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Functional composition of the Amazonian tree flora and forests

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Plants cope with the environment by displaying large phenotypic variation. Two spectra of global plant form and function have been identified: a size spectrum from small to tall species with increasing stem tissue density, leaf size, and seed mass; a leaf economics spectrum reflecting slow to fast returns on investments in leaf nutrients and carbon. When species assemble to communities it is assumed that these spectra are filtered by the environment to produce community level functional composition. It is unknown what are the main drivers for community functional composition in a large area such as Amazonia. We use 13 functional traits, including wood density, seed mass, leaf characteristics, breeding system, nectar production, fruit type, and root characteristics of 812 tree genera (5211 species), and find that they describe two main axes found at the global scale. At community level, the first axis captures not only the 'fast-slow spectrum', but also most size-related traits. Climate and disturbance explain a minor part of this variance compared to soil fertility. Forests on poor soils differ largely in terms of trait values from those on rich soils. Trait composition and soil fertility exert a strong influence on forest functioning: biomass and relative biomass production.

One way of explaining how plants cope with environmental conditions, and how they coexist, is to investigate their morphological, reproductive, physiological and phenological traits. Although derived from species characteristics, traits are defined, based on a tested or an assumed role they play on plant growth, survival and reproduction. In reality, no species can have traits to be competitive in every environment as most adaptations also come at a cost, causing trade-offs, i.e., the value of one trait cannot increase without the decrease of that of another. One example is the number of seeds a plant can produce. For a given amount of energy, a plant can make many small seeds but much fewer big seeds, known as the seed size - seed number tradeoff[1]. Another well-known trade-off, the "*worldwide leaf economics spectrum*"[2,3] captures various leaf traits, running "*from quick to slow return on investments of nutrients and dry mass in leaves, and operates largely independently of growth form, plant functional type or biome*"[2]. A similar worldwide spectrum has been described for wood traits[4] and more recently for roots[5].

The leaf-economics spectrum[2] is tightly related to resource capture and use[3,6]. Species that are specialised for resource rich environments, such as fertile soils, generally possess a high specific leaf area (SLA) which increases light capture per unit leaf biomass, and high phosphorus (P) and nitrogen (N) concentrations which increases metabolic rates, photosynthetic capacity, carbon gain and growth[2,7–9]. In contrast, species that are specialised for resource poor environments, such as infertile soils, produce thick, dense, and structurally well-defended leaves. Additionally, they have high leaf carbon concentrations and C:N ratios reflecting investments in structural and chemical defences such as lignin, tannins and soluble phenolics[10]. In combination, these traits increase leaf lifespan and nutrient conservation, while enhancing the length of the photosynthetic revenue from leaves[2,3]. Hence, in wet forests on infertile soils an evergreen leaf habit is important for nutrient conservation.

Another aboveground spectrum, known as the stature−recruitment trade-off, runs from small to tall species with increasing stem tissue density, leaf size, and seed mass[3,6,11–13]. Wood density relates to biomechanical resistance against biophysical hazards such as wind and pathogens, and can relate to increased resistance to drought-induced embolism[14]. Therefore wood density enhances a tree species' lifespan[4], and is a conservative trait that is beneficial on infertile soils, as it increases the biomass residence time[15]. Wood density has been shown to increase towards the northeast in Amazonia, presumably linked to poor soils[16,17]. Seed mass is a key functional trait that influences a plant's ecological strategy, dispersal, and establishment success[16] and decreases with soil fertility. Large seeds contain more carbohydrate and nutrient reserves, and produce larger, more robust seedlings which enhances seedling establishment and survival in low resource environments (such as nutrient-poor soils and the shaded wet forest understory)[16,18–21]. Seeds with a low mass (i.e. small seeds) often have wind-, bird- or bat-based dispersal, an ability to colonise larger areas, but lower success in individual seedling establishment[22,23], unless frequent disturbances make light available. As with wood density, seed mass has been shown to be much higher in eastern than western Amazonia[16].

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More recently a below ground economics spectrum was described, with two dimensions based on six fine root traits: a collaboration gradient running from a do-it-yourself strategy for acquiring resources to an outsourcing one relying on fungi, and a conservation gradient opposing fast-slow fine roots[5]. We have no root morphological data for the vast number of species in Amazonia but do have information on three important root traits (mycorrhiza, nitrogen-fixation, and aluminium accumulation). Most plant species are associated with vesicular arbuscular mycorrhiza[5,24], and distributed quite evenly across what was called the root economic space[5], while species associated with ectomycorrhiza were more found in the non-collaborative space[5]. Ectomycorrhizae (EM) are important for mono-dominant forests on very poor soils in Central Africa[25] and in Guyana[26–28] but are otherwise very rare in Amazonia[24,29]. Nitrogen fixation is thought to be an important trait on nutrient poor soils. However, earlier work has shown that non-nitrogen fixing 'caesalpinioid' Fabaceae dominate poor, acidic soil regions in Amazonia[16,29], perhaps because of a lack of trace elements necessary for nodulation. An additional reason might be that symbiotic nitrogen fixers prefer non-acidic, somewhat drier soils[24] and early successional forests[30,31], rather than shaded old growth forest because of the high energy requirements to maintain the rhizobial symbiotic bacteria. Aluminium accumulation occurs in only 18 tree families[32]. Some plant species accumulate aluminium that enters their roots into their leaves on soils with high aluminium content, to protect the toxic effect of aluminium on root tips. Aluminium accumulation is restricted to a number of families[33–35]. Aluminium accumulators are found mainly on aluminium rich soils, such as those of the Cerrado in Brazil[36,37] but no information is yet available on the distribution of aluminium accumulation in Amazonia.

At species level the leaf economics spectrum produces trade-offs as well: that of plant species being either slow growing and shade tolerant or fast growing but light demanding[38–41]. A similar trade-off is found among species growing on nutrient rich or nutrient poor soils[42,43]. In both cases an increasingly limiting resource (light, nutrients) leads to the need for conserving plant tissues, as they cannot easily be replaced under strongly limiting conditions. Thus, under favourable conditions, plants will show traits that allow them to grow fast at the cost of being less defended. Their fast growth, however, allows them to compensate for loss of their tissue to herbivores[44–46]. The slow/fast division in plant strategies has been observed much earlier and led to the much-used pioneer-climax tree division, with pioneers having cheap, large, thin, short-lived leaves, soft wood, small seeds, subsequent fast growth in high light but high mortality in shade. Climax species tend to have thick long-lived leaves, hard wood, slow growth but superior survival under shaded conditions[47,48]. Thus, "*species with large seeds, long-lived leaves, or dense wood have slow life histories, with mean fitness (i.e., population growth rates) more strongly influenced by survival than by growth or fecundity, compared with fast life history species with small seeds, short-lived leaves, or soft wood*"[49]. The link between the leaf economic spectrum and wood economic spectrum, however, is not that clear[4], and in a large study with 668 neotropical tree species and 16 leaf and wood traits it was shown that the traits of leaf-economic spectrum and those of the wood-economic spectrum were orthogonal rather than correlated. This suggests that the "*trade-offs operate independently at the leaf and at the stem levels*"[50], which is consistent across Amazonia[51].

Recently information became available on breeding systems of Amazonian trees and the production of nectar producing taxa world-wide[52]. We added these traits to our list to investigate their relationship with the above traits. While there is strong support for the leaf-economic-spectrum and stature-recruitment trade-off, it is less clear if different vegetative organs (leaf, stem and roots), reproductive strategies (breeding system, fleshy fruits, seed size), and symbioses (nitrogen fixing bacteria, mycorrhizae) align along these two main identified spectra (leaf-economic-spectrum and stature-recruitment trade-off) or represent independent, novel axes of strategy variation, thereby expanding the opportunities for niche differentiation and species coexistence.

Because plant species assemble to make up local communities, it is often assumed that these strategy spectra at the species level are filtered and translated into community-level functional composition[53,54]. However, in spite of ongoing studies, it remains unclear whether this is the case for different tropical forests and how this translates into ecosystem functioning (carbon storage and sequestration) at the regional scale, which at the smaller scale is known to be affected by soil fertility and forest dynamics[55]. Addressing these questions is especially critical for tropical ecosystems, as they provide by far the majority of the planet's species diversity and terrestrial ecosystem function[56].

Here, we investigate the relationship between 13 tree functional traits from 812 Amazonian tree genera, including above- and below-ground traits, and reproductive traits for the world's largest and most diverse tropical forest. We scale up from genus to community level across the entire Amazon region by calculating community-weighted mean (CWM) trait data for over 2000 tree-inventory plots in seven forest/soil combinations, mapping each trait and the result of the main strategy axis. We investigate potential drivers (climate, soil) of community trait values, and assess the implications of community trait values for forest functioning in terms of carbon storage and sequestration. We also test how life-histories, such as short-lived or (early) pioneers, long-lived pioneers, and old growth species – often used in models[12], and one life-history characteristic (observed maximum diameter) are related to the strategy axes of both genus-level and community-level analyses. Because it was recently shown that pre-Colombian people left a lasting imprint in some Amazonian forests[57–59], we also included information on the abundance of domesticated species[60] and the probability of finding evidence of human occupation (geoglyphs = human constructed earth works)[58] as factors potentially affecting forest traits composition and function.

Our main research questions are: (1) What plant-strategy spectra are found among Amazonian tree genera? (2) Are community-level strategy spectra similar to genus-level strategy spectra? (3) What are the main spatial gradients in functional composition across Amazonian forest types, and how does this relate to climate, large-scale disturbance, soil, and pre-Columbian human legacies? (4) How does community functional composition affect carbon storage and carbon sequestration?

If ecological filters are not modifying the relationships between traits from genera to communities, we may expect similar trait spectra at the genus and community levels. If the wood and leaf economic spectra, uncoupled at species level[50,51], react to soil fertility across Amazonia in a similar way, we expect convergence among traits within communities[9,61], and divergence among traits between communities driven by local and regional differences in soil[62]. We expect forest communities with, on average, slow traits to have high community mean wood density[16,17] but the relationship with forest productivity is less clear[55,63].

See Supplementary Box 1 for a description of the traits used and a discussion on their importance for tree ecology.

Results

Traits at genus level

To understand what plant-strategy spectra are found among Amazonian tree genera (question one), we started by identifying plant strategies at genus level. A principal component analysis was carried out on a dataset from all 2253 plots (Supplementary Fig. 1), including all 13 traits, using only the 535 genera with data for all traits, representing 90.8% of all individuals. Four leaf traits (N, P, SLA, C:N, Fig. 1, Table 1) were strongly related with Principal component 1 (PC1, Eigenvalue = 2.98), which explains 22.97% of variance in the data (Supplementary Table 1a). PC1 therefore represents the 'leaf economics spectrum' (LES) running from 'fast' productive leaves with high SLA and leaf nutrient concentrations to the left, to 'slow' well-defended leaves with high C:N to the right. Traits related to tree size and reproduction were mostly related to PC2 (Eigenvalue = 1.75), which explains 13.52% of the variance in the data and represents the "stature−recruitment trade-off', running from small species with fleshy fruits (FF) at the bottom to large species with somewhat large maximum diameter (Max), high seed mass (SM), high wood density (WD), a hermaphroditic breeding system (Her), and nectar (Supplementary Box 1). Life-history classification was based on

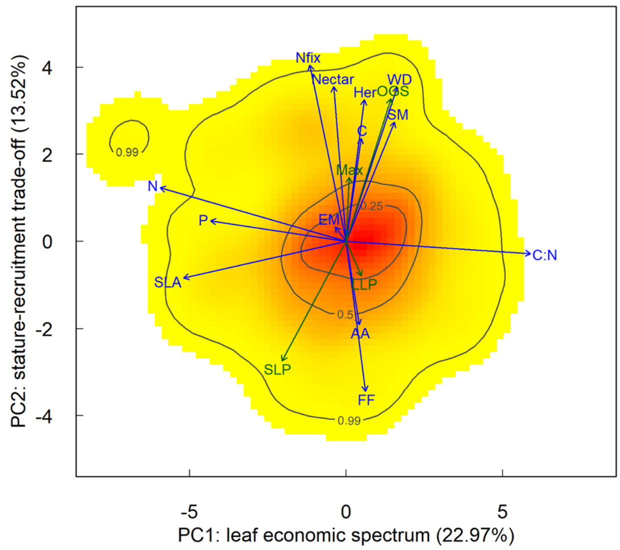

Fig. 1 | Trait space of 353 Amazonian tree genera on 2253 plots with genus level identification. Only genera with complete trait data were used (353 genera, of the 812 in our plots). PC1 has an Eigenvalue of 2.98 and represents the leaf economic spectrum (SLA, N, P, C:N). PC2 (Eigenvalue 1.62) represents the stature-recruitment trade-off (WD, SM) and is strongly linked to short lived pioneers (SLP, negatively) and old-growth species and maximum diameter (OGS, Max, positively). **Legend:** Colours indicate the probability of trait combinations in the trait space defined by the PCA (red = high probability; yellow = low probability). Contour lines indicate 0.99, 0.50, and 0.25 quantiles of the probability distribution. N leaf nitrogen concentration, C:N ratio of leaf carbon to leaf nitrogen, SLA specific leaf area, SM seed mass, P leaf phosphorus concentration, AA aluminium accumulation, Nfix atmospheric N-fixation, WD wood density (overlapping with OGS), C leaf carbon content, FF fleshy fruit, EM ectomycorrhiza, Her hermaphroditic, Nectar nectar producing. Life histories (dark green): OGS old-growth species, LLP long-lived pioneer, SLP short-lived pioneer[64]; Max, maximum diameter[165]. For description of the traits and units, see Supplementary box 1.

Table 1 | Percentage of variance explained for each trait for Amazonia

trait	PC1	PC2	PC3	R^2	p	type
N	0.824	0.019	0.004	0.847	0.001	LES
C:N	0.791	0.003	0.000	0.795	0.001	LES
SLA	0.630	0.010	0.010	0.650	0.001	LES
SM	0.091	0.160	0.382	0.634	0.001	SR/DIS
P	0.452	0.000	0.066	0.519	0.001	LES
AA	0.003	0.080	0.353	0.437	0.001	R
Nfix	0.048	0.366	0.007	0.422	0.001	R
Her	0.014	0.230	0.152	0.396	0.001	BR
FF	0.009	0.263	0.123	0.394	0.001	DIS
WD	0.101	0.260	0.018	0.379	0.001	SR
C	0.001	0.092	0.248	0.341	0.001	LES
Nectar	0.007	0.269	0.038	0.314	0.001	BR
EM	0.008	0.000	0.016	0.024	0.464	R

Traits are ordered in proportion to variance explained. *N* leaf Nitrogen concentration, *C:N* ratio of leaf carbon to leaf nitrogen, *SLA* specific leaf area, *SM* seed mass, *P* leaf phosphorus concentration, *AA* aluminium accumulation, *Nfix* atmospheric N-fixation, *Her* hermaphroditism, *FF* fleshy fruit, *WD* wood density, *C* leaf carbon concentration, *Nectar* nectar producing, *EM* ectomycorrhiza. For units see Supplementary Box 1. R^2 proportion of variance explained by trait; *p* significance level. Type: the spectrum or process the trait is important to: LES leaf economic spectrum, SR stature recruitment trade-off, *R* roots, mycorrhiza, N-fixing and Al-accumulation, *BR* breeding system, *DIS* trait important for dispersal.

seed mass and wood density[29,64]. Life histories were therefore closely linked with the stature-recruitment trade-off, being defined by three strategies, as follows: short-lived pioneers (SLP) with small seeds and soft wood occupying the small side, and old growth species (OGS) with large seeds and dense wood occupying the tall side of the spectrum. Long lived pioneers (LLP) are intermediate with light wood and relatively large seeds (Fig. 1, Supplementary Table 1c, Supplementary Fig. 2). Total functional richness was 87.7, SLP and LLP had partial functional richness of 71.6 and 69.1 respectively (Supplementary Fig. 2), while OGS had a partial functional richness of 60.6. We separately tested the contribution of Fabaceae, the most abundant and species-rich family in Amazonia (16% of all species and individuals). Fabaceae has remarkably high functional richness for a single family (60), compared to all other families combined (68.5; Supplementary Fig. 2). Fabaceae occupies the top of the trait space (Supplementary Fig. 2); it is almost entirely hermaphroditic (Her; 757 of 814 species), contains all Amazonian nitrogen-fixing species (Nfix) in our data (with the exception of *Trema*, Ulmaceae), and has on average relatively large seeds (SM)[16]. Aluminium accumulation was related to the third axis (Table 1), seed mass and leaf carbon content were also related to this axis. Ecto-mycorrhizal symbiosis was also related to the third axis but only explained 2.4% of the first three axes (Table 1).

Using only traits generally included in plant functional analyses (wood density, specific leaf area, leaf carbon content, leaf N content, leaf P content, leaf C:N ratio)[2,3,50], resulted in much higher explained variance for PC1 and PC2 of 41% and 19% respectively. As most other traits have eigenvalues close to one or much lower (Supplementary Table 1a) - they are either uncoupled from these two spectra or explain little variance in the data (Table 1).

Traits at tree community level

To identify tree community-level strategies (question 2), a second PCA was carried out using community weighted means (CWM) of 13 traits of the 2054 forest communities with species level identification (Fig. 2). Compared to the genus PCA, the trait loadings of the community PCA appear rotated to the right by 20–40 degrees. The CMW related to the leaf-economic-spectrum are still mostly associated with community PC1, similar to genus-level analysis. However, size and reproductive traits that were mostly associated with genus PC2, the stature-recruitment trade-off, in the analysis of the genera are now mostly weighing on community PC1 (PC1, eigenvalue 4.39, 33.8%, Supplementary Table 2a). Nitrogen fixation changed from a positive to a negative association with community PC2. Other traits mainly linked to PC2 are fleshy fruit, hermaphrodism, and nectar.

Community PC1 runs from forest communities with 'fast', acquisitive traits (SLA, N, P), to the left, to forest communities with 'slow', conservative' traits (C:N, wood density, seed mass) and high percentage of hermaphroditism to the right (Fig. 2, Table 2). Communities with fleshy fruits and nectar have the highest loading on community PC2 (Eigenvalue 2.27, 17.4%). We will use the term 'fast-slow forest spectrum' for PC1 of this second PCA of the forest communities. PC2 could be considered and axis of breeding system.

Comparing the trait associations at genus and community level

Question 2. asked if genus-level strategy spectra are similar to community-level strategy spectra. To assess if genera and forest communities show similar trait associations (Figs. 1, 2; Supplementary Fig. 3a, b), a Mantel test was carried out over distances of traits in PC space. The Mantel R (0.78, $p = 0.001$) suggests that a higher distance in genus-level trait values was also associated with a higher distance in plot CMW. This was mainly caused by the scores on the PC1's of each ordination, however, which were strongly correlated (Supplementary Fig. 3c) and less by the scores on the PC2's, which were not significantly correlated (Supplementary Fig. 3d).

We evaluated how environmental factors (soil pH, sum of bases, annual rainfall, cumulative water deficit, windthrow count, convective atmospheric potential energy), past human disturbances and management

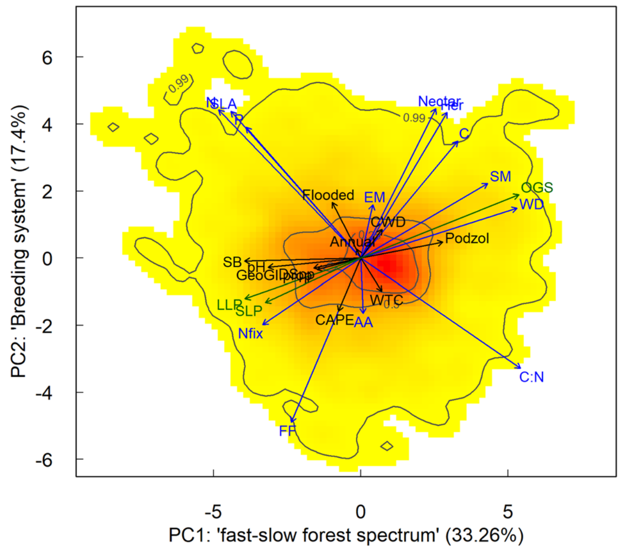

Fig. 2 | Trait space of 2054 tree communities with traits at genus and species level. PC1 has an Eigenvalue of 4.39 (explained variance 33.3%), and appears to be related to the 'leaf economic spectrum' (SLA, N, P, C:N) but also WD, SMC, and hermaphroditism contribute to this axis. Life-history forms SLP and LLP are also positively correlated with PC1. Environmental factors sum of bases and pH are strongly positively correlated to this axis. PC2 is linked to nodulation of Fabaceae and fleshy fruits and poorly correlated to the climatic factors used. Legend: Colours indicate the probability of trait combinations in the trait space defined by the PCA (red = high probability; yellow = low probability). Contour lines indicate 0.99, 0.50, and 0.25 quantiles of the probability distribution. N leaf nitrogen concentration, C:N ratio of leaf carbon to leaf nitrogen, SLA specific leaf area, SM seed mass, *P* leaf phosphorus concentration, AA aluminium accumulation, Nfix atmospheric N-fixation, WD wood density, C leaf carbon content, FF fleshy fruit, EM ectomycorrhiza, Her hermaphroditic, Nectar nectar producing. Life histories (dark green): OGS old-growth species, LLP long-lived pioneer, SLP short-lived pioneer[64]; Environmental variables: Annual, Annual precipitation (Bioclim12)[166]; CWD cumulative water deficit, CAPE Convective atmospheric potential energy[65], WTC Windthrow count[65]; PZ podzol, white-sand forest, FL flooded (swamp forest; várzea; igapó); pH, soil acidity; SB, log(sum of bases)[154]; G.prob, geoglyph probability[58]; DSpp, domesticated species[57]. Note that SLA, N and P are overlapping, as are DSpp, G.prob, pH and SB. For description of the traits and units, see Supplementary box 1.

(domesticated species[57] and geoglyph-probability[58]), as well as life history strategies are associated with community functional composition by a-posteriori plotting them in the PC trait space (question three). Soil explanatory variables (sum of bases, pH) and human impact (domesticated species, geoglyph probability) were mainly related to the 'fast-slow forest spectrum', although their explained variance is generally low (Supplementary Table 2c). Soil sum of bases explained most of the variance (33%) of the 'fast-slow forest spectrum', while pH explained 21.4% (Supplementary Figs. 4 a, b, 5). Domesticated species and geoglyph probability (Supplementary Fig. 4e, f) were also mainly aligned to the 'fast-slow forest spectrum' but explained <6% of the variance (Supplementary Table 2c). Climatic factors (annual precipitation, cumulative water deficit, windthrow count, convective atmospheric potential energy, flooding) are the best predictors of PC2, although all have an R^2 less than 7% (Supplementary Fig. 4c, d, Supplementary Table 2c).

Forest types differ in their functional composition, as indicated by the plot scores for the 'fast-slow forest spectrum'. Igapó, terra firme from the Guyana Shield, and especially the white sand podzol forests are, on average, 'slow' forests (TFBS, IG, TFGS, PZ) with positive scores for the 'fast-slow forest spectrum' (Fig. 3a). In contrast, terra firme on the Pebas formation and várzea (TFPB, VA) are, on average, 'fast' forests with negative scores for the 'fast-slow forest spectrum'. Forest types with low nutrient status (TFBS, IG, TFGS, PZ) are also positioned in the right part of the trait space (positive scores for the 'fast-slow forest spectrum'; Supplementary Figs. 5b, 6). Total

Table 2 | Variance explained by the community weighted means of 13 traits of 2054 tree communities in Amazonia

Trait	PC1	PC2	R^2	p	spectrum
N	57.98	28.91	0.869	0.001	LES
C:N	65.26	16.90	0.822	0.001	LES
SLA	52.27	26.53	0.788	0.001	LES
WD	57.03	4.59	0.616	0.001	WES
P	41.83	18.90	0.607	0.001	LES
Her	32.87	26.34	0.592	0.001	BR
FF	17.91	40.90	0.588	0.001	BR
Nectar	20.73	34.06	0.548	0.001	BR
SM	41.63	2.29	0.439	0.001	SES
C	26.95	9.54	0.365	0.001	LES
Nfix	22.95	5.29	0.282	0.001	R
EM	1.69	6.54	0.082	0.001	R
AA	0.00	5.90	0.059	0.001	R

Traits are ordered in variance explained. *N* leaf nitrogen content, *C:N* ration leaf carbon to leaf nitrogen, *SLA* specific leaf area, *WD* wood density, *P* leaf phosphorous content, *Her* hermaphroditism, *FF* fleshy fruit; Nectar, nectar producing, *SM* seed mass, *C* leaf carbon content, *Nfix* atmospheric N-fixation by Fabaceae, *EM* ectomycorrhiza. *LES* leaf economic spectrum, *WES* wood economic spectrum, *SES* dispersal, trait important for dispersal, roots, root trait. For units see Supplementary Box 1. PC1, the relative contribution of the environmental variable for PCA axis 1; PCA2 same for PCA 2. R^2 proportion of variance explained by environmental variable; *p*: significance level. Spectrum: *LES* leaf economic spectrum, *WES* wood economic spectrum, *BR* breeding R

functional richness of the complete dataset was 130.4. Forests on white sands and swamps had low functional richness (53.2, 55.4), terra firme ranged from 74.3 to 77.9, while the two flooded forest types várzea and igapó both had relatively high functional richness (95.1 and 86.7, respectively). Regions are also ranked from those with generally high soil fertility to those with low soil fertility (Fig. 3b, SWA > GS) and positioned from right (positive scores on the 'fast-slow forest spectrum'; low soil fertility) to left (negative scores on the 'fast-slow forest spectrum'; high soil fertility) in trait space (Supplementary Fig. 7). Most regions had identical functional richness ranging from 76.5–79.8, with Northwestern and Central Amazonia having a somewhat higher functional richness (Supplementary Fig. 7).

For the tree communities, the 13 community-weighted mean (CWM) traits showed similar spatial patterns across Amazonia, with values linked to the fast-soft, acquisitive end of the leaf economics spectrum both in the regions of north-western and south-western Amazonia and forest types (TFPB, VA) where relatively high soil-fertility and plant productivity are expected. Values linked to the slow-tough, conservative end were found in the regions (Central Amazonia, Guiana Shield, Southern Amazonia) and forest types (PZ, IG, TFGS, TFBS) with expected low soil fertility and productivity. Each trait is discussed in more detail in the Supplementary text and figures (Supplementary Figs. 8–25).

We mapped the 'fast-slow forest spectrum' (Fig. 4). Because the" 'fast-slow forest spectrum' is built up from the CWM's of the 13 traits, many of which correlate well with this axis the patters of the traits are fairly similar to the 'fast-slow forest spectrum' (Supplementary Figs 8–25). 'Slow' forests (with a positive score on the 'fast-slow forest spectrum') make up ~40% of all plots (Supplementary Fig. 26) and are found in areas with low soil fertility, such as the Guiana Shield and central Amazonia (yellow-beige colours in Fig. 4), where also most of the white sand forests are located. 'Fast' forests (negative score on the 'fast-slow forest spectrum', blue-purple colours in Fig. 4) make up ~30% of all plots (Supplementary Fig. 26) and are found in western Amazonia and southern Amazonia but not the areas directly bordering the Cerrado savanna area (for the delimitation of zones in Amazonia see Supplementary Fig. 1). The pattern of large-scale disturbances is quite similar to rainfall patterns in Amazonia (see Fig. 1 of ref. 65), and has little effect on trait data and on the 'fast-slow forest spectrum' (Supplementary

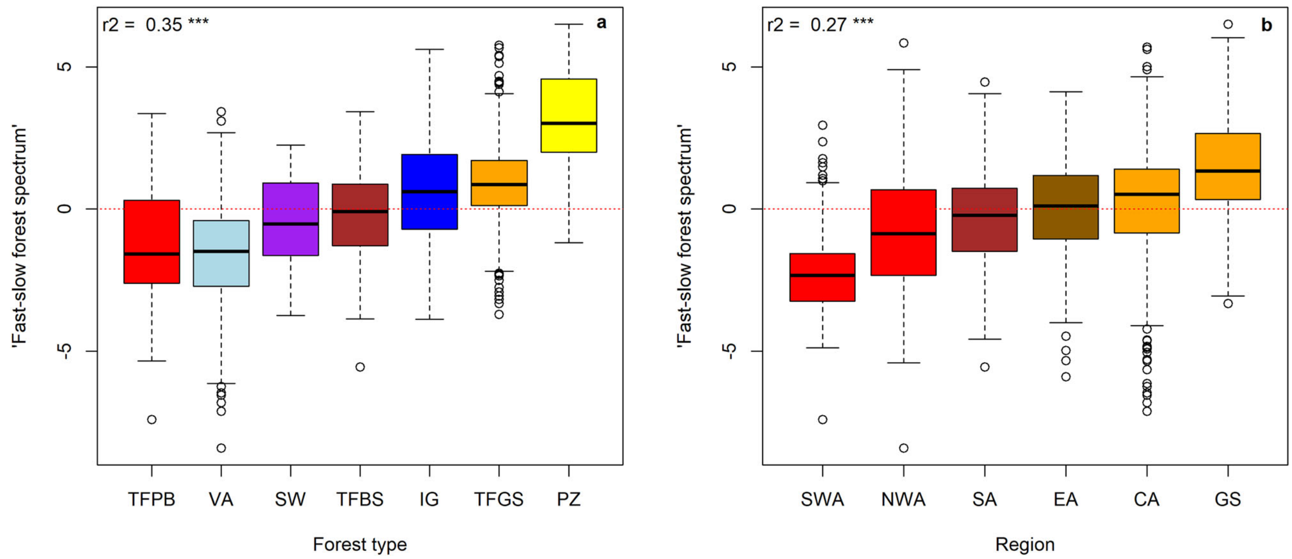

Fig. 3 | PC1 plot scores of community trait values related to forest types and Amazon regions. a 'The fast-slow forest spectrum' as determined by forest type. 'The fast-slow forest spectrum' is associated mostly with the economic spectra, and the order of forest types appears determined by general soil fertility (see Supplementary Fig. 29a). Note the very high value of the poorest soils in Amazonia (lowest sum of bases (Supplementary Fig. 29a), white sand podzol (PZ). **b'The fast-slow forest spectrum' as determined by Amazonian region**. The order of regions also appears follow general soil fertility (Supplementary Fig 29b). From rich to poor: TFPB terra firme Pebas Formation, VA várzea, SW swamp forest, TFBS terra firme Brazilian Shield, IG igapó, TFGS terra firme Guiana Shield, PZ white sand forest, SWA south west Amazonia, NWA northwest Amazonia, SA southern Amazonia, EA eastern Amazonia, CA central Amazonia, GS Guiana Shield. Colours follow the major forest type (SWA, NWA: TFPB; SA: TFBS; CA, GS: TFGS; EA: mix of TFBS, TFGS). Red dotted line: mean of all data.

Table 2c). To show that all traits are aligned to the 'fast-slow forest spectrum', we carried out an a-posteriori test, dividing the spectrum in three classes (fast < -1.2; medium -1.2 - 0.65, slow > 0.65 [Fig. 4], which have 29%, 31%, and 40% of all plots, respectively, Supplementary Fig. 25) and provide a boxplot for each trait by class. Individual CWM traits follow the same continuum as the 'fast-slow forest spectrum', although with different explained variance (R^2 values, Supplementary Figs 27, 28).

Community functional composition affects ecosystem functioning

Finaly, question four asked if functional composition had consequences for forest functioning. This is expected as the 'fast-slow forest spectrum' is strongly associated with soil fertility (Supplementary Fig. 4a, 5, Supplementary Table 2c, R2 = 32%, $P < < 0.001$). Indeed, above ground woody biomass (AGB) is significantly positively related to the 'fast-slow forest spectrum' (Fig. 5a). Forests with 'fast' traits have low biomass and those with 'slow' traits have high biomass. Absolute aboveground woody productivity (AGWP) is not significantly related to the 'fast-slow forest spectrum', suggesting that all forests have a similar, though variable, absolute productivity (Fig. 5b). Consequently, forests with high biomass have low relative AGWP (AGWP / AGB, Fig. 5c), whereas forests with a low biomass have a high relatively AGWP. Thus, relative AGWP is higher for forests with 'fast' trait values. Relative AGWP also increases with soil fertility (sum of bases, Fig. 5d). While the direct contribution of the 'fast-slow forest spectrum' and sum of bases to the AGWP is 33% and 27% explained variance, respectively, their combined contribution is 34% explained variance. Thus, their contribution is largely coinciding, strengthening the notion that fertility may be an underlying driver of both trait composition (PC2, the fast-slow forest spectrum), and productivity.

Discussion

Amazonian trees show two main strategy spectra

Across the globe, two main plant strategy spectra are found related to (1) plant size[12] and (2) leaf economics[3]. For Amazonian tree genera, the same two strategy spectra are found, but the order is reversed; the leaf economics spectrum (LES) is the spectrum describing most of the trait variance, probably reflecting adaptations to the strong Amazonian soil fertility gradient (see below). The size spectrum is only secondary (Fig. 1), presumably as we focus here solely on the tree life form compared to global analyses[3,6] that included many small herbaceous plant life forms. Across Amazonian tree genera, the wood economic spectrum (WD) was uncoupled from the LES (Fig. 1), as previously shown for Amazonian tree species[50,51,66]. This suggests that leaves and stems provide independent avenues for specialisation, potentially leading to more opportunities for niche differentiation and species coexistence.

We expand on previous analyses by showing that, even within trees, reproductive characteristics (breeding system, fleshy fruits, seed mass) are closely related to the size spectrum indicating that plant lifespan (tree size) and reproductive strategies are closely intertwined. Life history strategies were mainly related to the size-reproductive spectrum, in which small, short-lived pioneers produce many small animal-dispersed seeds to colonise ephemeral canopy gaps, whereas tall, long-lived old-growth species with durable wood (high wood density) produce large seeds which enables their seedlings to establish and survive successfully in the shade[47]. Long-lived pioneers lie somewhere in between trait-wise. The second axis reflects therefore the stature—recruitment trade-off which is often found in closed-canopy forests[11–13], where taller species have better access to light and smaller species have relatively high seed production and fast life cycle. It should be noted that long-lived pioneers and especially old growth species that produce large seeds generally have higher total seed mass production per fruiting event[67]. As they also live much longer they may thus have greater life-time seed production than short-lived pioneers[68].

Despite the global importance attributed to the LES, Amazonian pioneers and old growth species, surprisingly, do not differ much in their position on the LES. LES traits may be more important for the growth and survival of small seedlings and saplings that have a small total leaf area[41,69], compared to adult trees in which carbon gain is more determined by their large size and total leaf area than by leaf-level trait differences[2,70].

Plant strategies only partly translate into community strategies

Trait associations scale up from genera (Fig.1) to communities (Fig. 2) but not perfectly (Supplementary Fig. 3) and most traits are more strongly

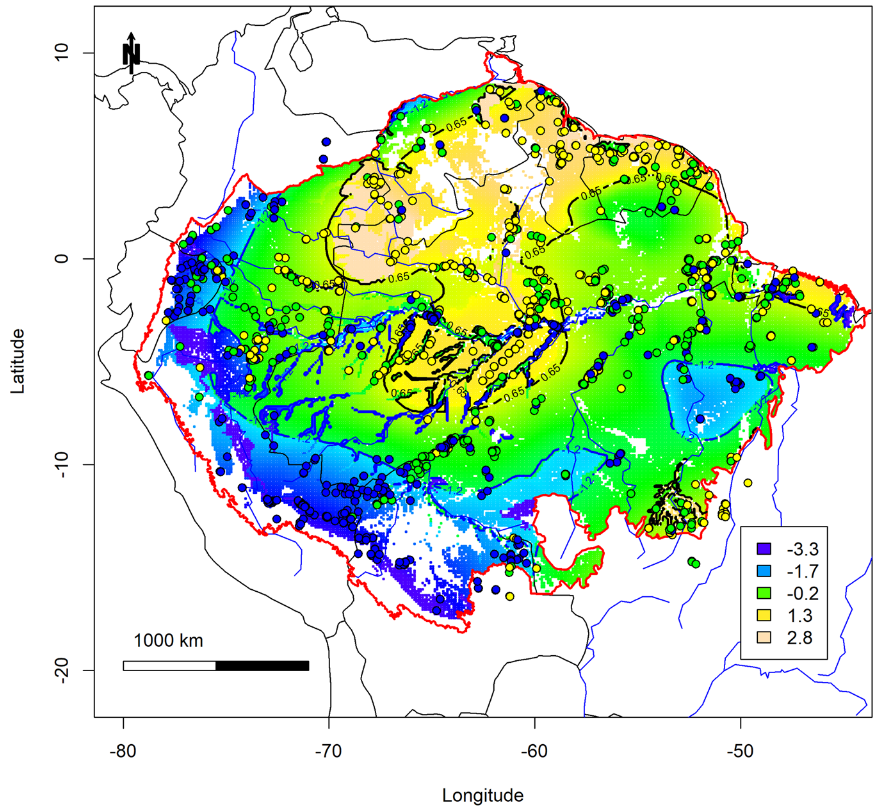

Fig. 4 | Functional characterisation of Amazonian forests. Forest with positive score on the 'fast-slow forest spectrum' (yellow, beige) are forests at the "slow", tough side of economic spectra (high CN ratio, low SLA, *N* and *P*), high wood density, low numbers of fleshy fruit, high levels of hermaphroditism, high in nectar producing individuals, occurring mainly on low to very low nutrient soils. Forests with negative score on the 'fast-slow forest spectrum' (blue, purple) are the opposite in terms of trait values and occur mainly on nutrient rich soils. The isolines divide Amazonia into three regions, tough-slow (PC1 > 0.65, yellow-beige), soft-fast (PC1 < -1.2 blue-purple) and intermediate (green). Colouring the plots based on their PC1 scores shows that their colour mostly matches the area colour, except if they are white sand plots (PZ) in a green area, and várzea plots (blue dots) in green and yellow areas. Note that the legend has been truncated at 2 standard deviations. Red polygon: Amazonian Biome limit[167]. Base map source (country.shp, rivers.shp), ESRI (http://www.esri.com/data/basemaps, © Esri, DeLorme Publishing Company).

related to the first PCA axis in the communities, the 'fast-slow forest spectrum'. At the community level, the LES traits, size and reproductive traits are all aligned with the first principal component (Supplementary Table 2c), resulting in one overall spectrum from 'fast' to 'slow' Amazonian forests, which closely parallels the soil fertility gradient (see below). For example, 'slow' forests on infertile soils tend to be tall, evergreen, densely shaded with low turnover dynamics and infrequent tree-fall gaps[71]. Under those conditions, high seed mass facilitates seedling establishment and survival[16,20,61,72,73]. Nutrient-poor conditions may select for species with dry fruits that tend to have low nutrient concentrations, high seed toxicity, and for hermaphroditic species that maximise fitness[1]. In low turn-over forests, tree species do not produce many small seeds but rather few large seeds, providing offspring with higher survival, a classic example of the "*high growth in light vs. low mortality in shade trade off*"[67,74]. In sum, the two plant strategy axes converge into one main community strategy axis because of strong environmental filtering by soils. This may explain why the pioneer-climax dichotomy[47] has been so appealing for such a long time.

Nearly all of the dry-fruited trees in the Amazon are hermaphroditic and, because wind- or unassisted-dispersal is not favoured in the sub-canopies of dense forests[75], which tend to be also tall. Heavy seed mass also tends to be associated with larger trees[76]. Very little is known on the nectar producing species in Amazonia but it appears positively associated with infertile soils and hermaphroditism. The link with infertile soils is most likely due to the fact that under conditions of high solar energy and abundant moisture but low soil nutrients, production of carbohydrate-rich exudates is favoured[77]. Flowers producing abundant nectar also tend to be large[78], rarely unisexual, but associated with hermaphroditic breeding systems. In contrast, wind-pollinated species produce large amounts of nitrogen-rich pollen[79], no nectar, and have mainly unisexual flowers.

Atmospheric N fixation was positively linked to the size-recruitment spectrum in the genus ordination (Fig. 1). Species in Fabaceae, the main N-fixers, are characterised by high wood density and large seeds. However, in the community ordination their position was reversed from a positive (Fig. 1) to negative relation (Fig. 2). Fabaceae, dominate the forests of the upper Rio Negro, Guyana and Suriname[16], but the species that dominate there are 'caesalpinoid' legumes that generally do not form N-fixing root nodules[16]. N-fixation is mainly found in the genera occurring in western Amazonia, which also have smaller seeds[16], which explains the reversal.

Areas along the Amazon main stem and other várzea rivers have negative scores for the 'fast-slow forest spectrum' and are known to be very fertile (see also Supplementary Fig. 29), having among the highest litter productivity of Amazonia[80]. It should be noted that the most fertile soils are also associated with regions of greatest soil instability[81,82], seasonal flooding (várzea), and in southern Amazonia with incidence of storms[83], making it difficult to disentangle effects of disturbance and soil fertility. The intermediate disturbance theory[84,85] has long held that in Amazonia, higher soil fertility would lead to faster tree growth and turn-over, gap dynamics, and heterogenous forest structure, ultimately yielding higher plant diversity[16,61,86]. Other studies have countered this conclusion[87]. Our data suggests that tree species richness has no relationship with the 'fast-slow forest spectrum' and also explains very little variance of the trait distribution (Supplementary Table 2c). In Amazonia, even though large windfall disturbances (from 5 to over 2000 ha) are not uncommon, their return frequency is between 27.000 years in Western Amazonia and 90.000 years in Eastern Amazonia[88]. Thus, it is unlikely that they contribute much to disturbance related species richness.

An Amazonian spectrum from slow to fast forests, driven by soil fertility

Amazonian forests show one major functional spectrum, running from 'fast' productive forest communities with high mean SLA, N, P, and fleshy fruits to 'slow' conservative forest communities with high C:N, wood density, seed mass, and high percentage of hermaphroditism (Fig. 2). This spectrum is best explained by soil fertility (sum of bases, light vs. lowmortality in shade pH; see Supplementary Figs. 4, 5), as has been suggested before for forest species and trait composition[16,62], but surprisingly little by macroclimate (annual rainfall, climatic water deficit,

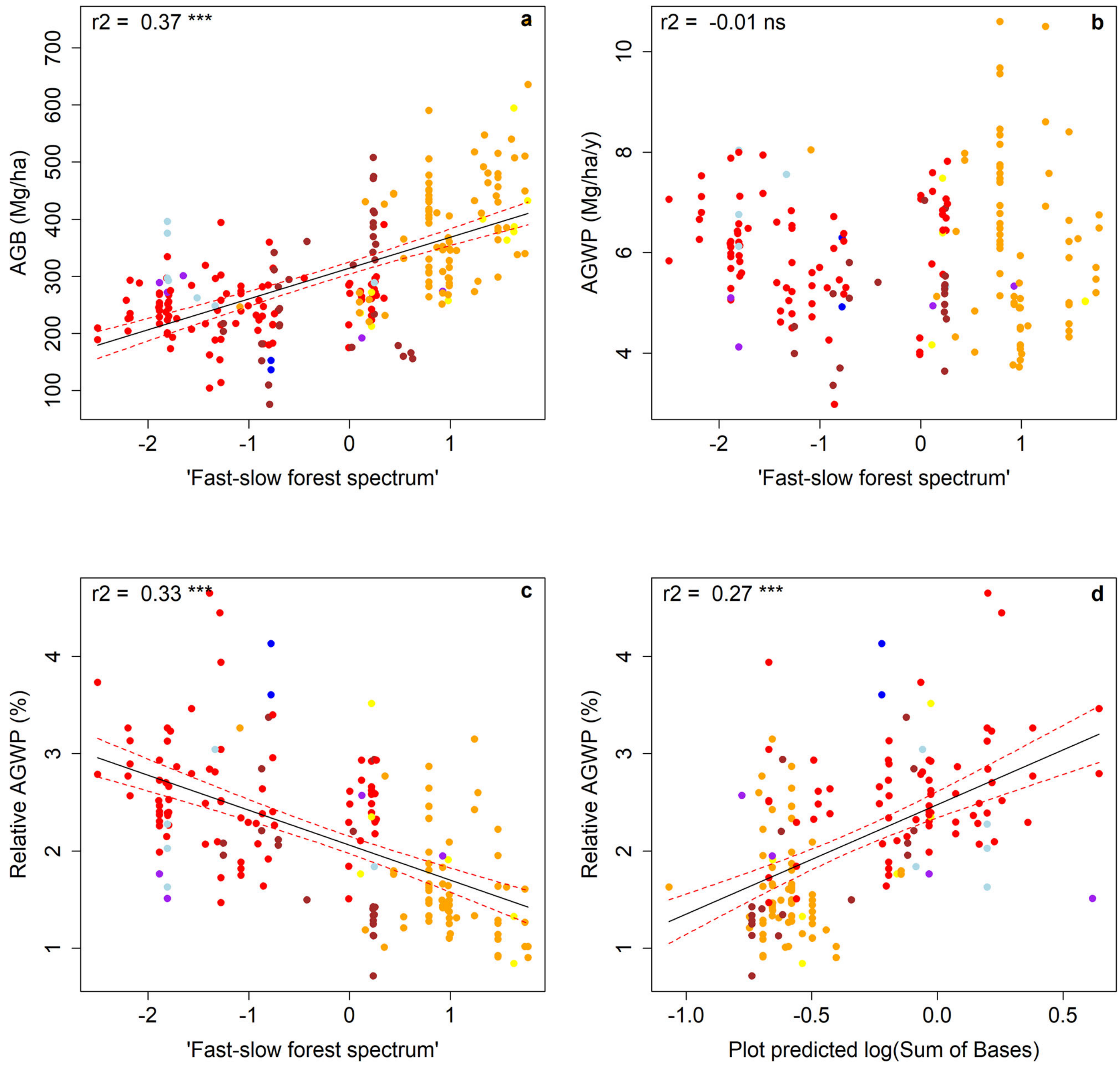

Fig. 5 | The 'fast-slow forest spectrum' and soil fertility as potential drivers of aboveground biomass and biomass productivity. a 'Slow' forests (positive value) have much higher above ground woody biomass (AWB) than 'fast' forests (negative values) **b** Absolute above ground woody productivity (AGWP) does not vary significantly with the **'fast-slow forest spectrum'**. **c** Biomass produced per biomass standing (= Relative AGWP [100*AGWP/AGB]) is highest in 'fast' forests (negative values for slow-fast forest spectrum). **d** Relative AGWP is positively correlated with predicted sum of bases[16]. Red lines indicate 95% confidence intervals. Biomass data from sources[55,83,168]. Colours: Red, terra firme Pebas formation; brown, terra firme Brazilian Shield; orange, terra firme Guiana Shield; yellow, white sand forest; purple, swamp forest; light blue, várzea.

and large-scale disturbance, Supplementary Table 2c, Supplementary Fig. 4). It was previously shown that species from communities of fertile soils have higher SLA and leaf nutrient concentrations than those from infertile soils and the sum of bases and pH explain respectively 30% and 18% of the trait variance[9]. A global study encompassing all biomes, ranging from grasslands to forests, found two main axes of community trait variance (i.e., plant stature and resource economics) that were only weakly associated with climate and soil conditions[11]. Functional composition of Amazonian forests is not driven by precipitation, possibly because all forest sites receive sufficient rainfall (>1800 mm/yr). Instead, functional composition and resource economics are strongly driven by soil fertility, as there is a major soil gradient running from the old weathered extremely nutrient poor soils from the Guiana Shield and the Brazilian Shield in the east, to the young and fertile soils formed by more recent Andean sediments[89]. This gradient drives strong assembly rules, sensu Keddy[90], arguably driven by soil characteristics in Amazonia[82]. We see strong convergence[9,61,62,91,92] of almost all traits when comparing low-productivity communities on poor soils to those with higher productivity and higher soil fertility. While soil fertility (total soil phosphorus [strongly related to sum of bases[9]]) was shown to be a strong driver of productivity in Amazonia, soil physical properties appear more important for forest turn-over[82], which is twice as high in western Amazonia compare to central and eastern Amazonia[81].

Although we did not include deciduousness in our analyses, it has been recently shown that increases in abundance of deciduous species is tightly linked to soil fertility and water availability[93,94]. Additionally, community leaf nutrients increase towards wetter forests on younger fertile soils in the western fringes of Amazonia[9,62,82,95] (Supplementary Figs. 11,12).

Studies comparing nutrient-poor igapó and nutrient-rich várzea forests showed that within genera similar results were found, with traits conferring a 'fast' lifestyle being more common in fertile várzea and those with a more 'slow' lifestyle were more common in infertile igapó[91,92]. Comparing congeneric species between terra-firme forest on clay soils and white-sand forest[96], the same result was found. Thus, it is likely that if we could have measured actual trait expression everywhere, the large-scale gradients would be reinforced.

Human legacies

We assessed to what extent the current functional composition of the Amazon is influenced by human legacies. Communities with 'fast' traits are significantly associated with the abundance of domesticated species (explaining 5.6% of the trait variance, Supplementary Table 2c) and geoglyph probability (explaining 5%, Supplementary Fig. 4, Supplementary Table 2c). This suggests that indigenous people may have domesticated faster growing species, and that long-term human presence and disturbance (open areas) may still have left its mark on the current vegetation[57,58]. The higher soil fertility (sum of bases) and access from the open Cerrado could be one of the reasons that pre-Columbian people settled the edges of Amazonia. At the Amazonian scale, areas with naturally higher soil fertility may have facilitated past human occupation by increasing productivity of agroforestry systems[97]. For instance, most domesticated tree and palm species benefit from fertile soils, and by contributing to enrich soil fertility through soil management practices, pre-Columbian people allowed domesticated species to persist in the forest over centuries[60]. Although the effect of anthropogenic soil enrichment on domesticated species likely plays a role at the landscape scale, depending on the extent of landscape transformations by pre-Columbian peoples, soil enrichment could potentially influence tree communities over broader scales. Therefore, part of the functional variation we observe across Amazonian tree communities could still be a legacy of pre-Columbian landscape domestication.

Community functional composition affects ecosystem functioning

Functional composition of Amazonian forests has consequences for ecosystem functioning. While the relationship between soil physical and chemical properties are not always clear[82], above ground woody biomass (AGB) is significantly, positively related to the 'fast-slow forest spectrum' (Fig. 5a) – indicating that 'slow' forests with conservative trait values and high wood density have high aboveground biomass[98]. Our map of the 'fast-slow forest spectrum' (Fig. 4) is indeed similar to an earlier ground-based biomass map[99]. Forest productivity is influenced by tree traits, frequency of disturbance and soil fertility (Fig. 2, Supplementary Table 2c). However, absolute aboveground woody productivity (AGWP) is not significantly related to the 'fast-slow forest spectrum' (Fig. 5b). Forests with high biomass have low relative biomass productivity (Fig. 5a, c), probably because a large proportion of the biomass is locked up in unproductive stems[100], whereas forests with low biomass have a higher biomass productivity, probably because of a higher light availability within the stand, and because a larger proportion of the biomass is in photosynthesising leaves[100]. Relative biomass productivity (aboveground woody productivity/aboveground woody biomass) is higher for forests with faster traits that produce a higher amount of woody biomass per standing biomass, and this effect is correlated with 'fast' trait values (Fig. 5), also increasing with soil fertility (sum of bases, Fig. 5d). Because soil fertility is a driver of both biomass productivity and the main explanatory variable for the 'fast-slow forest spectrum', soil fertility is likely the driver of forest productivity by both influencing the community traits and allowing higher growth rates directly. It has been predicted that a positive relationship exists between forest biomass and productivity[101]. However, forests with high productivity tend to have both high turnover[55,63], and low wood density[17], making this relationship more complex. We found no difference in net biomass productivity between the various forest types along the fast-slow forest spectrum but rather a high variability (Fig. 5b). Forests on poor soils tend to have high biomass but limited growth, while forests on rich soils have less biomass but higher relative growth. This does not lead to higher biomass, because of the lower wood density and much higher turn-over of the forests on rich soils[55] (see also Supplementary Fig. 30). The 'slow-fast forest spectrum' should also have consequences for other trophic levels. 'Slow' forests combine a slow growth with poor food quality as they have tough, well-defended, nutrient-poor leaves, few fleshy fruits, and large, often toxic seeds. Combined, this results in less food for animal life (e.g. less insects, insectivores, and frugivores). Conversely, 'fast' forests faster growth producing higher quality food sources (e.g. thinner leaves with lower C:N ratio, more fleshy fruit), resulting in a higher biomass of insects, mammals and birds[102].

Three functionally different Amazonian forest types

Based on the ordination analysis of 13 tree traits, Amazonia can broadly be divided into three regions with a different functional composition (Fig. 4). The very poor soils on the sandy deposits of the Roraima table mountains and the poor soils of the Guiana Shield, and the forests on white sands across other regions of Amazonia form one group. Forests that are part of this group generally have low diversity tree communities, except for the areas in central Amazonia with very high diversity[103]. This result strongly contrasts with our earlier notion that forest productivity/turnover and diversity are strongly positively linked[16,104]. The 'slow' forests are composed of mainly hermaphroditic species with tough, low palatability, low nutrient leaves with high C:N ratio, dense wood, dry fruit, and high levels of endemism[103,105]. Western and southern Amazonia are the 'faster' forest areas that select for the opposite trait characteristics than those mentioned above. Compared to the other two regions they are generally found on richer soils (Western Amazonia), drier areas (Southern Amazonia) and in várzea forests in the other two regions. They have high (Western Amazonia) to medium diversity (várzea forest)[103]. They are also characterised by high productivity[15] and high turnover[71,81].

Because the three forest functional types are based on tree traits with a strong influence on forest functioning, our map could be included in dynamic vegetation models[106] and earth system models[107], thus making better predictions on the role of Amazonia in global carbon and water cycling[108], the risk of tipping points[109], and the fate of the Amazon in the face of global change[110]. Because of the reliability of species identification, and lack of species-specific trait data, our current analysis and maps are based on average, genus-level data. When more data becomes available, the functional maps could be improved by including species-level trait values and hence accounting for interspecific (and perhaps intraspecific) trait variance.

Methods

Tree inventory data were taken from the May 2024 version of the Amazon Tree Diversity Network inventory data[111–114]. ATDN20240517 contains 2253 **genus-level plots** (with 1,198,408 individuals, 812 genera, 98.5% of all individuals identified at genus level), 2054 of which with **species composition** (the **species-level plots**, 1,010,524 individuals, 5211 species, 88% identified at species-level). Most of tree-inventories were for 1-ha size plots and sampled trees with a diameter at breast height (DBH, at 1.30 m or above tabular roots) over 10 cm (for plot metadata, see Appendix 1). Species synonymy was updated following ref. 115, but harmonising names with the World Flora Online[116], using the December 2023 snapshot the *WorldFlora* R package[117], with some modifications after Molino et al.[118].

Species with a *confer* (*cf.*) identification were accepted as belonging to the named species, while those with *affinis* (*aff.*) were accepted only at the genus level and therefore removed from the species analysis.

The 2253 genus-level plots (Supplementary Fig. 1) provided a total of 1,216,222 trees, of which 1,198,408 (98.5%) were identified at the genus level. Most plots (2153) had more than 90% of their individuals identified to genus (Supplementary Fig. 30). A total of 812 genera were recorded, of which *Eschweilera* (61,061 individuals), *Protium* (56,943), *Pouteria* (51.777), *Inga* (27,619), and *Oenocarpus* (22,907) were the five most abundant genera across all plots. Thirty-five genera made up 50% of all individuals and could be considered hyperdominant Amazonian tree genera[111,112]. A total of 149 genera had 10 individuals or less, while 42 genera had only one individual. The percentage of individuals with trait data ranged from 94-97% (leaf traits), through 99% (wood, seed) to 100% (root traits, fruit fleshiness, breeding system). For a list of all traits, their units and ecological information see Supplementary Box 1.

Most of our analyses were carried out at the genus level because over such a large and species rich region trees are more reliably identified at the genus level (Supplementary Fig. 31), and because for many species there is a lack of species-specific trait data. For several traits it has been shown that traits are phylogenetically conserved and most trait-level variance is found above the species level, as has been found for wood density[62,66,119,120], seed mass[121,122], and SLA[9]. We used the average of the trait data for all species within a genus, except for breeding system, which may vary largely within a genus and which was analysed at species level. Our analyses and maps do therefore not consider different species distributions within genera or variance of trait values within species due to plasticity and/or acclimation. For the traits included in our analysis, in Amazonia, SLA, N and C, are most determined by species identity, whereas leaf P is also strongly influenced by site growing conditions[9].

Traits were obtained from a number of sources. Wood density was mainly taken from[4,119]. Leaf traits were mainly from four large TRY datasets[9,14,50,51,66,123–127], with additional data from[128–134]. Seed mass was taken from[22,135,136] and various floras and tree guides[137–141]. Because seed mass varies over several orders of magnitude, we used logarithmic classes for seed mass[22,61]. For EM association we checked the most recent literature for confirmed EM tree species[142]. For nodulation we used[143,144]. For aluminium accumulation we used[32,145] and references therein. We considered a genus EM positive, nodulating or Al-accumulating if more than 50% of the species in that genus reported were positive for that trait. Nectar production was taken from[52] and mapped as a percentage by taxon. We first scored the percentage of species by genus and, if not available, we used the information by family. Breeding system may vary considerable in some genera and was taken at species level from[146] and descriptions from floras and monographs (in particular, *Flora e Funga do Brasil*). Jardim Botânico do Rio de Janeiro (http://floradobrasil.jbrj.gov.br/) issues of *Flora Neotropica* (https://www.springer.com/series/16365); and the Springer book series *The Families and Genera of Vascular Plants*[147–149] and other published revisions. We did not include adult tree height in our data, due to a lack of data for almost all genera.

We performed a principal component analysis (PCA) on the average trait values for all genera that had data for all traits (353 genera), scaling all data to a mean of zero and standard deviation of 1. While this is less than 50% of all genera, these 353 genera amounted to 90.8% of all individuals in our plots. While for several genera data is missing for particular traits, the percentage of individuals with trait data ranged from 94-97% (leaf traits), through 99% (wood, seed) to 100% (breeding system, root traits, fleshiness of fruits). Because of these high percentages we did not conduct data imputation. For all plots (communities) we calculated the community weighted mean of each trait, by calculating the average over all individuals of known taxonomy, thus using data of all genera. For discrete yes/no traits we used the percentage of individuals, rather than the mean.

The forest plots are subdivided in those that occur on floodplains (várzea (VA) and igapó (IG)), white sand podzols (PZ), terra firme (TF) and swamps (SW). For these four categories we constructed a separate spatial model of each trait across Amazonia with inverse distance weighting[103]. As an example, for all white sand plots and wood density we made a spatial interpolation. This interpolation was then used to predict the mean trait value for each pixel on the soil map that was considered a white sand area (Supplementary Fig. 32b, yellow pixels). The same was done for all plots in várzea and igapó combined, all plots established on terra firme and finally for swamp forests. The forest map (0.1 degree resolution, Supplementary Fig. 32a) was based on the Amazon lowland forest[112,150], divided in the major soils corresponding to the forest-soil combinations used[111,151] (Supplementary Fig. 31b). While the soil grid was based on the major soil type, the soil type of the plots was determined independently of this map and based on the field observation of the person that established the plot. It is thus possible that a plot on white sand is located in a grid cell classified as terra firme. Even so, it is used in the white sand spatial model (see ref. 103 for a more detailed explanation). For all maps we truncated the legend and its colours to values between the mean ± 2 times the standard deviation, to avoid that outliers in 5% the data would influence the visible pattern too much.

We calculated the percentage of variance explained by the model by combining the observed and predicted community weighted mean of all four spatial models, using a simple linear model[103].

Annual rainfall was extracted by plot location from the grid data from Worldclim 2[152]. The cumulative water deficit (CWD) was calculated as[153] and can be considered a parameter of the strength of the dry season. Soil fertility (sum of bases, SB) was extracted from the latest Amazonia wide map[154]. We used SB rather than the often-used CEC (cation exchange capacity), as the latter includes the full exchange complex, which on acid tropical soils often includes a large portion of Al^{3+} and H^+, which are in fact toxic for most species. Although we used the most recent soil-fertility map[154], the overwhelming predominance of soil data from terra firme sites resulted in an artificially high interpolated SB for white sand forests and low SB for Várzea forest (Supplementary Fig. 29). We may thus expect stronger relationship between functional composition, SB, and other soil variables when improved soil maps become available. Soil acidity (pH) is also an often-used index of soil fertility (a low pH being infertile). We extracted pH data from Soterlac[155], ISRIC wise[156], RAINFOR sites[95,151], and refs. 157–159. For pH, we created a loess interpolation model, based on all data available. We then estimated pH for each plot based on the loess interpolation, sensu[103]. Interpolated maps of SB and pH and boxplots for SB and pH based on plot data (sources as above) can be found in Supplementary Fig. 33. Large-scale disturbance was assessed in two ways: the density of large wind throws (5 – 2,223 ha; mapped at 0.25 degree resolution) caused by convective storms found on satellite images[65,88], and a map of convective available potential energy (CAPE), which is a strong driver of convective blowdowns[65].

We also calculated by plot four life-history characteristics: the fraction of short-lived pioneers (SLP); long-lived pioneers (LLP); old growth species (OGS)(Forestplots.net), and maximum observed diameter. Pioneers are defined after[64], by combining low wood density and low seed mass (wood density < 0.7 g/cm^3), where SLP have seed mass < 0.1 g and LLP have a seed mass >= 0.1 g, and OGS species have a wood density > 0.7 g/cm^3.

Domesticated species (Dsp) were taken from[57], we used the percentage of domesticated species per plot as a proxy of pre-Columbian legacy on the forest. Similarly, we used the probability of finding geoglyphs[58] as a second proxy of pre-Columbian influence on the forest.

Species richness/ha was calculated as in[103].

All analyses were carried out in the R programming environment, with custom made R[160] scripts, using the libraries *Funspace*[161] (for PCA and functional space analyses and images), *Vegan*[162] (Mantel test), and *Raster*[163].

Statistics and reproducibility

Statistic used are as described above. *P*-values for regression (Fig. 5) and ANOVA (Fig. 3) are calculated with standard linear models. Reproducibility was maintained by use of versioned scripts.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data necessary for producing the results reported here have been deposited on Figshare[164]. At Figshare we also provide a spatial model (at the scale of 0.1 degree) for each trait, a high-resolution map of the slow-fast-forest spectrum (Fig. 4), and plot-based community weighted averages for further research. Correspondence and requests for other materials, which is available upon reasonable request and following a ATDN data sharing agreement, should be addressed to Hans ter Steege.

Code availability

R code (version 4.3.1) and data to produce the figures and tables have been deposited on Figshare[164].

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H.t.S. & C.B. conceived the study. H.t.S. performed the analyses. H.t.S. wrote the first manuscript version, later with significant input from L.P., J.A.G., CF, W.M., O.L.P., E.P., B.G.L., J.E.G., M.J.E., T.R.B., M.N.U., M.v.d.S., M.M.P., M.M.G., F.C.D.. H.t.S. curated the A.T.D.N. data. A.L.e., G.P. curated the Forestplots data and approved the manuscript. L.P., M.v.S., H.t.S. provided trait data. I.A., L.S.C., F.W., F.D.A.M., D.L., R.P.S., H.t.S., C.V.C., J.E.G., M.C., O.L.P., M.T.P., W.E.M., D.S., J.F.M., L.D., J.D.C.R., J.o.S., M.I., M.P.M., J.R.S.G., J.F.R., O.B., A.Q., N.P., C.P., D.J.R., J.H., E.A., L.B., L.C., M.C.V.S., B.G.L., E.N., P.N., T.S.S., E.M.V., A.G.M., N.R., J.T., K.C., E.H., A.M., J.C.M., C.S., M.O., F.C., J.E., T.F., C.B., N.C., F.D.M., C.Z., T.K., B.S.M., B.H.M., R.V., B.M., R.A., D.D.A., H.C., J.E.H., M.B.M., M.F.S., A.S.A., J.L.C., S.L., W.L., L.M., G.B.M., J.S., T.R.S., E.F., M.A.L., J.L.L.M., H.E.M., H.L.Q., C.C.V., G.A., R.B., P.A., D.G.r, K.R., P.R.S., T.B., A.A.M., B.C., Y.F., H.F.M., M.R.S., L.F., J.R.L., F.C.D., J.A.C., J.J.T., G.D., R.G.V., A.L., M.R.P., A.V., I.V., F.C.V., A.A., L.A., F.D., V.F.G., W.N., D.N., M.C.P., D.A., F.B., Y.B., R.C., F.A.C., F.C.S., K.F., R.G., T.H., J., M.P.P, J.J.P, J.B., E.B., I.d., J.F., M.F., P.F., M.G., C.L., J.C.L, B.V., V.V., E.P., C.C., É.F., T.W.H., I.H., M.S., J.S.C., R.T.C., D.D., K.D., W.M., G.M., R.P., B.A.,

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