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Biogeographic constraints on the world-wide leaf economics spectrum

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ABSTRACT

Aim The world-wide leaf economic spectrum (LES) describes tight coordination of leaf traits across global floras, reported to date as being largely independent of phylogeny and biogeography. Here, we present and test an alternative, historical perspective that predicts that biogeography places significant constraints on global trait evolution. These hypothesized constraints could lead to important deviations in leaf trait relationships between isolated floras that were influenced by different magnitudes of genetic constraint and selection.

Location Global, including floristic regions of the Northern and Southern Hemispheres, eastern North America, East Asia (EAS), the Hawaiian Islands and tropical mainland floras.

Methods We use a large leaf-trait database (GLOPNET) and species native distribution data to test for variation in leaf trait relationships modulated by floristic region, controlling for climatic differences. Standardized major axis analyses were used to evaluate biogeographic effects on bivariate relationships between LES traits, including relationships of photosynthetic capacity and dark respiration rate ($A_{\text{mass}}-R_{\text{d-mass}}$), leaf lifespan and mass per area ratio (LL-LMA), and photosynthetic capacity and nitrogen content ($A_{\text{mass}}-N_{\text{mass}}$).

Results Independent of climate or biome, floras of different evolutionary histories exhibited different leaf trait allometries. Floras of the Northern Hemisphere exhibited greater rates of return on resource investment (steeper slopes for the trait relationships analysed), and the more diverse temperate EAS flora exhibited greater slopes or intercepts in leaf trait relationships, with the exception of the $A_{\text{mass}}-N_{\text{mass}}$ relationship. In contrast to our hypothesis, plants of the floristically isolated Hawaiian Islands exhibited a similar $A_{\text{mass}}-N_{\text{mass}}$ relationship to those of mainland tropical regions.

Main conclusions Differences in leaf trait allometries among global floristic regions support a historical perspective in understanding leaf trait relationships and suggest that independent floras can exhibit different tradeoffs in resource capture strategies.

Keywords

Convergent evolution, functional trait variation, leaf lifespan, leaf nitrogen, leaf respiration, photosynthetic rate, plant metabolic efficiency, plant strategy theory.

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INTRODUCTION

Wright *et al.* (2004) reported a general tradeoff surface ('leaf economic spectrum', LES) describing coordinated variation in leaf traits among global floras (see also Reich *et al.*, 1997, 1999;

Wright *et al.*, 2005a,b). This spectrum runs from species that have a quick return in leaf investment (i.e. low construction cost, low mass per area, short life span, high photosynthetic capacity, high respiration rate, high nutrient content) to those with contrasting traits associated with slow return on resource

investment. With the recognition of only subtle LES modulation from climate (Wright *et al.*, 2005b) and even smaller differences between growth forms (Wright *et al.*, 2005a) or biomes (Reich *et al.*, 1997, 1999), the broad generality of the LES has been presented as a robust framework for plant strategy evolution that is independent of phylogeography. These reportedly widespread general patterns in leaf trait relationships point toward global evolutionary convergence in the fundamental tradeoffs of plant resource economics (Shipley *et al.*, 2006; Donovan *et al.*, 2011; Tilman, 2011). Several mechanistic explanations of this reported global generality of the LES have been invoked, including the physical constraints of leaf physiology (Shipley *et al.*, 2006; Blonder *et al.*, 2011), genetic constraints and selection pressures against assumed inefficient trait combinations (Donovan *et al.*, 2011).

At its core, the leaf economics spectrum is an argument for the optimization of plant resource foraging across a range of environmental conditions, with different strategies across the gradient driven largely by resource availability (Fig. 1, shift A). Given a position along a resource gradient, LES theory assumes that species have had sufficient time and genetic variation to evolve an optimal strategy for converting resources into biomass through a maximally efficient carbon economy (Reich *et al.*, 1999; Donovan *et al.*, 2011). Although differences in environmental or biotic stresses between regions may require allocation of resources to processes not directly associated with carbon gain (such as defensive chemistry, frost or drought tolerance, etc.; Fig. 1, shift B), it has been argued that an increase in leaf tissue investment should give a similar return in carbon gain, as evinced by a common slope of leaf trait relationships among global floras (Reich *et al.*, 1997, 1999; Wright *et al.*, 2004). If LES trait relationships are indeed consistent among floras that have been isolated for long periods of evolutionary time, then either: (1) phylogenetic constraints on leaf-level carbon economy are minor across major plant lineages; (2) optimal carbon economies evolve relatively quickly once plant lineages colonize new areas of novel resource conditions; or (3) the core allometries of LES evolved early in vascular plant evolution and have been preserved as the major lineages colonized the Earth's land masses (Tilman, 2011).

An alternative hypothesis is that contingencies in the evolutionary development of historically isolated biotas, e.g. the large variation in age, spatial extent, and phylogenetic diversity (number of resident plant lineages) of the world's floras (Takhtajan, 1986), has precluded the emergence of a canonical, globally consistent set of leaf trait allometries. If an optimized carbon economy is largely the result of selection, with less efficient genotypes being eliminated over the course of plant evolution due to low fitness (Donovan *et al.*, 2011), then the level of efficiency of species carbon economics should be proportional to the competitive intensity experienced by plants in a particular region, which we reason is in part a function of the size and diversity of the flora (Dobzhansky, 1950). With substantial differences in evolutionary histories between modern global floras (Takhtajan, 1986), we predict that those floras that evolved in isolation should exhibit different sets of strategies in resource

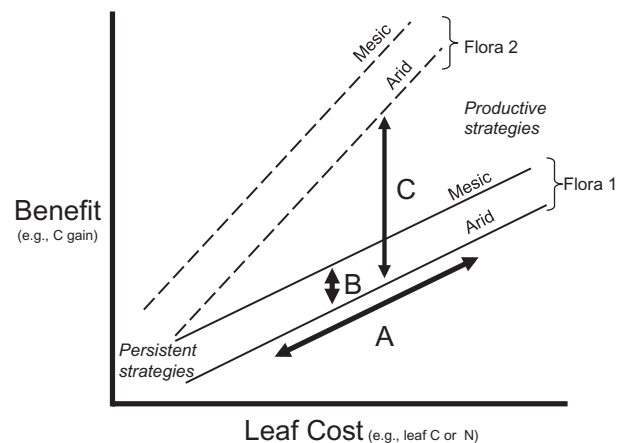


Figure 1 Hypothetical differences in leaf economic trait relationships that result from shifts along a common slope (A), a shift in the intercept of a common slope (B) or a shift in slope (C) between plants of different floristic regions. Plants of a given landscape show correlated variation along a common tradeoff axis ('leaf economic spectrum'), with different leaf economic strategies employed in niches along a resource gradient (A). However, when comparing regions with different abiotic conditions, important differences may arise as a function of ecosystem- or biome-level adaptations, where at a given leaf cost, species of one environment exhibit consistently greater carbon gain (B). This could be due to adaptive differences in resource allocation (i.e. metabolic versus structural) between environments (e.g. mesic versus arid conditions, less herbivory versus more herbivory), while showing the same basic tradeoff (slope). In addition, two isolated floras (solid and dashed lines) may show trait scaling differences, as illustrated through contrasting slopes (C). We hypothesize that after controlling for biome-level variation, regions with contrasting biogeographic histories should show slope differences in particular trait tradeoffs that reflect varying selection intensity for leaf function. In the absence of evidence for allocation differences (e.g. climate adaptations), shift B between regions cannot be ruled out as modulated by historical factors (e.g. herbivore pressure, edaphic differences). However, as interpreted from Leishman *et al.* (2010), the flora with the greater slopes (dashed lines) evolved a fundamentally different resource-use tradeoff, defined by acquiring greater returns per unit resource invested. Therefore, we would expect differences in intercept (shift B) or slope (shift C) when comparing floras in the same biome type but with different historic selection pressures.

economics, beyond ecosystem differences in allocation (Reich *et al.*, 1999; Wright *et al.*, 2001). This difference should be most clearly demonstrated through the existence of different trait allometries (i.e. slopes), where, per unit increase in leaf cost traits, the summed benefits are greater in the flora with greater genetic variation and historical selection pressures for metabolic function (Fig. 1, shift C). A shift in slope for leaf economic traits signifies the regions that follow different carbon capture strategies (*sensu* Leishman *et al.*, 2010). LES modulations have been reported in the form of differences in slope or *y*-intercept between sites of different climates (Wright *et al.*, 2005b), but

biogeographic differences independent of climate have not been examined.

It is well known that plant and animal lineages released from competition and predation pressures after colonization of oceanic islands evolve along different trait trajectories than mainland lineages (Carlquist, 1974; Brown, 1995; Lomolino *et al.*, 2010), and this 'naïve' evolutionary status of island assemblages is a frequent reason given for their high susceptibility to invasion from mainland lineages (Vermeij, 2005). Small or historically isolated floras may also be more susceptible to phylogenetic constraints that limit regional trait evolution, a phenomenon that is well described in the plant invasion literature (Mack, 2003) and could in theory limit the expression of leaf-level trait allometries (Donovan *et al.*, 2011). The degree to which allopatric trait convergence is realized, even within a biome type, can be constrained by these important historical differences between regions (Cody & Mooney, 1978).

We utilized the GLOPNET data set (Wright *et al.*, 2004) to analyse plant trait relationships according to their native floristic region. Prior studies have analysed such relationships in the context of climate (Wright *et al.*, 2005b), biome (Reich *et al.*, 1997, 1999), growth form (Wright *et al.*, 2004, 2005a), phylogeny (e.g. Ackerly & Reich, 1999; Walls, 2011) or habitat factors (e.g. soil fertility; Ordoñez *et al.*, 2009). However, these analyses lack the ability to evaluate differences between global floras as a result of historical influences. Testing for biome-level variation in LES trait relationships (e.g. Reich *et al.*, 1999), based solely on ecological similarities that ignore evolutionary differences, obscures the detection of potential differences arising from historical constraints. Potential historical constraints include the presence or absence of given plant clades through evolutionary time (phylogenetic constraints), past physical barriers to dispersal, climatic/geological events, and other relict biogeographic processes (including past biotic interactions), all of which influence the evolutionary trajectories of distinct floristic regions. Evaluation of the relative influence of biogeography requires a comparison of climatically similar phytogeographic regions that reflect evolutionarily meaningful units based on shared evolutionary histories (Takhtajan, 1986). Past studies have measured the influence of phylogeny on leaf trait patterns (Ackerly & Reich, 1999; Walls, 2011). However, there have been no studies to date which compare LES relationships at the level of floristic regions, the level that would reflect the larger-scale phylogenetic and biogeographic constraints in trait evolution. We expected that isolated floras would exhibit significantly different strategies of leaf carbon economics relative to larger, more connected and diverse floras, which we assume experienced greater competitive intensities for longer periods of evolutionary time (Dobzhansky, 1950; MacArthur, 1972).

We chose three different trait relationships to quantify the potential for carbon gain per resource cost using key leaf-level tradeoffs. These included relationships of leaf photosynthetic capacity and dark respiration ($A_{\text{mass}}-R_{\text{d-mass}}$), leaf longevity and leaf mass per area (LL-LMA) and photosynthetic capacity and leaf nitrogen concentration ($A_{\text{mass}}-N_{\text{mass}}$). A given flora was said

to follow 'fundamentally different carbon capture strategies' (*sensu* Leishman *et al.*, 2007, 2010) if resident species displayed a greater increase of a carbon gain trait per unit increase in a cost trait (i.e. a steeper slope; Fig. 1, shift C). Resource allocation differences can also be shown if resident species displayed consistently greater carbon gain trait values at any given value of a cost trait (i.e. a greater y -intercept; Fig. 1, shift B). Differential allocation could be due to either abiotic differences between sites or core strategy differences for historical reasons. Therefore, floras with similar climates could theoretically exhibit slope or y -intercept shifts if historical differences can explain their leaf physiologies (Fig. 1).

We tested the following hypotheses:

1. H₁: Northern Hemisphere (NH) floras exhibit a greater slope or intercept in LES trait relationships than those of the Southern Hemisphere (SH), showing significant deviations from the presumed global generality of LES tradeoffs. Controlling for climate differences, this first comparison was motivated by the contrasting evolutionary histories of the predominantly vicariant floras of former Gondwanaland (current SH floras) and the larger, more connected floras of former Laurasia (current NH floras) (Morrone, 2009). With smaller component areas as Gondwana broke apart, lower phylogenetic diversity and greater isolation relative to the NH, the floras of the SH historically came into contact with fewer plant lineages and may have experienced lower selection pressure for resource-use economy.
2. H₂: plants of East Asia (EAS) show greater slopes or intercept in LES trait relationships than plants of eastern North America (ENA), despite both floristic regions lying largely within the north temperate mesic forest biome. The potential for a more efficient resource economy of EAS plants than those from ENA is suggested by several lines of evidence. A diversity bias exists with disjunct genera between ENA and EAS, having twice as many species in EAS than ENA, resulting from large-scale historical differences between the regions rather than habitat differentiation (Qian & Ricklefs, 2000). We reason that the greater diversity of the EAS flora has led to a more intense competitive environment and therefore greater selection pressure for resource-use efficiency in EAS plants. Additionally, there is a clear recorded invader bias with a large proportion of recent invaders to ENA being of EAS origin (Fridley, 2008), but not the converse (Weber *et al.*, 2008). This invader bias may be at least partly attributable to the greater resource economy of EAS species, which provides supplementary evidence to support our prediction of the scalings of LES traits between EAS and ENA.
3. H₃: the endemic flora of Hawaii exhibits a reduced slope or intercept in LES trait relationships in comparison to tropical mainland floristic regions. This prediction is based on the small area and younger age of the islands, the low phylogenetic diversity of the native flora and the recognition that Hawaii represents the most isolated floristic region in the world (Takhtajan, 1986). It is also consistent with empirical evidence from controlled studies involving native and alien Hawaiian species (e.g. Pattison *et al.*, 1999; Funk, 2008).

METHODS

Floristic region and leaf trait data

We combined the extensive GLOPNET data set (Wright *et al.*, 2004) with species native distribution data to test hypothesized differences in the leaf economies among select global floras. The native range of each species was assigned to one or more of the global floristic regions of Takhtajan (1986). This scheme represents the most current understanding of phylogeographic regions based on areas of endemism and major centres of plant diversification (see Fridley, 2008). Based on core geographic ranges, each species was grouped as a NH or SH species. Species with distributions spanning both Northern and Southern Hemispheres were excluded from the hemispheric contrasts due to the inability to assign these pan-tropical ranges as exclusively within the NH or SH. Native species distributions were assigned primarily through floristic information from the USDA Germplasm Resources Information Network (USDA, ARS, National Genetic Resources Program, 2010). Additional source floras were consulted as appropriate for confirmation of the extents of geographic ranges. The original GLOPNET data set (Wright *et al.*, 2004) contains 2548 entries and 2021 different plant species from 175 sites. Trait data for 346 entries were excluded for the current analysis due to insufficient distribution data, species originating in human cultivation or an unclear native origin (see Appendix S1 in Supporting Information for floristic region assignments). See Wright *et al.* 2004 for additional details on the specific measurements protocols and compilation of leaf data in the GLOPNET data set.

The trait combinations selected have clear predicted functional meaning without providing redundant interpretations, including the scaling of photosynthetic capacity to dark respiration ($A_{\text{mass}}-R_{\text{d-mass}}$; potential carbon gain–carbon maintenance cost), leaf longevity to leaf mass per area (LL–LMA; duration for potential resource gains per proxy measure of leaf cost) and photosynthetic capacity to leaf nitrogen concentration ($A_{\text{mass}}-N_{\text{mass}}$; photosynthetic N-use efficiency). We interpret leaf-level performance from these traits and can only speculate on whole plant fitness.

Data analysis

Three floristic region contrasts were chosen: (1) the land masses of the NH and SH; (2) ENA (Takhtajan region 3, North American Atlantic region) and EAS (Takhtajan region 2, eastern Asiatic region); and (3) the Hawaiian Islands (Takhtajan region 21, Hawaiian region) and mainland tropical regions (aggregated Caribbean, Amazonian and Malesian regions, Takhtajan regions 18, 23, 25). Because a ‘mainland’ source flora contrast for Hawaii was not intuitively clear, several alternative tropical floras were explored. The flora that colonized the Hawaiian floristic region is thought to have dominantly arisen from the Malesian islands, as well as from tropical mainlands of Central America and Australia (Takhtajan, 1986). Because fitted lines for species of these regions did not significantly differ in slope or intercept (analysis

not shown), species from the tropical mainland and island regions of the Caribbean, Amazon and Malesia were aggregated to form the comparison. Some of the species in the data set had geographic ranges which spanned more than one floristic region. In a few cases, species were excluded from a given floristic analysis if they were represented in both regions of interest (e.g. several circumboreal or cosmopolitan species were excluded from the EAS–ENA comparison).

Controlling for extrinsic factors of climate, biome and growth form between floras

To ensure LES contrasts between floras were not the result of climatic differences, we used site climate data from Wright *et al.* (2004) to compare climate distributions between regions. If differences were found for a given comparison, we controlled for climate by re-running the analysis using only data from sites that did not differ significantly in climate. This was only true for the NH–SH comparison (see Results). There was no significant difference in climate variables for sites used in the EAS–ENA analysis [mean annual temperature (MAT) rainfall, potential evapotranspiration (PET); see Table 1 for sample sizes, *t*-tests, all $P > 0.2$] or the Hawaii–tropical mainland MAT contrast [$n_1 = 5$ sites (HI), $n_2 = 22$ sites (mainland), $t = 0.27$, d.f. = 13, $P = 0.79$]. We did not preclude edaphic differences as a driver in potential trait variation for this contrast (see Discussion). In addition, chi-square contingency tests were performed to assess any biases between floristic regions in the composition of woody and non-woody growth forms represented in the data set. No consistent bias was found (analysis not shown), and growth form is not considered a major driver of these relationships (Wright *et al.*, 2005a).

Testing for differences in resource economics between evolutionarily distinct floras

Leishman *et al.* (2007) advocate the use of scaling relationships to infer metabolic function and ‘fundamental’ resource capture strategies because resource-use efficiency ratios (e.g. photosynthetic nitrogen use efficiency; $A_{\text{max}}/\text{leaf N}$) can be affected by differences in slope, intercept or shifts along a common slope. Allometric relationships for each floristic region contrast were analysed through standardized major axis (SMA) regression implemented in the *smatr* package for R (Warton, 2007; R Development Core Team, 2010). SMA regression line fitting minimizes residual variance in both *x* and *y* dimensions and is preferred in analysing bivariate allometric relationships, as opposed to predicting *y* from *x* in classical regression (Warton *et al.*, 2006). Testing in the SMA regression routine involves first testing for common slopes between groups. If the slopes do not differ (homogeneity), the lines fitted to the groups may represent a shift along their common slope and/or shifts in the *y*-intercept. The data were \log_{10} -transformed to sufficiently meet the assumptions of SMA regression.

Slope homogeneity was tested for each set of floristic contrasts. If the slope differed between floras (heterogeneity), the

Table 1 Standardized major axis regression parameters, coefficients of determination and sample sizes for each floristic contrast and trait relationship.

Floristic region contrast	Photosynthetic capacity–dark respiration ($A_{\text{mass}}-R_{\text{d-mass}}$)	Leaf longevity–leaf mass per area (LL–LMA)	Photosynthetic capacity–leaf N ($A_{\text{mass}}-N_{\text{mass}}$)
Northern Hemisphere	$\log A_{\text{mass}} = 1.27 \log R_{\text{d-mass}} + 0.67$; $r^2 = 0.61$; $n = 112$; 11 sites	$\log \text{LL} = 1.85 \log \text{LMA} - 2.84$; $r^2 = 0.45$; $n = 394$; 34 sites	$\log A_{\text{mass}} = 1.84 \log N_{\text{mass}} + 1.54$; $r^2 = 0.58$; $n = 447$; 44 sites
Southern Hemisphere	$\log A_{\text{mass}} = 0.98 \log R_{\text{d-mass}} + 0.91$; $r^2 = 0.42$; $n = 134$; 11 sites	$\log \text{LL} = 1.42 \log \text{LMA} - 1.87$; $r^2 = 0.30$; $n = 157$; 15 sites	$\log A_{\text{mass}} = 1.39 \log N_{\text{mass}} + 1.65$; $r^2 = 0.28$; $n = 159$; 16 sites
East Asia	$\log A_{\text{mass}} = 1.04 \log R_{\text{d-mass}} + 1.10$; $r^2 = 0.57$; $n = 12$; 6 sites	$\log \text{LL} = 2.25 \log \text{LMA} - 3.61$; $r^2 = 0.57$; $n = 59$; 14 sites	$\log A_{\text{mass}} = 1.54 \log N_{\text{mass}} + 1.52$; $r^2 = 0.60$; $n = 53$; 19 sites
Eastern North America	$\log A_{\text{mass}} = 1.31 \log R_{\text{d-mass}} + 0.63$; $r^2 = 0.65$; $n = 84$; 7 sites	$\log \text{LL} = 1.70 \log \text{LMA} - 2.53$; $r^2 = 0.49$; $n = 137$; 15 sites	$\log A_{\text{mass}} = 1.76 \log N_{\text{mass}} + 1.63$; $r^2 = 0.48$; $n = 174$; 15 sites
Hawaii	Insufficient data ($n = 0$)	Insufficient data ($n = 0$)	$\log A_{\text{mass}} = 1.88 \log N_{\text{mass}} + 1.49$; $r^2 = 0.26$; $n = 22$; 5 sites
Mainland tropics	Insufficient data ($n = 27$)	Insufficient data ($n = 77$)	$\log A_{\text{mass}} = 1.81 \log N_{\text{mass}} + 1.51$; $r^2 = 0.24$; $n = 67$; 22 sites

A_{mass} ($\text{nmol g}^{-1} \text{s}^{-1}$), leaf photosynthetic rate; $R_{\text{d-mass}}$ ($\text{nmol g}^{-1} \text{s}^{-1}$), leaf dark respiration rate; LL (months), leaf longevity; LMA (g m^{-2}), leaf mass per area; N_{mass} (%), leaf nitrogen content.

flora with a greater slope showed a greater increase in trait x per increase in trait y . When comparing leaf economic traits, slope differences between two groups have been interpreted as the groups following different strategies of resource capture (Leishman *et al.*, 2007, 2010). When the groups shared a common slope, a common slope was fitted. If the common slope relationship differed in intercept, the flora with the greater y -intercept exhibited greater resource returns at any given value of cost trait x . Likewise, when fitted lines shared a common slope, groups may be shifted along a common axis, where floras follow identical allometry but lie on different points of the same tradeoff surface (Warton *et al.*, 2006). Heterogeneity in slopes or intercepts of lines separately fitted for each region indicated differences among floras in the execution of a common ecological strategy, rather than habitat-driven shifts within floras, for the trait relationships analysed.

RESULTS

NH–SH contrasts

As predicted, slope heterogeneity was detected in all three relationships in the hemispheric contrasts. Comparing potential carbon gain (A_{mass}) with carbon respiratory costs ($R_{\text{d-mass}}$), leaf longevity (LL) with leaf mass (LMA), and potential carbon gain with leaf nitrogen content (N_{mass}), the slopes of the fitted lines for each trait contrasts were significantly different (Table 1, Fig. 2a–c). Species native to the NH exhibited consistently higher slope values in all three trait relationships. This indicates that in the bivariate relationships explored, the scaling of the NH species traits showed significantly higher returns per increase in resource investment.

Because these slope differences could be function of MAT (Wright *et al.*, 2005b), differences in mean site MAT between

regions were tested. Sites in the SH had higher MAT on average (see Table 1 for sample sizes; two-sided tests; Fig. 2a, $t = -1.31$, d.f. = 16.42, $P = 0.21$; Fig. 2b, $t = -2.99$, d.f. = 34.15, $P < 0.01$; Fig. 2c, $t = -3.882$, d.f. = 34, $P < 0.001$). These mean site differences were caused by several low-MAT sites ($\text{MAT} < 0^\circ \text{C}$, $n = 7$) in the NH and several high-MAT sites ($\text{MAT} > 20^\circ \text{C}$, $n = 7$) in the SH. When excluding these sites in the highest and lowest MAT classes ($\text{MAT} < 0^\circ \text{C}$ and $\text{MAT} > 20^\circ \text{C}$), the resulting sites did not differ in MAT [t -tests; mean $n_1 = 25.67$ (NH), mean $n_2 = 14.33$ (SH), all $P > 0.1$], and SMA analyses were rerun using this data subset. The conclusions remained the same for all three relationships (tests for SMA heterogeneity, $P < 0.05$). Robust to climate, the points in Fig. 2a–c include sites of all climates.

EAS–ENA contrasts

EAS–ENA regional floras exhibited variable results with respect to the direction of the hypotheses (Fig. 2d–f). Notably, despite small EAS sample size ($n = 12$) and sites having similar climates, the $A_{\text{mass}}-R_{\text{d-mass}}$ relationship showed a clear shift in intercept. Against our expectation, the slopes of this relationship when fitted separately by region were statistically insignificant, but assuming common slopes, EAS species exhibited consistently higher A_{mass} for a given $R_{\text{d-mass}}$ (Table 1). A significant shift in slope was detected for the LL–LMA relationship in the EAS–ENA contrast (Table 1, Fig. 2e). The SMA line fitted with ENA species had a significantly steeper slope, indicating higher returns in leaf longevity per increase in leaf dry mass production. Common slopes were found for $A_{\text{mass}}-N_{\text{mass}}$ fitted lines between EAS–ENA floras. The scaling showed a significant shift in intercept (Fig. 2f). Unexpectedly, plants from EAS had lower average values of A_{mass} at all values of N_{mass} than those from ENA (Table 1).

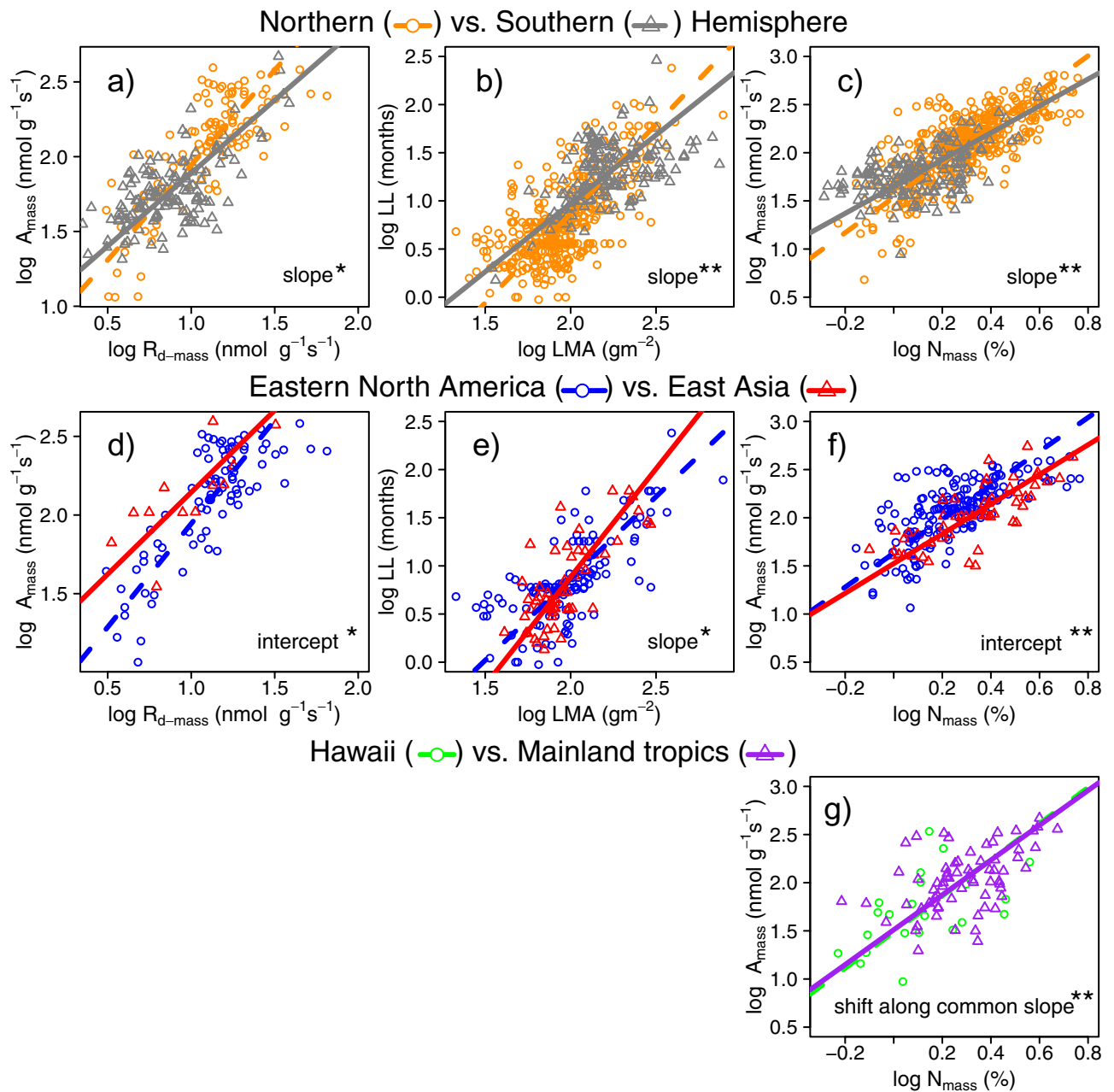


Figure 2 Leaf economic spectrum trait relationships for each floristic contrast and results of tests of differences in standardized major axis (SMA) slope, intercept, and shift along common SMA slope. For Northern–Southern Hemisphere floras: (a) photosynthetic capacity–dark respiration rate ($A_{\text{mass}}-R_{\text{d-mass}}$); (b) leaf longevity–leaf mass per area (LL–LMA); (c) photosynthetic capacity–leaf nitrogen content ($A_{\text{mass}}-N_{\text{mass}}$). For eastern North American–East Asian (ENA–EAS) floras: (d) $A_{\text{mass}}-R_{\text{d-mass}}$; (e) LL–LMA; (f) $A_{\text{mass}}-N_{\text{mass}}$. For Hawaiian and aggregated mainland floras: (g) $A_{\text{mass}}-N_{\text{mass}}$. Only significant ($P < 0.05$) test results are shown (* $P < 0.01$; ** $P < 0.001$).

Hawaiian islands–tropical mainland contrast

Insufficient data for plants endemic to the Hawaiian floristic region precluded analysis of relationships involving LL or R_{d} . However, SMA regression analysis of $A_{\text{mass}}-N_{\text{mass}}$ yielded significant results. Against expectation, lines fitted separately for Hawaiian and ‘mainland’ tropical floras exhibited common slopes for $A_{\text{mass}}-N_{\text{mass}}$ and failed to show a shift in intercept (Table 1). Rather, a shift along a common slope was detected,

with Hawaiian species exhibiting consistently lower values of both A_{mass} and N_{mass} relative to their mainland counterparts (Fig. 2g).

DISCUSSION

The generality of the LES (Wright *et al.*, 2004, 2005a), which predicts commonality of tradeoffs in resource capture between

floras, was tested against alternative predictions generated from biogeographic influences on trait evolution. We found evidence against a globally uniform rate of carbon gain per resource invested (a general LES axis), in favour of a historical alternative, which asserts that isolated lineages can follow different metabolic trajectories based on phylogenetic constraints and contrasting selective pressures. In contrast to previous geographic analyses that acknowledge modest LES trait variation of leaf trait as a function of biome (e.g. Reich *et al.*, 1999; Wright *et al.*, 2004) or climate (e.g. Wright *et al.*, 2005b), we present a novel biogeographic analysis of global leaf trait data that compares regions with known evolutionary histories. This approach sheds light on biogeographic differences that would otherwise be obscured using approaches that implicitly combine multiple floras that may be similar in terms of broad vegetation types or modern climate regimes but, individually, have distinct evolutionary histories.

Apart from the Hawaiian–mainland comparison, all trait relationships explored supported the broad hypothesis that biogeographic influences can result in different leaf trait relationships (Fig. 1, shifts B and C). This was represented by significant differences in the allometric scaling of slope between floristic regions for key leaf-level resource tradeoffs. The associated biological significance of these statistical differences is in need of further exploration. Significant shifts in slope for NH–SH comparisons and shifts in intercept or slope for EAS–ENA comparisons, given no significant differences in climate regimes, indicate the existence of broad-scale differences in plant resource capture strategies (Leishman *et al.*, 2010). These differences were detected despite the inevitable variation in trait measurement procedures and growth conditions between studies represented in the GLOPNET database, and our necessary assumption that a species' current native range accurately reflects evolutionary processes that shaped modern floras as defined by Takhtajan (1986).

What explains deviations from a more general, world-wide LES? We suggest that evolutionary processes operating at the scale of a floristic region – an area of plant diversification that has been isolated from other regions during a large part of its evolutionary history, particularly during the Tertiary (Good, 1974; Takhtajan, 1986) – can either constrain the evolution of metabolic efficiency through a lack of genetic variation, or can slow the adaptive process if competitive intensity is low (Dobzhansky, 1950). For example, the potential for higher carbon assimilation (A_{\max}) at a given respiration rate (R_d) is theoretically constrained by the biophysical requirements of photosynthetic machinery (i.e. more carbon must be invested to allow for greater carbon gain; Lambers *et al.*, 2008). It is largely assumed that selective pressures prevent plants with less efficient leaf functioning from persisting (Reich *et al.*, 1999; Donovan *et al.*, 2011), but this perspective assumes that past evolutionary forces have acted globally, with sufficient selection leading to the past extinction of all plants in floras with unfit trait combinations. We question this assumption, particularly in light of the evolution of metabolic efficiencies of the flora and fauna of oceanic islands, where lower predation and competition pres-

ures have promoted the evolution of a wide variety of plant and animal physiologies that have never evolved on mainlands (Carlquist, 1974; Brown, 1995). By extension, we argue that continental regions that vary in their historical isolation, area, geological history and phylogenetic diversity can exhibit similar variation in floristic trait evolution. Relative to floras of similar environments, plants of a floristic region may theoretically be restricted in their capacity to evolve similarly unconstrained optimal solutions, limiting evolutionary convergence (Cody & Mooney, 1978).

The biogeographic differences in resource capture strategies shown here are in direct contrast to the argument of Tilman (2011), who hypothesized identical tradeoff surfaces for floras world-wide (the 'universal tradeoff hypothesis') based on the historical lack of extinction after biotic interchange. The patterns we report here argue that either the universal trade-off hypothesis is wrong (in favour of the alternative 'biogeographic superiority hypothesis'), or that tradeoffs are sufficiently multivariate so as to preclude testing this hypothesis with bivariate data. Although we cannot exclude this latter possibility with our analysis given the limited trait data currently available, our study is novel in demonstrating incongruent bivariate tradeoff surfaces across different biogeographic regions.

Several case studies provide empirical evidence that highlight regional constraints of phylogeny and floristic-wide evolutionary histories on LES trait relationships. For example, endemic species of the Balearic Islands in the Mediterranean were found to have lower photosynthetic capacity (A_{\max}) at a given leaf mass per area (LMA) than non-endemic species, which may reflect their collapsing geographic ranges (Gulías *et al.*, 2003). Similarly, in comparison to their native competitors, some plant invasion studies that control for habitat, phylogeny and ontogeny have found that invasive species have higher resource use efficiencies than natives (Funk & Vitousek, 2007; Funk, 2008), lower construction costs at a given LMA (Osunkoya *et al.*, 2010) and higher photosynthetic capacity at a given respiratory cost (Pattison *et al.*, 1999). Adding support to these case studies, we have shown differences in the allometric scaling of plant economic traits in large-scale comparisons of entire regional floras of contrasting evolutionary history.

LES differences were particularly evident in the trait scaling between the species of the NH and SH, suggesting a less efficient resource economy of SH floras (Fig. 2a–c). During the break-up of the most recent unified landmass of Pangaea roughly 180 million years ago, two large landmasses were formed: Laurasia in the NH and Gondwanaland in the SH (Lomolino *et al.*, 2010). Upon further break-up, the landmasses of Laurasia were periodically connected through land bridges, allowing for significant biotic interchange. In contrast, vicariance played a more critical role in the floristic development of the landmasses of Gondwanaland (Sanmartín & Ronquist, 2004; Morrone, 2009). With fewer landmass connections and component landmasses of smaller areas, the current SH floras are a product of reduced phylogenetic diversity compared with the flora of the NH (Takhtajan, 1986). We propose that these southern landmasses had less competitive biotic

environments and therefore experienced weaker selection for efficient resource utilization. Differences in plant physiological functioning between these regions have been shown before with respect to particular stresses; for example, SH tree lines generally occur lower in intercept than those in the NH (Körner & Paulsen, 2004) and SH plants exhibit lower frost resistance (Bannister, 2007). We suggest reduced metabolic functioning for SH plants, which continue to evolve largely in isolation from the northern temperate flora (excepting alien invaders), extends to their overall carbon economy.

Slope differences were clear between NH and SH floras, but there appear to be additional differences in the relative locations of the clouds of points illustrating bivariate relationships between groups (Fig. 2a–c). Because slope heterogeneity was detected for all relationships, there was no statistical basis for fitting common slopes to detect a shift along a common axis. However, separate mean values of each variable indicate systematic differences between hemispheres. SH species in the data set had lower mean values of A , R_d , N and higher mean values of LL and LMA. Although we excluded climate biases in the data, the directionality of these differences in mean trait values could be partially explained by the greater preponderance of nutrient-poor soils in the SH sites.

Functional differences observed in EAS and ENA can also be explained with respect to their evolutionary histories (Fig. 2d–f). Although natural ecosystems in both regions are dominated by mesophytic forest communities that were colonized by similar lineages throughout much of the Tertiary (Donoghue & Smith, 2004), large changes in lineage representation since at least the Pleistocene in ENA have led to the development of modern-day floras with deep contrasts in species diversity, phylogenetic diversity and levels of endemism (Qian & Ricklefs, 2000). EAS has roughly twice the number of species as ENA and is represented by 50 more plant families (247 vs. 192; Heywood *et al.*, 2007; including 22 endemic families vs. 1 in ENA; Takhtajan, 1986). Given the historical differences between the two regions, detected differences in leaf physiology (Fig. 2d,e) follow the prediction that regions with more competitive evolutionary histories (i.e. EAS) ultimately lead to greater metabolic efficiencies. The slope differences of the analysed trait relationships in EAS and ENA species are consistent with the recent finding that the most effective natural area invaders in ENA are of EAS origin (Fridley, 2008). The present study suggests that this EAS bias in ENA invasions may be due in part to more effective carbon use strategies by EAS lineages.

In addition to slope differences, y -intercept shifts were found for the EAS–ENA comparison (Fig. 2d,f). When controlling for ecosystem differences, the ecological meaning of a y -intercept difference between floras was not immediately clear. As any allocation differences were presumably not modulated by environmental pressures, this shift between the regions could be due, in part, to the same historical drivers generating slope differences. Consistently greater photosynthetic returns at any given leaf respiration values (Fig. 2d) are consistent with higher metabolic functioning in the EAS flora than that of ENA.

The direction of the shift in intercept for the $A_{\text{mass}}-N_{\text{mass}}$ relationship for EAS–ENA was contrary to our hypothesis of greater metabolic efficiency of EAS species. This difference was not consistent with the $A_{\text{mass}}-R_{\text{d, mass}}$ and LL–LMA patterns for the EAS–ENA contrast (Fig. 2d,e). Whether the discrepancy results from nutrient conditions particular to some of the samples included in the GLOPNET data set, or from floristic differences in nutrient efficiencies that we have not considered, cannot be determined from the present data. In addition, the Hawaiian–mainland analysis for the $A_{\text{mass}}-N_{\text{mass}}$ tradeoff suggests a shift along a common slope, rather than the hypothesized differences in slope or intercept, indicating a common resource axis among floras of Hawaiian, Malesian and tropical mainland regions. This may be indicative of environmental differences between these regions that dominated the expression of trait relationships across floras, as Hawaiian species, having diversified on nutrient-poor volcanic soils (Vitousek *et al.*, 1993), exhibited consistently lower values of both A_{mass} and N_{mass} . Similar findings in shifts along common slopes toward slower returns on leaf economics for key traits were found in a recent study of Hawaiian endemics when contrasted with alien competitors (Peñuelas *et al.*, 2010). However, we note that controlled studies using a common garden approach to trait measurements of Hawaiian native and alien plants reported clear scaling differences in LES trait relationships in the direction of our hypothesis (Baruch & Goldstein, 1999; Pattison *et al.*, 1999; Funk, 2008).

There is broad consensus for a general LES that places constraints on the evolution of plant form and function and underlies the modern development of plant strategy theory (Grime, 1977; Chapin, 1980; Reich *et al.*, 1999, 2003; Wright *et al.*, 2004, 2005a). Although LES studies have stopped short of defining an absolute set of optimal trait relationships, most studies emphasize the global generality of LES patterns (Wright *et al.*, 2005a) and global evolutionary convergence in leaf trait relationships (Reich *et al.*, 1997). In contrast, we assert that deviations from a canonical set of leaf allometric relationships across global floras should be expected given a Darwinian perspective of natural selection operating in isolated regions. Our argument is supported by the present biogeographic analysis of a suite of bivariate trait relationships, which detected significantly different allometries in the scaling of $A_{\text{mass}}-R_{\text{d, mass}}$, LL–LMA and $A_{\text{mass}}-N_{\text{mass}}$ across floristic regions that share common bioclimatic characteristics. We expect such biogeographic differences to be magnified in trait comparisons that control for other types of site variation (e.g. Pattison *et al.*, 1999; Funk, 2008; Osunkoya *et al.*, 2010). Further mechanistic elucidation of the biogeographic signature of plant resource economics will help to refine our understanding of the historical assembly of regional floras and the continuing re-assembly of global floras through modern invasions.

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REFERENCES

- Ackerly, D.D. & Reich, P.B. (1999) Convergence and correlations among leaf size and function in seed plants: a comparative test using independent contrasts. *American Journal of Botany*, **86**, 1272–1281.
- Bannister, P. (2007) A touch of frost? Cold hardiness of plants in the southern hemisphere. *New Zealand Journal of Botany*, **45**, 1–33.
- Baruch, Z. & Goldstein, G. (1999) Leaf construction cost, nutrient concentration, and net CO₂ assimilation of native and invasive species in Hawaii. *Oecologia*, **121**, 183–192.
- Blonder, B., Violle, C., Bentley, L.P. & Enquist, B.J. (2011) Venation networks and the origin of the leaf economics spectrum. *Ecology Letters*, **14**, 91–100.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago, IL.
- Carlquist, S. (1974) *Island biology*. Columbia University Press, New York.
- Chapin, F.S. (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 233–260.
- Cody, M.L. & Mooney, H.A. (1978) Convergence versus non-convergence in Mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics*, **9**, 265–321.
- Dobzhansky, T. (1950) Evolution in the tropics. *American Scientist*, **38**, 209–221.
- Donoghue, M.J. & Smith, S.A. (2004) Patterns in the assembly of temperate forests around the Northern Hemisphere. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 1633–1644.
- Donovan, L.A., Marherali, H., Caruso, C.M., Huber, H. & de Kroon, H. (2011) The evolution of the worldwide economics spectrum. *Trends in Ecology and Evolution*, **26**, 88–95.
- Fridley, J.D. (2008) Of Asian forests and European fields: eastern U.S. plant invasions in a global floristic context. *PLoS ONE*, **3**, e3630.
- Funk, J. (2008) Differences in plasticity between invasive and native plants from a low resource environment. *Journal of Ecology*, **96**, 1162–1173.
- Funk, J. & Vitousek, P. (2007) Resource-use efficiency and plant invasion in low-resource systems. *Nature*, **446**, 1079–1081.
- Good, R. (1974) *The geography of the flowering plants*, 4th edn Longman, London.
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1194.
- Gulías, J., Flexas, J., Mus, M., Cifre, J., Lefi, E. & Medrano, H. (2003) Relationship between maximum leaf photosynthesis, nitrogen content and specific leaf area in Balearic endemic and non-endemic Mediterranean species. *Annals of Botany*, **92**, 215–222.
- Heywood, V.H., Brummitt, R.K., Culham, A. & Seberg, O. (2007) *Flowering plant families of the world*. Firefly Books, Richmond Hill, ON.
- Körner, C. & Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, **31**, 713–732.
- Lambers, H., Chapin, F.S. & Pons, T.L. (2008) *Plant physiological ecology*, 2nd edn, Springer, New York.
- Leishman, M.R., Haslehurst, T., Ares, A. & Baruch, Z. (2007) Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. *New Phytologist*, **176**, 635–643.
- Leishman, M.R., Thomson, V.P. & Cooke, J. (2010) Native and exotic invasive plants have fundamental similar carbon capture strategies. *Journal of Ecology*, **98**, 28–42.
- Lomolino, M.V., Riddle, B.R., Whittaker, R.J. & Brown, J.H. (2010) *Biogeography*, 4th edn, Sinauer Associates, Sunderland, MA.
- MacArthur, R.H. (1972) *Geographical ecology*. Harper & Row Publishers, New York.
- Mack, R.N. (2003) Phylogenetic constraint, absent life forms, and preadapted alien plants: a prescription for biological invasions. *International Journal of Plant Sciences*, **164**, S185–S196.
- Morrone, J.J. (2009) *Evolutionary biogeography: an integrative approach with case studies*. Columbia University Press, New York.
- Ordoñez, J.C., van Bodegom, P.M., Witte, J.M., Wright, I.J., Reich, P.B. & Aerts, R. (2009) A global study of relationships between leaf traits, climate, and soil measures of nutrient fertility. *Global Ecology and Biogeography*, **18**, 137–149.
- Osunkoya, O.O., Bayliss, D., Panetta, F.D. & Vivian-Smith, G. (2010) Leaf trait co-ordination in relation to construction cost, carbon gain and resource-use efficiency in exotic invasive and native woody vine species. *Annals of Botany*, **106**, 371–380.
- Pattison, R.R., Goldstein, G. & Ares, A. (1999) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia*, **117**, 449–459.
- Peñuelas, J., Sardans, J., Llusà, J., Owen, S.M., Carnicer, J., Giambelluca, T.W., Rezende, E.L., Waite, M. & Niinemets, Ü. (2010) Faster returns on ‘leaf economics’ and different biogeochemical niche in invasive compared with native plant species. *Global Change Biology*, **16**, 2171–2185.
- Qian, H. & Ricklefs, R.E. (2000) Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature*, **407**, 180–182.
- R Development Core Team (2010) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From the tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences USA*, **94**, 13730–13734.

- Reich, P.B., Ellsworth, D.S., Walter, M.B., Vose, J.M., Gresham, C., Volin, J.C. & Bowman, W.D. (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80**, 1955–1969.
- Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M. & Walters, M.B. (2003) The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences*, **164**, S143–S164.
- Sanmartín, I. & Ronquist, F. (2004) Southern Hemisphere biogeography inferred by event-based models: plant vs. animal patterns. *Systematic Biology*, **53**, 216–243.
- Shipley, B., Lechowicz, M.J., Wright, I. & Reich, P.B. (2006) Fundamental trade-offs generating the worldwide leaf economics spectrum. *Ecology*, **87**, 535–541.
- Takhtajan, A. (1986) *Floristic regions of the world*. University of California Press, Berkeley, CA.
- Tilman, D. (2011) Diversification, biotic interchange, and the universal trade-off hypothesis. *The American Naturalist*, **178**, 355–371.
- USDA, ARS, National Genetic Resources Program (2010) Germplasm Resources Information Network (GRIN), United States Department of Agriculture, Agricultural Research Service. Available at: <http://www.ars-grin.gov/cgi-bin/npgs/html/paper.pl?language=en> (accessed 24 November 2010).
- Vermeij, G. (2005) Invasion as expectation: a historical fact of life. *Species invasions: insights into ecology, evolution, and biogeography* (ed. by D.F. Sax, S.D. Gaines and J.J. Stachowicz), pp. 315–339. Sinauer Associates, Sunderland, MA.
- Vitousek, P.M., Walker, L.R., Whiteaker, L.D. & Matson, P.A. (1993) Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park. *Biogeochemistry*, **23**, 197–215.
- Walls, R.L. (2011) Angiosperm leaf vein patterns are linked to leaf functions in a global-scale data set. *American Journal of Botany*, **98**, 244–253.
- Warton, D. (2007) *SMATR: (standardized) major axis estimation and testing routines*. [translated to R by Ormerod, J.] R package, version 2.1. Available at: <http://web.maths.unsw.edu.au/~dwarton> (accessed 13 November 2010).
- Warton, D.I., Wright, I.J., Falster, D.S. & Westoby, M. (2006) Bivariate line fitting methods for allometry. *Biological Reviews*, **81**, 259–291.
- Weber, E., Shi-Guo, S. & Li, B. (2008) Invasive alien plants in China: diversity and ecological insights. *Biological Invasions*, **10**, 1411–1429.
- Wright, I.J., Reich, P.B. & Westoby, M. (2001) Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology*, **15**, 423–434.
- Wright, I.J., Reich, P.B., Westoby, M. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Garnier, E., Hikosaka, K., Lamont, B.B., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D.I. & Westoby, M. (2005a) Assessing the generality of global leaf trait relationships. *New Phytologist*, **166**, 485–496.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Warton, D.I. & Westoby, M. (2005b) Modulations of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography*, **14**, 411–421.

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Appendix S1 List of species and floristic region assignments.

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