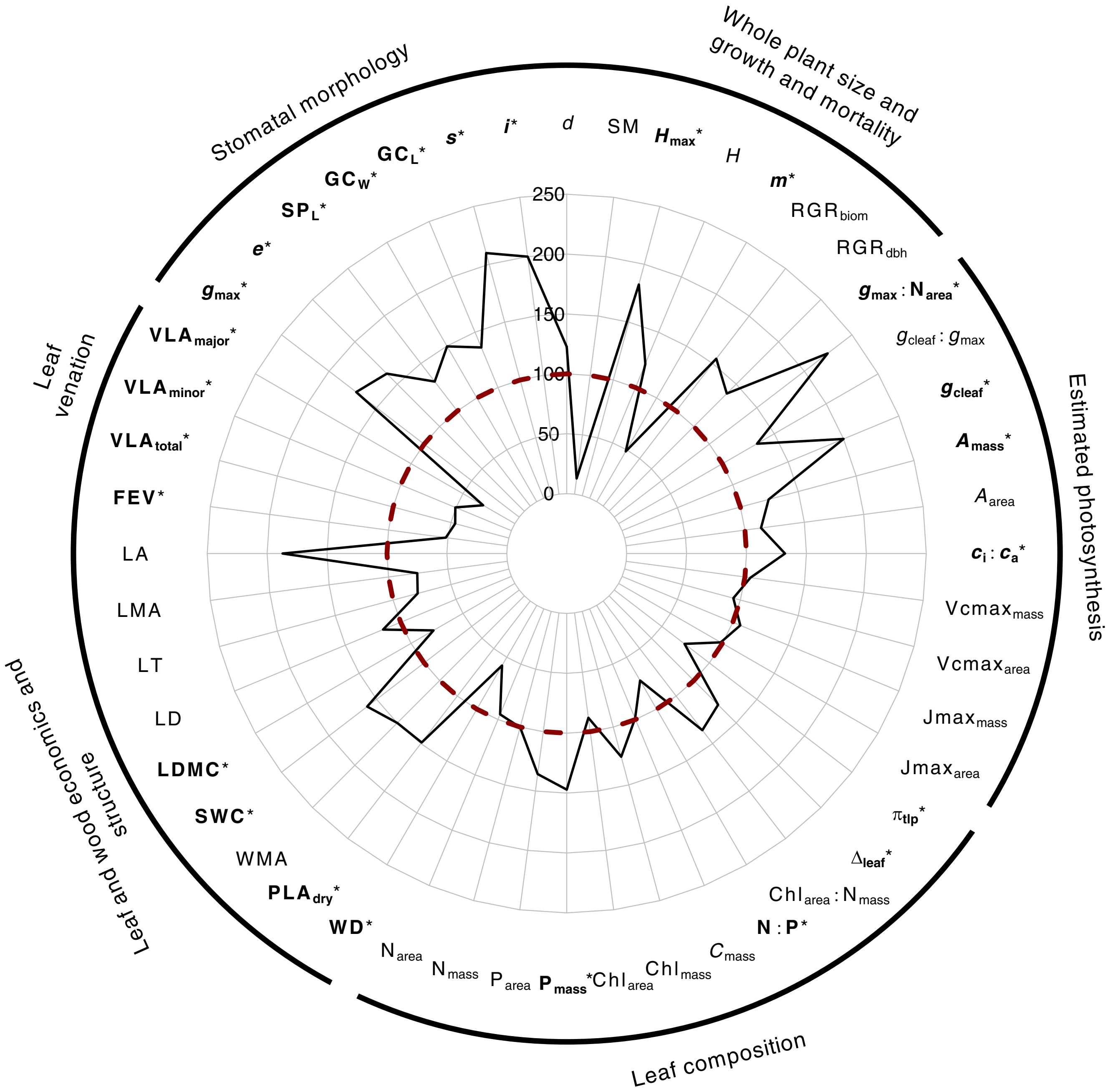

FIGURE 2 Radar graph illustrating per cent difference in trait means between MWF and LDF species. The LDF species means were fixed arbitrarily as the 100% reference values (the dark red dashed line), and the black line indicates the per cent difference between MWF species and LDF species. Traits are arranged according to putative traits modules previously defined (Table 1). Bold and * indicate $p < 0.05$

seven with RGR_{biom} and two with m across all 35 species (Supporting Information Table S4). Thus, RGR_{dbh} and RGR_{biom} were positively correlated with d, i and g_{max} (r ranged from 0.57 to 0.64; $p < 0.05$; Supporting Information Tables S4 and S8; Figure 4a,b), RGR_{biom} was negatively correlated with LMA and VLA_{minor} ($r = -0.5$ and -0.56, respectively; $p < 0.05$; Supporting Information Tables S5 and S9; Figure 4d,e) and positively correlated with P_{mass} and $\bar{A}_{mass}$ ($r = 0.48$ and 0.51, respectively; $p < 0.05$; Supporting Information Tables S4 and S8; Figure 4c,f), and m was positively correlated with both N_{mass} and $\bar{A}_{mass}$ ($r = 0.5$ and 0.61, respectively; $p < 0.05$; Supporting Information Table S8; Figure 4g,h).

Given that species' RGRs did not differ between forests, trait–RGR correlations within forests were tested but not explored (Table 2, Supporting Information Tables S2, S5 and S6). However, the forests differed in m, and in its trait correlations. In the MWF, m was positively correlated with LMA, LD, N_{area}, P_{area} and P_{mass}, and with photosynthetic traits on both mass and area basis, $Jmax_{area}$, $Jmax_{mass}$, $Vcmax_{area}$, $Vcmax_{mass}$, $\bar{A}_{area}$, $\bar{A}_{mass}$ and $\bar{g}_{cleaf}$ (r ranged from 0.72 and 0.89; $p < 0.05$; Supporting

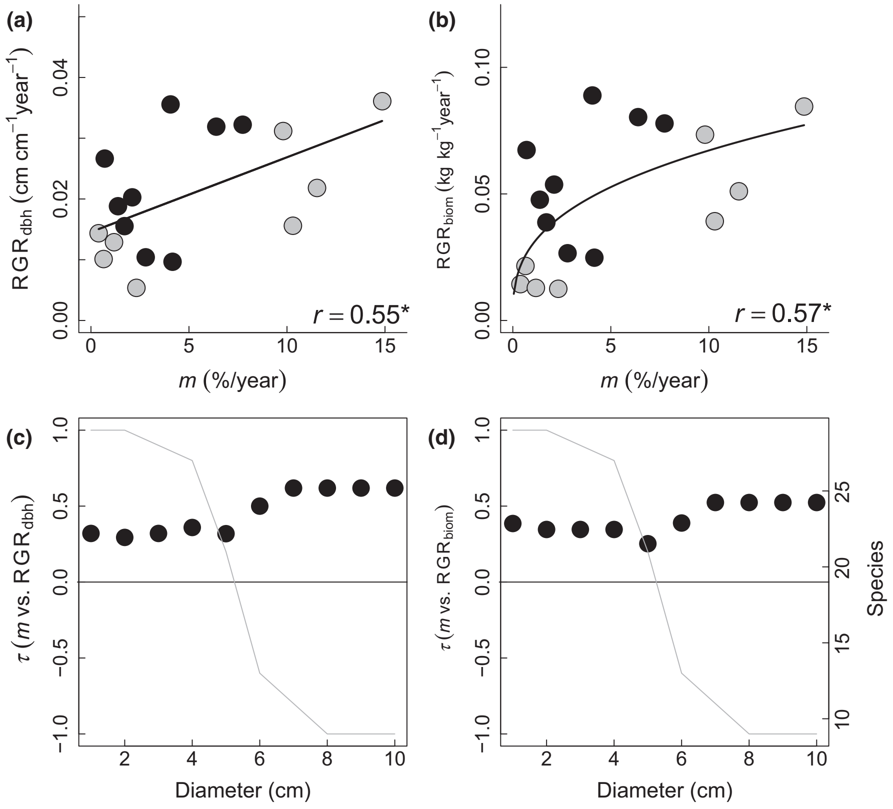

FIGURE 3 Relationships between relative growth rate (RGR) and mortality rate (*m*) across species of Hawaiian wet and dry forest. The top panels show the relationships across species between mean values for *m* and (a) relative growth rate in terms of diameter at breast height, RGR_{dbh} and (b) in terms of above-ground biomass, RGR_{biom}. The bottom panels show that the correlation of mortality with RGR is robust across size modules by plotting the Kendall correlation coefficient (τ) between *m* and (c) RGR_{dbh} and (d) RGR_{biom} against plant size class, with the grey line showing the number of species in each 1-cm diameter class (lower in larger size classes). *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Top row: black symbols, Montane Wet Forest (MWF) species; grey symbols, Lowland Dry Forest (LDF). $RGR_{dbh} = 0.01 + 0.001 * m$; $RGR_{biom} = 0.03 * m^{0.35}$. Bottom row: Filled symbols represent significant correlations. We use Pearson correlation coefficient in plots (a) and (b) because the species means for *m*, RGR_{dbh} and RGR_{biom} calculated across all individuals were normally distributed or became so after log-transformation, whereas we used Kendall's correlation coefficient in plots (c) and (d) because after stratifying by plant size, *m* remained non-normally distributed even after transformation. Notably, the *RGR-m* relationships can be discerned with either coefficient; when calculating Kendall's coefficient for panels (a) and (b), Kendall's τ was 0.32 ($p = 0.07$) and 0.35 ($p = 0.048$) respectively; for panels (c) and (d), correlations were considered significant when the 99% credible interval of τ did not include zero

Information Table S5). In the LDF, *m* was negatively correlated with LA, LMA, LT, $Jmax_{area}$, $Vcmax_{area}$, $\bar{A}_{area}$ and $\bar{g}_{cleaf}$ (*r* ranged from −0.76 and −0.91; $p < 0.05$; Supporting Information Table S6). Notably, the direction of the correlation across species between *m* and LMA differed between forests, resulting in positive relationships between *m* and area-based photosynthetic traits in the MWF and negative relationships in the LDF (Figure 5a,b). Further, *m* was positively correlated with P_{mass} in the MWF ($r = 0.89$; $p < 0.01$; Supporting Information Table S5; Figure 5c) and negatively correlated with LA in the LDF ($r = -0.76$; $p < 0.05$; Supporting Information Table S6; Figure 5d).

3.5 | Functional traits and size-dependent plant relative growth and mortality rates

Many more trait correlations with relative growth rate were resolved when accounting for tree size using the Bayesian approach. Whereas three traits were correlated with RGR_{dbh} without accounting for size class, when using the Bayesian approach to account for plant sizes, 18 traits were correlated with RGR_{dbh} within at least one size class. Within given size classes RGR_{dbh} was positively correlated with *d*, *i*, g_{max}, LDMC, LD, C_{mass}, c_i:c_a, $\bar{g}_{cleaf}$, g_{max}:N_{area} (Figure 6a), H_{mean} and H_{max} and negatively correlated with *e*, SWC, WMA, LA, PLA_{dry}, $\bar{g}_{cleaf}$:g_{max} and SM ($\tau > 0$).

When accounting for plant size, we found correlations of *m* with 18 traits. In all size classes, *m* was positively correlated with N_{mass}, $Jmax_{mass}$, $Vcmax_{mass}$ and $\bar{A}_{mass}$ ($\tau > 0$) and negatively correlated with LT ($\tau < 0$). Within given size classes, *m* was positively correlated with *d* (Figure 6c), VLA_{major}, N_{area}, P_{mass} (Figure 6d), N:P and $\bar{g}_{cleaf}$ and negatively correlated with *s*, GC_L, GC_W, WMA, C_{mass}, Chl_{area}:N_{area} and g_{max}:N_{area} ($\tau > 0$).

Notably, the finding of a greater number of significant relationships between traits and vital rates when stratifying by tree size was not based on the (appropriate) use of different correlation

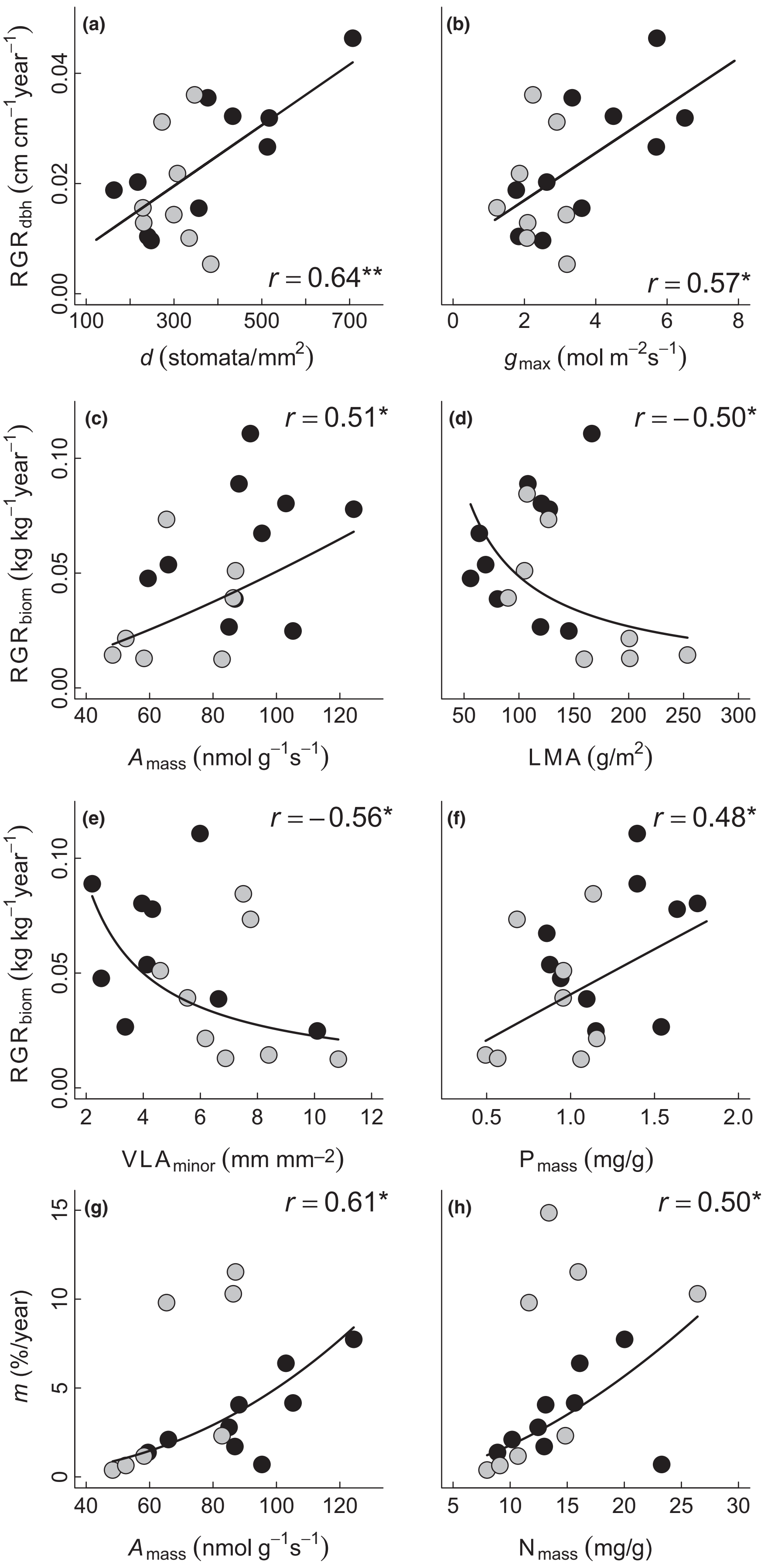

FIGURE 4 Trait–vital rate relationships across Hawaiian wet and dry forest species, including relationships between relative growth rate in terms of diameter at breast height (RGR_{dbh}) and (a) stomatal density and (b) maximum stomatal conductance; between relative growth rate in terms of above-ground biomass (RGR_{biom}) and (c) time integrated CO_2 assimilation rate per mass, (d) leaf mass per area, (e) minor vein density and (f) phosphorus per mass; and between mortality rate (*m*) and (g) time integrated CO_2 assimilation rate per leaf dry mass, (h) nitrogen per leaf dry mass. Black symbols, Montane Wet Forest (MWF) species; grey symbols, Lowland Dry Forest (LDF) species. $RGR_{dbh} = 3.02e^{-03} + 5.51e^{-05} * d$; $RGR_{dbh} = 0.01 + 0.004 * g_{max}$; $RGR_{biom} = 10e^{-03} * \bar{A}_{mass}^{1.35}$; $RGR_{biom} = 2.53 * LMA^{-0.858}$; $RGR_{biom} = 0.17 * VLA_{minor}^{-0.87}$; $RGR_{biom} = 0.041 * P_{mass}^{0.97}$; $m = 8e^{-05} * \bar{A}_{mass}^{2.40}$; $m = 0.04 * N_{mass}^{1.67}$. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$

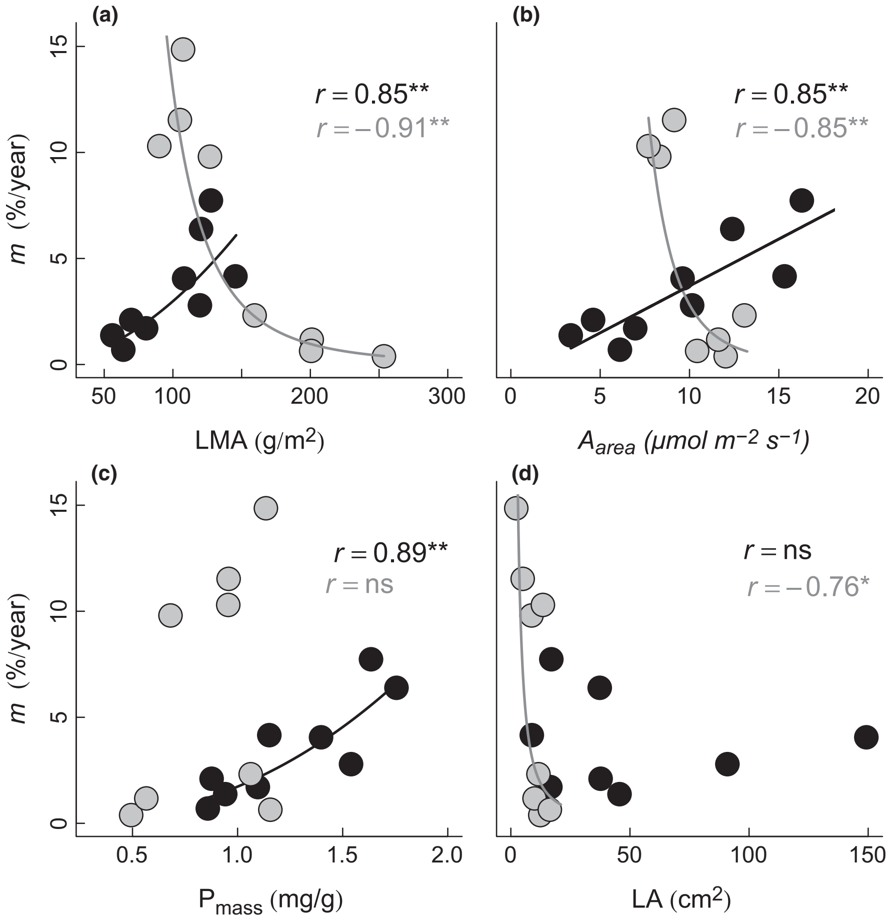

FIGURE 5 Contrasting relationships between mortality rate and functional traits across forests, including (a) leaf mass per area, (b) time integrated CO_2 assimilation rate per leaf area, (c) phosphorus concentration per leaf mass and (d) individual leaf area. Black symbols and curve, Montane Wet Forest (MWF) species; grey symbols and curve, Lowland Dry Forest (LDF) species. In (e), the black and grey lines and *r* values represent the fit and Pearson's regression coefficients including only MWF species and LDF species respectively. $m_{MWF} = 5e^{-04} * LMA^{1.89}$ and $m_{LDF} = 4e^{8} * LMA^{-3.74}$; $m_{MWF} = -0.72 + 0.44 * \bar{A}_{area}$ and $m_{LDF} = 764{,}699 * \bar{A}_{area}^{-5.43}$; $m = 1.73 * P_{mass}^{2.38}$; $m = 74.53 * LA^{-1.46}$. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

methods selected according to the distribution of the data, that is, the Pearson *r* for the analyses of trait–vital rate correlations when averaging across all individuals for each species, and the Kendall tau when testing these correlations while stratifying by plant size (see Section 2). To test this, we also determined the trait–vital rate correlations using Kendall tau when averaging across all individuals for each species, and as for the Pearson test, seven traits were correlated with RGR_{dbh} and/or RGR_{biom} and seven were correlated with *m*. Thus, the finding that more trait–vital rate relationships are significant when stratifying by plant size is robust to the use of different correlation tests.

3.6 | Predicting RGR_{dbh}, RGR_{biom} and *m* from functional traits

To predict RGR_{dbh}, RGR_{biom} and *m*, we built multiple regression models that included the seven non-redundant traits most strongly correlated with vital rates among the 26 hypothesized a priori to influence vital rates (*d*, VLA_{minor}, LMA, WD, N_{mass}, P_{mass} and $\bar{A}_{mass}$) and a term for forest membership (site; coded as 0 for MWF species and 1 for LDF species). The variable selection procedures (Supporting Information Table S9) indicated that *d*, VLA_{minor}, P_{mass} and $\bar{A}_{mass}$ were the best predictors for RGR_{dbh} (adjusted $R^2 = 0.72$; $p < 0.001$; Table 4, Figure 7a); *d*, VLA_{minor}, LMA and P_{mass} for RGR_{biom} (adjusted $R^2 = 0.70$; $p < 0.01$; Table 3, Figure 7b); and VLA_{minor}, LMA, P_{mass}, $\bar{A}_{mass}$ and site for *m* (adjusted $R^2 = 0.71$; $p < 0.001$; Table 4, Figure 7c).

4 | DISCUSSION

4.1 | Trait variation between Hawaiian wet and dry forests

We found strong novel trait variation between Hawaiian wet and dry forests, demonstrating that these forests are highly distinct not only in climate and species composition, but also in an extensive set of traits. While previous studies have shown that wet and dry forests differ in functional traits (Brenes-Arguedas, Roddy, Kursar, & Tjoelker, 2013; Lohbeck et al., 2015; Markesteijn et al., 2010; Santiago, Kitajima, Wright, & Mulkey, 2004; Wright et al., 2004), by including a far wider range of traits related to resource acquisitiveness and stress tolerance, our analyses highlight their power in multiple comparative and predictive applications of trait-based ecology.

The trait differences between forests aligned with their variation in vital rates. While the species of the two forests did not differ on average in RGR, the MWF species showed lower mortality

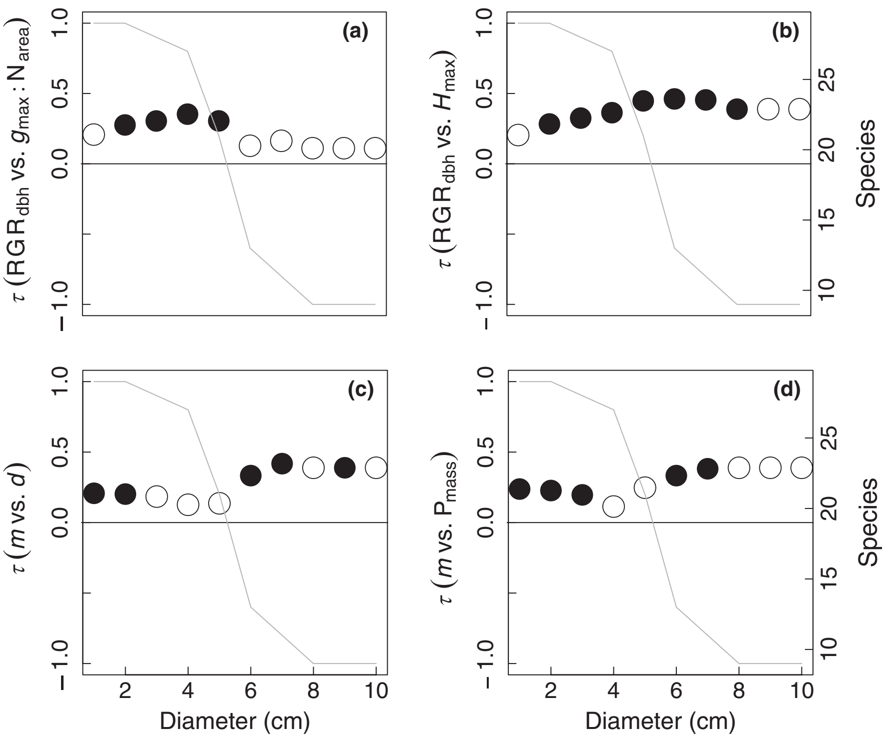

FIGURE 6 Estimating the influence of plant size on the correlation of relative growth rate and mortality with given functional traits. Each panel shows the plot of the size-dependent Kendall correlation coefficient (τ) between: (a) relative growth rate and the ratio of maximum stomatal conductance to leaf nitrogen per area, $g_{\max}$:$\mathrm{N_{area}}$; (b) relative growth rate and maximum height, $H_{\max}$; (c) mortality rate and stomatal density, *d*; and (d) mortality rate and phosphorus concentration, $\mathrm{P_{mass}}$. Open symbols represent non-significant associations (the 99% credible interval of τ included zero), and filled symbols significant correlations (the 99% credible interval of τ did not include zero). The grey line shows the number of species in each 1-cm diameter class

rates than the LDF species, consistent with previous work showing higher mortality in drier forests elsewhere (Gaviria, Turner, & Engelbrecht, 2017; Laura Suarez & Kitzberger, 2010). The lower mortality of the MWF species is consistent with the greater supply of water and soil nutrients, related to greater accumulated weathering, organic material formation, N-fixation, and nutrient retention capacity, and its richer microbial community. The positive relationship of RGRs and *m* across all species was consistent with that found across species in temperate (Iida et al., 2014; Seiwa, 2007) and tropical forests (Kitajima, 1994; Philipson et al., 2014; Wright et al., 2010). Our finding of greater trait variation within the wet forest than the dry forest supports the expectations from first principles that the low-resource availability in the dry forest would act as a strong environmental filter resulting in functional convergence, and/or promote greater niche overlap among species in the dry forest via fewer potential biotic interactions (Kraft, Crutsinger, Forrestel, & Emery, 2014; Lebrija-Trejos et al., 2010; Nathan et al., 2016; Weiher & Keddy, 1995).

The greater soil resources in the MWF led to the expectation that species would possess traits associated with photosynthetic productivity and rapid growth. Consistent with this expectation, MWF species had higher values on average for *i* and *s*, dimensions of guard cells ($\mathrm{GC_L}$, $\mathrm{GC_W}$ and $\mathrm{SP_L}$) and *e*, $g_{\max}$, SWC, $\mathrm{PLA_{dry}}$, $\mathrm{P_{mass}}$, Chl_{area}:$\mathrm{N_{area}}$, $\bar{A}_{\mathrm{mass}}$, $\bar{g}_{\mathrm{cleaf}}$, c_i:c_a, $g_{\max}$:$\mathrm{N_{area}}$, Δ_{leaf} and $H_{\max}$, and lower values for LDMC, WD and N:P. By contrast, the higher temperature and lower rainfall of the LDF led to the expectation that species would possess drought tolerance traits. Indeed, LDF species had higher vein densities, $|\pi_{\mathrm{tlp}}|$, WD and LDMC and lower values for $\mathrm{PLA_{dry}}$, stomatal dimensions, SWC and c_i:c_a ratio and $\bar{A}_{\mathrm{mass}}$. Finally, the greater understorey shade of the MWF led to expectations of shade adaptation, confirmed for the lower values for vein densities and LDMC (Baltzer et al., 2008; Chave et al., 2009; Farquhar et al., 1989; Li et al., 2015a; Niinemets, 2001; Stratton, Goldstein, & Meinzer, 2000; Wright et al., 2004). Beyond these average differences among forests, trait values were consistent with known life-history differences among species within and across forests. For example, *Acacia koa*, the fastest growing species overall, had notably high values for stomatal dimensions and index, and estimated rates of electron transport and gas exchange; drought-tolerant *Osteomeles anthyllidifolia* had high $|\pi_{\mathrm{tlp}}|$ and WD and low c_i:c_a ratio and $\bar{A}_{\mathrm{mass}}$; and shade-tolerant *Hedyotis hillebrandii* had high values for stomatal dimensions and LA, and low vein densities and WD.

4.2 | Trait correlations across species of wet and dry forests

Our work supported the hypothesis that traits would be intercorrelated within modules corresponding to a given organ or function (Li et al., 2015b; Sack et al., 2003a). These trait associations can indicate allometric relationships that arise developmentally, such as those found among stomatal traits, vein densities and leaf size (Brodribb, Field, & Sack, 2010; Sack et al., 2012). Other trait–trait relationships within modules would arise from co-selection for optimal function, for example, traits potentially contributing to maximum gas exchange and RGR (Scoffoni et al., 2016), such as high $g_{\max}$ and $\mathrm{P_{mass}}$; or to drought tolerance (Bartlett, Klein, Jansen, Choat, & Sack, 2016), such as high $|\pi_{\mathrm{tlp}}|$ and $\bar{A}_{\mathrm{mass}}$; or to shade tolerance (Givnish et al., 2005), such as high LA and low WD.

TABLE 4 Models selected by maximum likelihood to estimate relative growth rate in terms of diameter at breast height (A, $\mathrm{RGR_{dbh}}$) or above-ground biomass (B, $\mathrm{RGR_{biom}}$) or mortality rate (C, *m*). Independent variables included in the tested models were those of each module (Supporting Information Table S8) that were most correlated with each dependent variable. We present the Pearson's coefficients for the relationships of each predicted variable vs. each independent variable using untransformed and log-transformed data, the multiple regression coefficient estimates and per cent contribution of each trait to model fit. Full models and detailed model selection procedures using AICcs are presented in Supporting Information Table S9

Model	Pearson's correlation coefficient	Multiple regression analyses coefficient estimate	Hierarchical partition analyses (%)
(A) $\mathrm{RGR_{dbh}} \sim d + \mathrm{VLA_{minor}} + \mathrm{P_{mass}} + \bar{A}_{\mathrm{mass}}$			
Intercept	–	$2.09e^{-02*}$	–
d	0.67^{**}, 0.43	$7.76e^{-05***}$	53.2
$\mathrm{VLA_{minor}}$	−0.44, −0.49	$-3.32e^{-03*}$	27.6
$\mathrm{P_{mass}}$	0.39, 0.25	$-2.43e^{-02*}$	10.9
$\bar{A}_{\mathrm{mass}}$	0.36, 0.28	$2.51e^{-04}$	8.3
Adjusted multiple R^2	–	0.72^{***}	–
(B) $\mathrm{RGR_{biom}} \sim d + \mathrm{VLA_{minor}} + \mathrm{LMA} + \mathrm{P_{mass}}$			
Intercept	–	$6.58e^{-02*}$	–
d	0.65^{**}, 0.40	$2.01e^{-04***}$	51.9
$\mathrm{VLA_{minor}}$	−0.50, -0.56^{*}	$-4.78e^{-03*}$	20.0
LMA	−0.35, −0.48	$-2.32\ e^{-04}$	13.7
$\mathrm{P_{mass}}$	0.39, 0.25	$-2.30e^{-02}$	14.4
Adjusted multiple R^2	–	0.70^{**}	–
(C) $m \sim \mathrm{VLA_{minor}} + \mathrm{LMA} + \mathrm{P_{mass}} + \bar{A}_{\mathrm{mass}}$ + site			
Intercept	–	−2.59	–
$\bar{A}_{\mathrm{mass}}$	0.49, 0.73^{**}	0.18^{**}	39.1
Site	–	6.65^{**}	31.2
LMA	−0.35, −0.38	−0.03	15.9
$\mathrm{P_{mass}}$	0.16, 0.42	−3.39	7.7
$\mathrm{VLA_{minor}}$	−0.13, −0.17	−0.60	6.1
Adjusted multiple R^2	–	0.70^{**}	–

$^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

The numerous trait correlations across species result in a reduced trait “dimensionality,” by which most trait variation may be captured by few axes (Diaz et al., 2016). However, that finding does not in fact imply that traits are functionally redundant, as correlated traits can contribute semi-distinctly to function and their consideration as separate parameters improves predictive and mechanistic modelling (John et al., 2017; Sterck et al., 2011). For example, while LMA is correlated with other traits that share structural or compositional bases (Finegan et al., 2015; John et al., 2017) such as LDMC or WMA, photosynthetic rates and nutrient concentrations, these traits can play non-redundant roles in determining functions such as shade and drought tolerance and in influencing RGR and *m* (Supporting Information Tables S4–S6 and S10).

4.3 | Trait associations with relative growth rates and mortality rates

Several novel trait correlations were found with mean RGRs and *m* across species that were expected from theory and that have potential for generality, including the relationships of $\mathrm{RGR_{dbh}}$, $\mathrm{RGR_{biom}}$ and/or *m* to $\bar{A}_{\mathrm{mass}}$ and *d*, and several relationships were confirmed, such as with H_{max}, LMA and WD, that were reported in previous studies of temperate (Iida et al., 2016) and/or tropical forests (Finegan et al., 2015; Hérault et al., 2011; Liu et al., 2016; Wright et al., 2010). The contrasting correlations of traits with *m* between the MWF and LDF, such as LMA and $\bar{A}_{\mathrm{area}}$ (Figure 5a,b), and the correlations of traits with *m* in one but not the other forest, such as for $\mathrm{P_{mass}}$ and LA (Figure 5c,d), highlight the context dependence of trait–vital rate relationships. In the MWF, a high LMA was associated with higher *m*, as expected given ist representing the more shade-tolerant species in the understorey, which tend to have higher mortality (Kobe & Coates, 1997; Lusk et al., 2008). Conversely, in the LDF, high LMA was related to lower *m*, as expected given its potential contribution to greater drought tolerance via a lower surface area: volume ratio, and/or a greater mechanical protection contributing to longer leaf life span and reduced respiration costs (Falcão et al., 2015; Wright, Westoby, & Reich, 2002; Wright et al., 2004).

Hawaiian forests also showed contrasting relationships of certain traits to vital rates than previously reported. For example, vein density contributes mechanistically to greater hydraulic conductance, photosynthetic productivity and RGR across diverse species, all else being equal (Brodribb & McAdam, 2017; Iida et al., 2016; Li et al., 2015a; Sack & Frole, 2006; Sack & Scoffoni, 2013; Sack et al., 2013; Scoffoni et al., 2016). However, RGR was negatively related to vein density across the species of both forests. This negative correlation may reflect the co-variation of vein

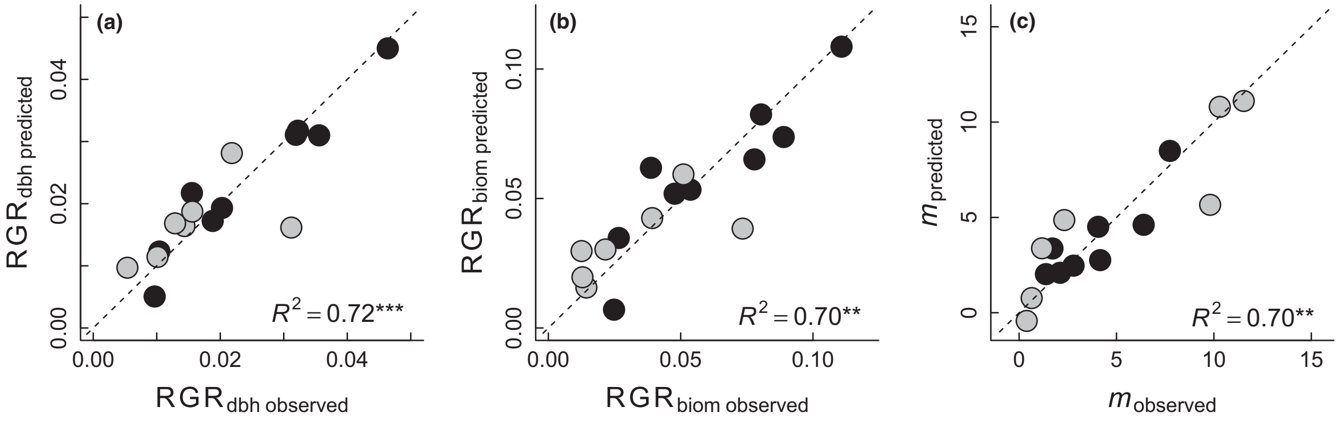

FIGURE 7 Relationship between observed growth rate in terms of diameter at breast height ($\mathrm{RGR_{dbh}}$), above-ground biomass ($\mathrm{RGR_{biom}}$) and mortality rate (m) and the values predicted from models using the plant traits most correlated with each dependent variable: (a) $\mathrm{RGR_{dbh}} = 2.09\mathrm{e}^{-02} + (7.76\mathrm{e}^{-05} * d) - (3.32\mathrm{e}^{-03} * \mathrm{VLA_{minor}}) - (2.43\mathrm{e}^{-02} * \mathrm{P_{mass}}) + (2.51\mathrm{e}^{-04} * \bar{A}_{\mathrm{mass}})$; (b) $\mathrm{RGR_{biom}} = 6.58\ \mathrm{e}^{-02} + (2.01\mathrm{e}^{-04} * d) - (4.78\mathrm{e}^{-03} * \mathrm{VLA_{minor}}) - (2.32\mathrm{e}^{-04} * \mathrm{LMA}) - (2.3\mathrm{e}^{-02} * \mathrm{P_{mass}})$; (c) $m = -2.59 - (0.60 * \mathrm{VLA_{minor}}) - (0.03 * \mathrm{LMA}) - (3.39 * \mathrm{P_{mass}}) + (0.18 * \bar{A}_{\mathrm{mass}}) + (6.64 * \mathrm{site})$. The dashed line represents the 1:1 relationship. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

density with other traits negatively related to RGR, including traits not considered, such as root traits, and/or it may arise from the high values for LDF species, which is consistent with their adaptation to higher *RGR* in the more limited periods when water is available, though this high *RGR* is not achieved integrated over time (Sack & Scoffoni, 2013).

Our study also confirmed the hypothesis that stratifying by plant size improved the frequency of correlations of vital rates with given traits. Stratifying by size has previously been shown to improve resolution of correlations of RGR and *m* with traits such as vein densities, LA, LMA, SWC, LT, $\mathrm{N_{mass}}$ and $\mathrm{P_{mass}}$, WD and H_{max} (Iida et al., 2014, 2016; Prado-Junior et al., 2016), and our study expanded this finding to a wider range of traits. Stratifying by size reduces the confounding influence of ontogenetic shifts in vital rates on cross-species comparisons (Hérault et al., 2011). Notably, when we examined trait correlations with RGR and *m* for plants of given sizes, as in previous studies conducting this analysis, our trait values were only for the sampled trees of typical mature size. Future studies may further improve resolution of correlations by also considering ontogenetic variation in trait values.

4.4 | Trait-based predictions of vital rates

Our study showed the value of a broad suite of functional traits for predicting vital rates. Models based on seven selected traits could explain more than 70% of the variation in $\mathrm{RGR_{dbh}}$, $\mathrm{RGR_{biom}}$ and *m* (Table 4, Supporting Information Table S9, Figure 7). The most parsimonious models for all three vital rates retained minor vein density and P per mass and two of them included stomatal density, time integrated $\mathrm{CO_2}$ assimilation rate and LMA. These findings highlight the potential of an approach based on an extensive suite of functional traits and the continued need to refine our mechanistic understanding of how suites of traits drive processes at the scale of individuals and whole forests.

4.5 | Conclusions and limitations of the study

We conclude that the use of an extensive suite of functional traits contributes power to (a) discover and resolve variation across species expected from their contrasting adaptation, (b) compare functional convergence across ecosystems, (c) highlight novel trait–trait and (d) trait–vital rate associations, and (e) the mediating role of plant size in these associations, and (f) to predict RGR and *m* across species. Recent studies have applied trait data to mechanistic process models to predict forest vital rates, niche differentiation and productivity (Fyllas et al., 2014; Marks & Leichowicz, 2006; Sterck et al., 2011). We propose that including an extensive suite of traits in such models will be a powerful avenue for future research on the functional ecology of contrasting communities, including vital rates and ultimately their responses to climate change and shifts in species' distributions. An important avenue for future research is to consider the incorporation of extended traits into estimating and testing species' habitat preferences within and across forests, extending from recent work showing substantial power even based on few traits, such as leaf size, wood density, LMA and seed size (Shipley et al., 2017).

We note that some of our study questions were carried out by comparing single forests of each type, and our findings suggest that the approach has value for further testing replicate forests of each type. Additionally, models are needed of the specific processes involved in vital rates, in which traits can be included along with climate, to resolve how specific trait variation scales up to influencing RGR and *m*. Our approach focused on the correlations of single traits and suites of traits with RGR and *m*, a central approach in trait-based ecology. However, given that upper level processes such as growth or species niche preferences depend on multiple traits, given that correlations may not actually reflect causal mechanisms, due to patterns of co-variation with other traits (John et al., 2017; Shipley et al., 2017). Further, while our models predicting vital rates included site as a factor, that approach does not fully incorporate trait–climate interactions, suggesting the value of mechanistic trait-based models that include climatic factors.

Including an extensive suite of functional traits can sharpen our characterization of species adaptation to their ecosystem and climatic preferences as well as predicting vital rates. Including traits in mechanistic process models for growth and species' distributions will increase predictive power further. Such prediction is increasingly critical for species conservation, especially in ecosystems such as Hawaiian forests, which are threatened in the face of development and ongoing climate change (Fortini et al., 2013). Future work should also consider intraspecific variation in the wider set of traits, and its role in shaping species distributions within and between forests, as well as trait determination of microsite differences among species (Inman-Narahari et al., 2014). Given the power to predict vital rates, this work can enable scaling up from the traits of component species to ecosystem and eventually global vegetation processes, highlighting the enormous promise of increasing mechanistic information—from measurements, to analyses, to models—for clarifying and predicting processes in species and community ecology.

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AUTHORS' CONTRIBUTIONS

C.D.M. and L.S. conceived ideas and experimental design. C.D.M., C.S., F.I., G.J., M.B. and L.S. collected trait data. F.I., R.O., S.C., C.G. and L.S. organized and collected forest census data. C.D.M. and L.S. analysed the data and wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

DATA ACCESSIBILITY

All trait data collected for this paper are archived in the Dryad Digital Repository: https://doi.org/10.5061/dryad.cq47n7s (Medeiros et al., 2018).

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SUPPORTING INFORMATION

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

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