Global leaf trait estimates biased due to plasticity in the shade

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The study of leaf functional trait relationships, the so-called leaf economics spectrum[1,2], is based on the assumption of high-light conditions (as experienced by sunlit leaves). Owing to the exponential decrease of light availability through canopies, however, the vast majority of the world's vegetation exists in at least partial shade. Plant functional traits vary in direct dependence of light availability[3], with different traits varying to different degrees, sometimes in conflict with expectations from the economic spectrum[3]. This means that the derived trait relationships of the global leaf economic spectrum are probably dependent on the extent to which observed data in existing large-scale plant databases represent high-light conditions. Here, using an extensive worldwide database of within-canopy gradients of key physiological, structural and chemical traits[3], along with three different global trait databases[4,5], we show that: (1) accounting for light-driven trait plasticity can reveal novel trait relationships, particularly for highly plastic traits (for example, the relationship between net assimilation rate per area (A_a) and leaf mass per area (LMA)); and (2) a large proportion of leaf traits in current global plant databases reported as measured in full sun were probably measured in the shade. The results show that even though the majority of leaves exist in the shade, along with a large proportion of observations, our current understanding is too focused on conditions in the sun.

Leaf structural, chemical and physiological traits are key characteristics of plant function[2,6,7], and form part of a coupled whole plant economic spectrum that encapsulates evolutionary histories, competitive strategies and acclimation to resource constraints[1,2]. The spectrum describes the return on investments of nutrients and carbon[2], and as such plays an important role in our understanding of whole ecosystem structure, function and potential responses to climate change. Recent efforts have thus used observations from global databases of leaf traits to improve global models of ecosystem function and distribution[8,9], moving from the strict characterization of vegetation in plant functional types to a more continuous plant trait field approach.

The consideration of observed trait variation along major axes of a continuous spectrum has shed much light on the ecological tradeoffs running from a slow to a quick return of investments in nutrients and dry mass[1,2]. One major issue with this approach, however, is that the leaf economic spectrum is defined for high-light conditions[2]. Although almost all species can grow under full light, many species are better adapted to the shade. Plant functional types also differ in their capacity to reach full-sun conditions at the top of the canopy (e.g. herbs versus trees). Even in relatively open canopies, light gradients are typically as large as 10- to 20-fold[10–12]. In fact, due to the exponential decrease of light availability with increasing leaf area, much of global vegetation grows in at least partially shaded conditions.

Key leaf traits are highly sensitive to integrated light during development[3,13–17]. For instance, LMA, photosynthetic capacity per area (A_a) and leaf nitrogen content per leaf area (N_a) demonstrate high light-driven plasticity, whereas others such as leaf nitrogen content per leaf dry mass (N_m) and photosynthetic capacity per leaf dry mass (A_m) often vary less[3]. Large differences also exist in plasticity among plant functional types. For example, in the fast return end of the economics spectrum, in herbs, N_m and A_m vary more than LMA, whereas the opposite is true in the low return end of the economics spectrum[3]. Light-driven trait plasticity could therefore alter trait scaling in both the slow and the fast return ends of the economics spectrum.

The existence of light-driven plasticity, large light gradients and species with a preference for shade, along with difficulties in sampling from top-of-canopy positions for some ecosystems, suggest that a proportion of observations in current trait databases were obtained from leaves that developed in shaded conditions. As low-light conditions lead to lower trait values for particularly plastic traits[3], the presence of samples from shaded leaves in global trait databases would lead to an underestimation of full-sun trait values, particularly for highly plastic traits such as A_a. Light-driven trait plasticity could also importantly alter the derived scaling slopes among key leaf traits and the strength of statistical relationships.

Despite the large influence of light on leaf traits with high light-driven plasticity, the effect of light-driven trait plasticity has yet to be considered in the leaf economics spectrum. It is also unclear to what extent existing large-scale vegetation plant databases used for developing the leaf economics spectrum[2], parameterizing land surface models[8,9] and in comparisons to remote sensing approaches[18,19] actually include specimens sampled at low light. In this study we examine these issues using a light-standardized canopy trait plasticity (CANTRIP[3,20]) database of leaf structural, chemical and physiological traits[3], along with a combined dataset consisting of three previously published global leaf trait databases (the Poorter[4], Niinemets[5] and Glopnet[2] databases, henceforth the PNG dataset, see Methods) that do not account for the effect of light-driven trait plasticity[2,4,5]. We use the combined datasets to examine the effect of low light during development (i.e. shading) on reported trait values, estimate the prevalence of traits measured in shaded environments in the global databases and quantify the effect of light-driven trait plasticity on the global leaf economics spectrum.

Trait values were significantly lower when the sampled leaves developed under lower-light conditions (Fig. 1). This was particularly true for the area-based traits, N_a and A_a, and LMA, where light-driven trait plasticity resulted in a roughly 60% reduction in trait values for a 90% reduction in light level, compared to values under full-sun conditions (Fig. 1). The effect of shading was consistent from the fast to the slow return ends of the leaf economic spectrum. The same was not true for the mass-based traits, where shading had a small effect on both N_m and A_m (Fig. 1). Overall, species level traits in the PNG dataset consistently under-predicted
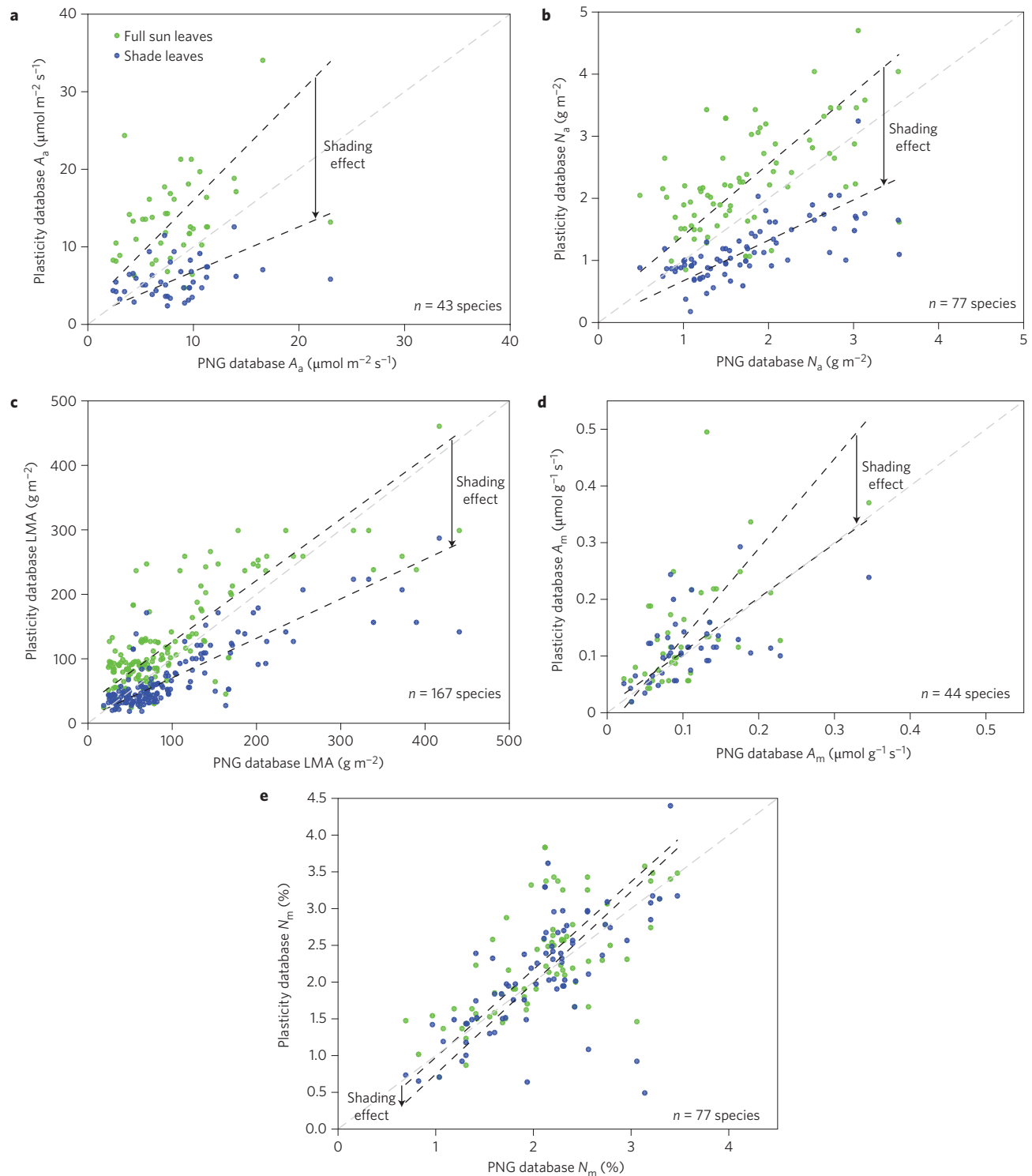
Figure 1 | Comparison of trait values from different databases. A comparison of trait values for full-sun (green) and shaded (blue) leaves from the CANTRIP plasticity database with values from three published datasets (the combined PNG dataset) of leaf mass per area (LMA), net assimilation rate (A) and nitrogen content (N) on both a mass (m) and area (a) basis. The CANTRIP database values account for the effect of within-canopy changes in integrated light.

the corresponding full-sun trait values in the plasticity database (Fig. 1). The under-prediction was strongest for the area-based traits A_a and N_a, and for LMA at the faster return end of the leaf economic spectrum.

We used the species and trait specific plasticity gradients to calculate the extent of shading that would be required to explain the observed difference between the trait values in the plasticity database and those in the PNG datasets. The difference between the two datasets suggests a large contribution of traits from shaded leaves (Fig. 2). The largest effect of the presence of trait values sampled from shaded leaves was evident in values of A_a across plant functional types (PFTs), which also showed a large underestimation of high-light trait values in the PNG dataset and strong light-driven trait plasticity in the plasticity database
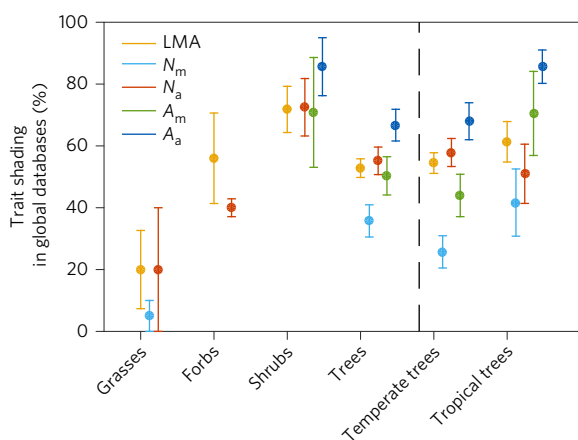
Figure 2 | The effective shading by trait and plant functional type. The extent of shading in existent trait databases is estimated using light-driven trait plasticity on a per-species basis to scale reported trait values in the PNG dataset to full-light conditions. Shading is quantified as the percentage reduction in the effective Q_{int} from full-sun values in the CANTRIP plasticity database to the corresponding species trait values in the PNG dataset. Values presented represent the mean (±1 s.e.m.) across all species in a PFT for each trait.

(Fig. 1). On the contrary, N_m represented the lowest degree of shading (Fig. 2), with the lowest underestimation in the PNG datasets and the lowest light-driven trait plasticity in the plasticity database (Fig. 1). The proportion of trait shading in global databases was different for different PFTs, with grasses, which largely grow in full-sun conditions and have easily accessible canopies, showing the smallest contribution from shade leaf trait values. Shrubs showed the highest proportion of shade leaf trait values, followed by trees and forbs. For trees, tropical canopies showed a consistently higher proportion of leaf traits measured in the shade than did temperate trees (Fig. 2), perhaps owing to the difficult-to-access complex canopies and strong light gradients tropical forests typically exhibit.

The consideration of light-driven trait plasticity altered both the strength and nature of the derived relationships along the leaf economics spectrum (Fig. 3). For A_a, in particular, which shows strong light-driven plasticity within canopies, the slope of the relationship with LMA was positive (at $p = 0.15$) for the PNG dataset, which contains a mix of both high- and low-light leaf samples, but was negative ($p < 0.01$) when only high-light trait values in the plasticity database were considered. The lack of a strong relationship between LMA and A_a in global databases has been previously reported[2]. Here we show that accounting for trait plasticity can reveal significant trait tradeoffs when the influence of shading on trait values is removed.

Light-driven trait plasticity has a large effect on trait values through vegetation canopies, with trait plasticities dependent on plant functional type and driven by plant functional type dependent combinations of plasticities in different underlying traits. For example, light-dependent plasticity in A_a is highly conserved across functional types, but is associated with different combinations of plasticities in underlying traits in different plant functional types[3]. For woody species, large light-dependent changes in LMA are responsible for the observed changes in A_a, whereas in herbaceous species changes in A_a are dependent on light-driven changes in N_m and nitrogen use efficiency[3]. This complex interplay of functional type independent plasticities associated with functional type dependent plasticities in underlying traits can potentially change the nature and strength of functional relationships between traits characterized by the leaf economic spectrum.

Comparisons of full-sun traits estimated for the plasticity database, which directly accounts for the effect of light-driven trait plasticity, to three existing datasets that do not directly account for shading[2,4,5] suggests that a large proportion of traits in those datasets correspond to shaded conditions. Our results show that this is associated with a large underestimation of key trait high-light values, which can alter derived trait relationships (Fig. 3). The underestimation is larger for those traits with high light-driven plasticity, such as A_a. The results emphasize that a proper accounting of the integrated light load of sampled leaves is necessary to better understand leaf functional relationships both across species and within canopies.

Leaf trait acclimation to integrated light has been reported to stabilize about 30–60 days after leaf formation in both woody and herbaceous canopies[21,22], but age-dependent modifications are possible for some plant growth forms[23] and such modifications can further alter the correlative relationships within the leaf economics spectrum[24]. In particular, in evergreen woody species, M_a and N_a plasticity has been reported to decrease with increasing leaf age, with limited changes in A_a plasticity[23]. In forbs, N_a plasticity increased, whereas in grasses, N_a plasticity decreased with increasing leaf age, potentially reflecting life form differences in age-dependent changes in light availability. Unfortunately, there are very few studies that use replicate sampling when reporting age effects[23], which makes it difficult to distinguish between exceptional and characteristic responses, and this thus limits the generality of the conclusions that can be drawn. In addition, only a few studies have looked at a suite of relevant functional traits simultaneously, which complicates inference about the structural, chemical and physiological coordination of canopy functioning due to age-driven changes in plasticity. Although a full characterization of age-driven trait plasticity remains elusive[23], current evidence suggests that both light and age effects should be considered in the analysis of leaf trait values.

The presence of shade leaf trait values in global trait databases is in some cases unavoidable, as many species preferentially grow in the shade or are infrequently found in full sun. Light penetration through canopies declines exponentially, following Beer's Law, which implies that the majority of Earth's leaf area exists in at least partial shade. In addition, field campaigns focused on leaf traits often have difficulty sampling from full-sun conditions. In many instances such sampling requires canopy cranes or other means of access to the top of the canopy that are not feasible in remote locations, dense vegetation or canopies with complex architecture[25]. In such cases a shotgun is sometimes used (for example, ref. 26) to sample upper canopy leaves, although this is problematic when photosynthesis measurements need to be taken because disruption to water flow can lead to irreversible cavitation of the sampled branches. Although the logistical difficulties provide real problems, the outcome of sampling difficulties is that existing global datasets have a mix of leaves from full-sun and shaded conditions. We argue that the frequent statement in studies of leaf functional trait relationships that leaves were collected in full-sun conditions is, more often than not, flawed.

Recent reports have questioned the use of mass normalized traits in the examination of the leaf economic spectrum[27,28], suggesting that the normalization of area proportional traits by mass induces strong correlations due to large inter-species variation in LMA. Such criticisms have been defended on the basis that mass normalized traits are an equivalently logical basis of expression as area-based traits, and that LMA is often not the dominant source of between-species variability[29,30]. In a recent analysis, Niinemets et al.[3] showed that concerns regarding the mass normalization of traits were not relevant within the context of light acclimation of photosynthetic traits due to the existence of a spectrum of trait responses to within-canopy light gradients within the leaf
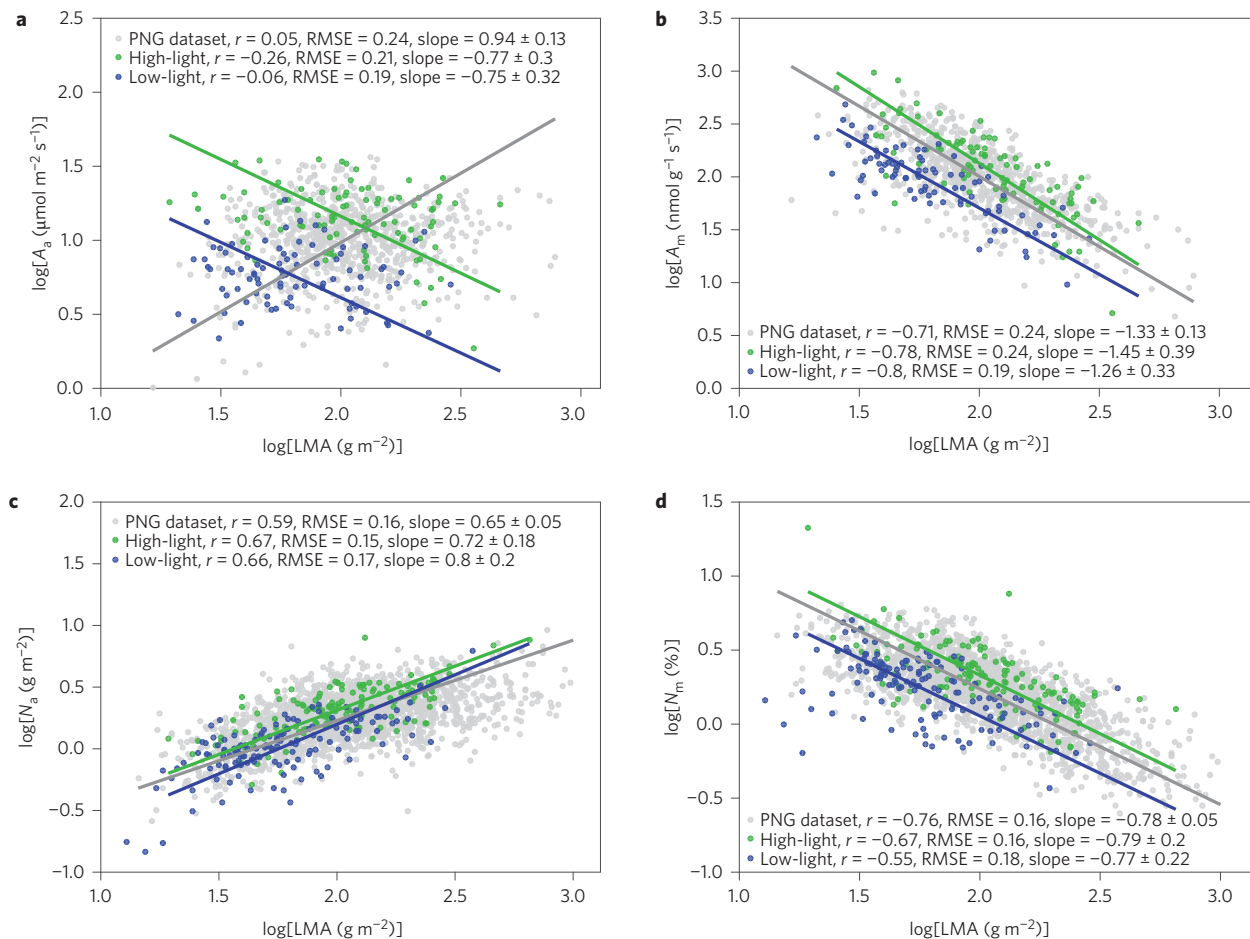
Figure 3 | The effect of plasticity on the leaf economic spectrum. Relationships between LMA and A and N on both a mass (m) and area (a) basis, for high-light (green, 40 mol m^{-2} d^{-1}) and low-light (blue, 3 mol m^{-2} d^{-1}) traits from the CANTRIP plasticity database, along with trait values from the PNG dataset (grey dots), all on a log$_{10}$ scale. Coloured lines represent reduced major axis regressions. All correlations (r) are significant at $p < 0.01$, with the exception of the LMA ~ A_a relationships for both the PNG dataset ($p = 0.15$) and low-light traits ($p = 0.56$); RMSE, root-mean-square error. For non-transformed relationships see Supplementary Fig. 3.

economic spectrum. Within-canopy acclimation results from different combinations of traits varying through plant canopies in different plant functional types, both at the fast and the slow return end of the spectrum[3]. We examine the impact of shading on both area- and mass-based traits, and find greater plasticity (Fig. 1), and thus a greater effect on leaf functional trait relationships (Fig. 2), for area-based traits. It should be noted that the relatively large light-driven plasticity of A_a may explain the weaker published A_a relationships in the leaf economic spectrum[2]. We show that area-based trait relationships are stronger when accounting for light-driven plasticity (Fig. 3).

Although trait databases on occasion record sampled leaves as originating from either full-sun or shaded conditions, such dichotomous categories of 'sun' and (in particular) 'shade' are highly ambiguous. In reality, leaves experience strong light gradients within a canopy[3], across gap-understory continua[4,31] and with changes to light availability during their development[22]. The extent of light-driven trait plasticity necessitates a more detailed reporting of the daily average leaf-incident integrated photosynthetically active quantum flux density during leaf development. Recent developments in terrestrial laser scanning (e.g. ref. 32) along with radiative transfer modelling[33] offer promising paths forward. Properly accounting for plasticity in studies of leaf functional trait relationships is necessary to improve our understanding of trait variation and the nature of economic tradeoffs within the whole plant economic spectrum[1].

Methods

We used four different datasets in our analysis: a global database of canopy trait plasticity (CANTRIP)[3,20] and three published datasets of global trait variation[2,4,5]. We focused on the five key traits most commonly reported across datasets: leaf mass per area (LMA), the light saturated assimilation rate and nitrogen concentration on both a mass (A_m, N_m) and an area (A_a, N_a) basis.

Worldwide database of within-canopy plasticity in leaf traits. The worldwide CANTRIP[3,20] database is comprised of foliage structural, chemical and physiological traits that play an important role in photosynthetic acclimation within vegetation canopies[3]. The data stems from an extensive literature survey of studies that included within-canopy variation for at least three different canopy positions for over 800 different canopies. All studies included explicit measurements of within-canopy light conditions or cumulative leaf area. Particular emphasis was made to standardize estimates of average incident integrated light available during growth for all leaves, in recognition of the strong effect of large gradients of within-canopy light regimes on plant functional traits. The daily average incident integrated photosynthetically active quantum flux density on a horizontal surface during leaf development was used as an estimate of leaf integrated light conditions (Q_{int}). Q_{int} was averaged for the 50 days after the start of leaf development, or for the actual number of days since the start of leaf development for leaves younger than 50 days or for leaves with an average life span of less than 50 days. This approach is motivated by reports that foliage trait acclimation to integrated light stabilizes about 30–60 days after leaf formation in both woody and herbaceous canopies[21,22].

The full database includes 831 measured within-canopy gradients for 304 species, covering most canopy forming vascular plant functional types. Here we focus on LMA (g m^{-2}, 532 gradients), N_m (%, 374 gradients), A_m (nmol g^{-1} s^{-1}, 242 gradients), N_a (g m^{-2}, 535 gradients) and A_a (μmol m^{-2} s^{-1}, 411 gradients). All traits, particularly those on an area basis, were characterized by strong

light-dependent within-canopy variations. See Supplementary Information Fig. S1 for the distribution of sites used, and Niinemets et al.[3] for a more detailed description of the methods used and the characteristics of the database.

The observed trait plasticity gradients were used to calculate species-level trait values at multiple Q_{int} levels, for comparison with published trait values in existing datasets (see below). For the examination of the effect of light-driven trait plasticity on the leaf economics spectrum, we used values at both at high light (i.e. full sun, $Q_{int} = 40$ mol m^{-2} d^{-1}) and low light (i.e. shade $Q_{int} = 3$ mol m^{-2} d^{-1}) conditions. A standard value for full-sun Q_{int} is required to harmonize across trait measurements. We chose 40 mol m^{-2} d^{-1} for full-sun Q_{int} based on the distribution of full-sun PPFD during leaf development for trait values in the plasticity database (Supplementary Fig. S2). Given that in closed plant canopies light availability at the bottom leaves is typically 1–5 mol m^{-2} d^{-1} [3,17,34], we chose a moderately conservative value of 3 mol m^{-2} d^{-1} to represent the lower end of the light range. Equivalent analyses at higher light levels of 6 mol m^{-2} d^{-1} and 12 mol m^{-2} d^{-1} (corresponding to medium forest canopy gaps of approximately 30 m diameter[35]) are presented in the Supplementary Information (Figs S4, S5, S6, S7). We do not control for the effects of leaf age on trait values, but the majority of leaves sampled (82%) were less than one year old, with 49% of leaves being 4 months old or less. Per-species canopy gradients of each trait were used to estimate the degree of shading that would be required to explain the difference between full-sun trait values and values published in the global datasets described below. The CANTRIP database is publicly available from the GitHub digital repository (https://github.com/trevorkeenan/traitPlasticity)[20], and will be updated as more data becomes available.

Previously published trait values. To test the effect of light-driven plasticity on trait functional relationships, and the extent in existing datasets, we combined three global trait databases for comparison to the trait values in the plasticity dataset. Datasets used include the global Glopnet database[2], which comprises trait values for 1978 species, the Niinemets et al.[5] database, which comprises trait values for 597 species, and the Poorter et al.[4] database, containing trait values for 587 unique species. We refer to this combined dataset as the Poorter, Niinemets, Glopnet (PNG) dataset. The combined PNG dataset comprises observations from all vegetated continents, and represents a wide range of vegetation types, from arctic tundra to tropical rainforest, including temperate and boreal forests, grasslands and deserts. Site elevation ranges from below sea level to over 5,000 m, mean annual temperature ranges from −16.5 to 27.5 °C and mean annual rainfall ranges from 133 to 5,300 mm per year. Comparison of PNG trait values to those in the CANTRIP[3,20] plasticity database was performed on a per-species basis. Note that observations for all traits were not available for all species in the PNG dataset. The number of common species observations varied by trait, with 167 species with LMA measurements, 77 species with N_m and N_a measurements, and 44 species with A_m and A_a measurements.

We estimated the proportion of trait values that were measured in the shade in the PNG dataset by examining the difference between the full-sun trait values in the plasticity dataset and the corresponding species' trait values reported in the PNG dataset. We used the plasticity gradient for each species in the plasticity dataset to estimate the effective value of integrated light (EQ_{int}) that corresponds to the mean PNG value for that species. EQ_{int} could be interpreted as the mean Q_{int} at which a particular species is measured on average in the PNG dataset. We report effective shading as the percentage reduction from full-sun Q_{int} to the species and trait specific EQ_{int} corresponding to the trait values in the PNG dataset.

Data availability. The Canopy Trait Plasticity (CANTRIP) database presented in this manuscript is publicly available from the GitHub digital repository (https://github.com/trevorkeenan/traitPlasticity)[20].

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Author contributions

T.F.K. and Ü.N. conceived the analysis. T.F.K. performed the analysis and both authors participated in drafting the manuscript.

Additional information

Supplementary information is available for this paper.

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Competing interests

The authors declare no competing financial interests.