

Leaf economics traits predict litter decomposition of tropical plants and differ among land use types

Maartje Anne Bakker^{*1,2}, Geovana Carreño-Rocabado^{1,2} and Lourens Poorter^{1,2,3}

¹Forest Ecology and Forest Management Group, Center for Ecosystem Studies, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands; ²Instituto Boliviano de Investigación Forestal, P.O. Box 6204, Santa Cruz, Bolivia; and ³Resource Ecology Group, Center for Ecosystem Studies, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands

Summary

1. Decomposition is a key ecosystem process that determines nutrient and carbon cycling. Individual leaf and litter characteristics are good predictors of decomposition rates within biomes worldwide, but knowledge of which traits are the best predictors for tropical species remains scarce. Also, the effect of a species' position on the leaf economics spectrum (LES) and regeneration light requirements on decomposition rate are, until now, unknown. In addition, land use change is the most immediate and widespread global change driver, with potentially significant consequences for decomposition.

2. Here we evaluate 14 leaf and litter traits, and litter decomposition rates of 23 plant species from three different land use types (mature forest, secondary forest and agricultural field) in the moist tropics of lowland Bolivia.

3. Leaf and litter traits were closely associated and showed, in line with the LES, a slow–fast continuum ranging from species with tough, well-protected leaves (high leaf density, leaf dry matter content, force to punch and litter C : N ratio) to species with cheap, productive leaves [high specific leaf area (SLA) and nutrient concentrations in leaves and litter].

4. Fresh green leaf traits were better predictors of decomposition rate than litter traits, and leaf nitrogen concentration (LNC) was a better predictor of decomposition than leaf phosphorus concentration, despite the widely held belief that tropical forests are P-limited.

5. Multiple regression analysis showed that LNC, SLA and chlorophyll content per unit leaf area had positive effects on decomposition, explaining together 65–69% of the variation. Species position on the LES and regeneration light requirements were also positively related to decomposition.

6. Plant communities from agricultural fields had significantly higher LNC and SLA than communities from mature forest and secondary forest. Species from agricultural fields had higher average decomposition rates than species from other ecosystems and tended to be at the fast end of the LES.

7. Both individual traits of living leaves and species' position on the LES persist in litter, so that leaves lead influential afterlives, affecting decomposition, nutrient and carbon cycling.

Key-words: chlorophyll, decomposition, functional traits, global change, land use, leaf economics spectrum, nitrogen, phosphorus, specific leaf area, tropical forest

Introduction

Decomposition is a key ecosystem process that connects all trophic levels. Through the activity of decomposers

and trophic transfer, nutrients like nitrogen and phosphorus are made available to primary producers and higher trophic levels (Campbell & Reece 2002; Wardle *et al.* 2004). Litter decomposition is controlled by three main factors: environmental conditions, the decomposer community and substrate quality (Pérez-Harguindeguy *et al.* 2000; Toledo Castanho & Adalardo de Oliveira 2008).

*Correspondence author. E-mail: maartjebakker@gmail.com

Environmental conditions such as climate and soil have occasionally been found to be the best predictors of litter decomposition (Aerts 1997). However, Cornwell *et al.* (2008) showed in a global meta-analysis that the traits of plant species exert a dominant control over litter decomposition rates.

Both litter and fresh leaf traits have successfully been used to predict litter decomposition rate, and both sets of traits have advantages. Where litter traits shed light on the initial quality of decomposing leaves, fresh leaf traits are more closely linked to the plant's growth strategy and are more widely available. Decomposition rate has been found to correlate positively with litter nitrogen (Kurokawa & Nakashizuka 2008; Parsons & Congdon 2008), phosphorus (Alvarez-Sánchez & Becerra Enríquez 1996; Cornwell *et al.* 2008; Parsons & Congdon 2008) and cation concentrations (Mg, K and Ca; Alvarez-Sánchez & Becerra Enríquez 1996), while it correlates negatively with molecules consisting of large carbon chains, such as lignin and cellulose (Vaiereetti *et al.* 2005; Kurokawa & Nakashizuka 2008; Parsons & Congdon 2008).

Taking a step further away from the decomposition process, fresh leaf N, Mg, K and Ca concentration, and total base content (Cornelissen & Thompson 1996; Santiago 2007; Parsons & Congdon 2008) turned out to be good predictors of decomposition rate. Leaf nitrogen concentration (LNC) was better at predicting decomposition rate than litter nitrogen concentration (Cornwell *et al.* 2008). Physical leaf properties are also related to decomposition rate. Specific leaf area (SLA; leaf area divided by leaf dry mass) has a positive effect on litter decomposition rate (e.g. Cornelissen *et al.* 1999; Vaiereetti *et al.* 2005; Santiago 2007; Kurokawa & Nakashizuka 2008), while leaf dry matter content (LDMC; ratio leaf dry : fresh mass; Kazakou *et al.* 2006; Cortez *et al.* 2007; Cornwell *et al.* 2008; Kurokawa & Nakashizuka 2008) and leaf toughness (Cornelissen & Thompson 1997; Cornelissen *et al.* 1999) have a negative effect.

There is no unambiguous answer to the question whether chemical or physical traits determine decomposition rate – and in fact, both groups are closely associated, because they are both the result of the plant's strategy. Plants follow different physiological strategies that lead to roughly the same fitness levels for coexisting species. They produce either low-quality leaves at low energy costs, or high-quality leaves at high structural costs, thus showing a trade-off between either fast growth and high photosynthesis or slow growth and persistent, long-lived leaves (Wright *et al.* 2004; Poorter & Bongers 2006; Santiago 2007). This continuum is referred to as the leaf economics spectrum (LES). In tropical forests, for example, the LES ranges from slow-growing shade-tolerant tree species to fast-growing pioneer species with high light requirements for regeneration (Poorter & Bongers 2006).

The 'economic' value of a leaf influences its afterlife, because many of the physiological and protective features of green leaves persist through senescence and after shedding. For example, traits that make leaves resistant to physical damage and herbivores (such as high leaf toughness, LDMC

and low SLA and nutrient concentrations) are at the same time effective barriers against soil decomposers. Leaf palatability and litter decomposition rates are therefore positively correlated (Grime *et al.* 1996).

So far, leaf economic value has never been related directly to litter decomposition rate, although several previous studies have shown the relevance of individual leaf traits associated with the LES to decomposability (Kazakou *et al.* 2006; Cortez *et al.* 2007; Fortunel *et al.* 2009). Also, for tropical rain forest trees, there is a striking lack of published studies on the relation between individual leaf traits and litter decomposition rate. Although some work has been done on the influence of environmental conditions like soil, climate, water availability and decomposer organisms on decomposition rate (e.g. Sherman 2003; Rueda-Delgado, Wantzen & Tolosa 2006; Powers *et al.* 2009), knowledge of the relation between leaf traits and decomposition rate is scarce in this part of the world (but see Santiago 2007, 2010; Kurokawa & Nakashizuka 2008).

Furthermore, no study has explicitly evaluated the consequences of land use change on leaf decomposition rates in the tropics. Human-induced changes on land use lead to major changes in plant community composition (Boyle & Boyle 1994; Huntley *et al.* 1997) and ecosystem processes (Chapin *et al.* 2000; Díaz & Cabido 2001) such as litter decomposition and nutrient cycling (Vitousek 1997; Vitousek *et al.* 1997). The relation between land use, green leaf traits of the plant community and decomposability has been shown for herbaceous communities across Europe (Fortunel *et al.* 2009), Chinese grasslands (Zheng *et al.* 2010), and Australian grasslands and forests (Dorrough & Scroggie 2008), but never for slash-and-burn agriculture and secondary forest succession in tropical ecosystems. Yet, it is important to observe changes in plant communities and ecosystem processes in the tropics, because especially in poor, largely rural tropical countries people rely directly on ecosystem services that plant communities provide, like food, shelter and water regulation (Díaz *et al.* 2006).

Here we present the results of a decomposition study with 23 plant species with different growth strategies from a range of common land use types in the moist tropics of lowland Bolivia. The following questions were addressed: (i) How are green leaf and litter traits associated? (ii) Which leaf and litter traits are good predictors of decomposition rate? (iii) How do leaf traits and decomposition rates differ between species that are typical for different land use types? We had the following corresponding hypotheses: (i) not only leaf traits but also litter traits show a slow-fast continuum, in line with the LES; (ii) litter traits are better predictors of decomposition than green leaf traits because they directly affect decomposers; P is a better predictor than N because tropical soils are P-limited, and not only individual leaf and litter traits predict decomposition rate, but also the position of a leaf on the LES; and (iii) leaf nutrient concentrations and decomposition rates are lowest for mature forest species, intermediate for secondary forest species, and highest for agricultural species.

Materials and methods

STUDY SITE AND SPECIES

Fieldwork was carried out in northeastern Bolivia (department Santa Cruz, province Guarayos). Mean annual temperature in the region is 25.3 °C. Annual precipitation is 1580 mm (range 1269–1871 mm, data collected at La Chonta sawmill from 1994 to 2006), with a dry season (<100 mm per month) from May until September and 1 month (July) during which potential evapotranspiration exceeds rainfall. The area is situated on the southwestern border of the Brazilian Shield, characterized by rolling hills with thin soil mostly derived from gneiss, granitic and metamorphic rocks (Crochane 1973; Navarro & Maldonado 2004). Soils have been described as inceptisols with 10–15% of the area being covered by anthropogenic soils (Paz-Rivera & Putz 2009). Inceptisols are soils of relatively new origin and are usually arable and fertile.

Land use types selected for this study were the moist tropical forest of the timber concession of La Chonta (15°47'S, 62°55'W) and agricultural systems close to Ascensión de Guarayos (15°54'S, 63°11'W). The agricultural systems consist of slash-and-burn agriculture in which local subsistence farmers fell and burn a patch of (secondary) forest. Crop cultivation takes place for 2–6 years. Then the sites are abandoned for a fallow period of 5–20 years and a secondary forest develops. Research took place in agricultural fields and in secondary forests aged between 5 and 15 years. Common crop species in the shifting cultivation systems are corn, rice, cassava, banana and peanut.

For each land use type (mature forest, secondary forest and agricultural field) three 0.5 ha plots were established (50 × 100 m). A vegetation survey was made in each plot. The methodology differed between land use types, because of the differences in vegetation structure. For mature forest, all trees with a diameter at breast height (DBH) > 10 cm were identified and measured. Because stems tend to be smaller in secondary forests, in these forests also four subplots of 10 × 10 m were established in which trees between 5 and 10 cm DBH were measured. In the agricultural field five 100 m transects were laid out, and every 10 m species touching or being within 10 cm of the transect were identified. Thus 50 measurements were made in each plot. The relative abundance of a species was calculated based on its basal area (for the secondary and mature forest species), or based on its relative frequency (for the agricultural fields).

A total of 24 plant species, which belonged to the most abundant species (in terms of basal area or cover) was selected (Table 1): 18 trees, three palms, one shrub and two herbs. Species differed in their light requirements for regeneration (i.e. the inverse of shade-tolerance), expressed as the average juvenile crown exposure of a 2 m tall sapling of the species, occurring in the forest. The juvenile crown exposure (CE_{juv}) varied from one for a species whose saplings were only found in the shaded understory, to three for a species whose saplings were only found with full overhead light in gaps (Poorter & Kitajima 2007). CE_{juv} was only available for 17 tree species (Poorter & Kitajima 2007).

COLLECTION OF LEAF AND LITTER MATERIAL

To measure fresh leaf traits, outer-canopy leaves were collected from sun-exposed plants of 23 species (for all species but *Oryza*). Seedlings were avoided. Leaves of truly shade-tolerant species, never found in full sunlight, were collected from the least shady places found. Relatively young but fully expanded and hardened leaves from adult plants were chosen, if possible without pathogen and herbivore dam-

Table 1. Twenty-four tropical species included in the study, their land use type (MF, mature forest; SF, secondary forest; AF, agricultural field), guild (TST, total shade-tolerant; PST, partial shade-tolerant; LL, long-lived pioneer; SLP, short-lived pioneer; PALM, palm; H, herb; S, shrub) and decomposition rate (% biomass loss after 8 weeks)

Species	Land use type	Guild	Decomposition
<i>Ampelocera ruizii</i>	MF	TST	33.2
<i>Attalea phalerata</i>	MF	PALM	19.7
<i>Ficus boliviana</i>	MF	LLP	43.3
<i>Ficus eximia</i>	MF	LLP	24.0
<i>Hura crepitans</i>	MF	PST	75.3
<i>Licaria triandra</i>	MF	TST	20.8
<i>Ocotea sp.</i>	MF	PST	18.1
<i>Ocotea sp.</i>	MF	PST	20.8
<i>Pourouma cecropiifolia</i>	MF	PST	12.6
<i>Pouteria macrophylla</i>	MF	PST	35.1
<i>Pseudolmedia laevis</i>	MF	TST	24.6
<i>Schizolobium parahyba</i>	MF	LLP	47.0
<i>Stylogyne ambigua</i>	MF	TST	21.0
<i>Syagrus sancona</i>	MF	PALM	67.9
<i>Terminalia oblonga</i>	MF	PST	51.2
<i>Zanthoxylum sprucei</i>	MF	LLP	60.2
<i>Attalea speciosa</i>	SF	PALM	20.7
<i>Cecropia concolor</i>	SF	SLP	38.3
<i>Cecropia polystachya</i>	SF	SLP	18.6
<i>Heliocarpus americanus</i>	SF	SLP	67.0
<i>Trema micrantha</i>	SF	SLP	46.8
<i>Arachis hypogea</i>	AF	H	87.6
<i>Manihot esculenta</i>	AF	S	81.9
<i>Oryza sativa</i>	AF	H	60.8

age and without substantial epiphyll cover. Leaves were generally collected from five individuals per species, 4–5 leaves per individual (cf. Cornelissen *et al.* 2003). A minimum of five individuals and two leaves per individual was used. For palms, which have few extremely large leaves, a minimum of three individuals and two leaves per individual was measured. Whole twig sections with the leaves still attached were collected. The partial hydration method (Vaieretti *et al.* 2007) was used: samples were put in sealed plastic bags in which air was exhaled, so that leaves closed their stomata because of the high CO₂-concentration and thus remained water-saturated. Measurements took place as soon as possible after collecting, certainly within a few days. Leaves were not removed from the twigs until just before measurement.

To collect litter material 30 rectangular litter traps (70 × 100 cm) were installed in the mature forest and leaf litter was collected from September 2007 until April 2008 on a monthly basis. Litter was stored in an air-conditioned building until the litter decomposition experiment was started in May 2008. Litter was then sorted per species and species that contributed enough material were used in the experiment. Palm leaves were collected afterwards, because palm fronds remain on the plant for several months after senescence. The most recent senesced frond was taken that had no remaining green pigment. In addition, just prior to the experiment freshly shed, senesced and undecomposed leaf litter was collected for species from the agricultural systems and secondary forests by collecting leaves from the soil surface or by gently shaking plants.

LEAF AND LITTER TRAIT MEASUREMENT

For most species from mature forest leaf traits had already been measured by Rozendaal, Hurtado & Poorter (2006). We used the same

method as in those measurements. In general, measurements were done on the leaf lamina only. For a few species the petiole was included in the measurements, but its effect on calculated trait values is believed to be negligible (Cornelissen *et al.* 2003). For species with compound leaves, leaf area and mass were based on the total of leaflets plus rachis, with the exception of palms, for which only leaflets were used.

Leaf area (LA, cm²) was determined by scanning the leaves with a flatbed scanner and analysing the pictures with pixel-counting software (ImageJ; National Institutes of Health). Leaf thickness (LTh, mm) was measured with a micrometre, as close as possible to the middle of the leaf, avoiding the veins. For determining fresh mass (g), leaves were rehydrated during the night in plastic bags filled with moist tissue. Following the rehydration procedure, the leaves were cut from the branch and gently blotted dry with tissue paper to remove any surface water before measuring water-saturated fresh mass. Each leaf sample was then dried in the oven at 60 °C for at least 72 h and its dry mass (g) was determined.

Force to punch (F_p , N cm⁻²) is an indicator for the resistance of plants to herbivory (Coley 1983). F_p was measured with a penetrometer, which measures the mass that is needed to penetrate the leaf, between the veins, with the head of a nail. The weight on the nail was gradually increased until the nail penetrated the leaf. F_p was calculated as $\text{mass} \times 9.81 \text{ per } (\pi \times r^2)$, in which mass was expressed in kg and r represents the radius of the head of the nail in cm (0.181 in our study). Specific force to punch (SF_p) was calculated as F_p divided by leaf thickness, and is an indicator of the leaf material toughness (cf. Y. Onoda *et al.*, unpublished data). Chlorophyll content per unit area (Chl, in SPAD-units) was determined with a chlorophyll metre (SPAD-502; Konica Minolta, Osaka, Japan). The correspondence between SPAD values and independent measurements of chlorophyll contents is very good (Anten & Hirose 1999). For a pooled sample of leaves per species, the LNC (nitrogen mass per unit leaf mass, %) and leaf phosphorus concentration (LPC, phosphorus mass per unit leaf mass, %). LNC is a proxy for the photosynthetic capacity of the leaf. For leaf litter, nitrogen (LitterNC, %), phosphorus (LitterPC, %) and carbon concentrations (LitterCC, %) were measured.

From these data the following parameters were derived: SLA (one-sided area of a fresh leaf divided by its oven-dry mass, expressed in cm² g⁻¹), as a measure of the amount of leaf area for light capture per unit biomass invested; LDMC (oven-dry mass of a leaf divided by its fresh mass, expressed in g g⁻¹); leaf density (LD, in g cm⁻³); and litter carbon : nitrogen ratio (LitterC : N).

LITTER DECOMPOSITION EXPERIMENT

Litter decomposition rate was determined using the litter bag technique. Per species, 16 bags (size 10 × 15 cm) with 1 g of air-dried litter were prepared. Litter bags had a mesh size of 2.5 mm. This mesh size prevents the loss of small litter fragments but allows access of mesofauna (Swift, Heal & Anderson 1979). Mesh size may affect absolute decomposition rate, but it does not significantly change the species ranking based on litter mass loss (Cornelissen & Thompson 1997). Leaf litter used in the decomposition experiment was buried in the state in which it was found. This means that some compound leaves, for example, peanut leaves, had their rachis attached, while others, such as *Schizolobium parahyba* were decomposed without rachis. Although palm leaves fall down as a whole, their woody rachae were not included in the experiment. This could have led to an overestimation of their decomposition rate.

The litter bags were placed in an experimental litter bed in the tropical moist forest of La Chonta. Such a purpose-built outdoor leaf-mould bed normally hosts a naturally developed decomposer community. The bed had been established by clearing a flat area in the forest understorey and consisted of 16 randomized blocks in which each block (0.5 × 0.75 m²) contained one sample of each species. On 24 and 25 May 2008, the bags were buried at *c.* 4–5 cm depth. Since the experiment started at the beginning of the dry season, and since humid conditions are favourable for decomposers, the leaf decomposition bed was watered daily with *c.* 5 L water per m². This amount of water corresponds to the precipitation per day in La Chonta averaged throughout the year.

After one and two months, eight bags per species were collected from the decomposition bed. The content of the litterbags was gently brushed clean, after which the litter was oven-dried at 65 °C for 48 h and weighted. Decomposition rate (Dec, in %) was calculated as the percentage of initial dry mass lost after one or two months. A 5 g subsample per species had been set aside before the start of the experiment, in order to establish the relationship between the air-dry litter placed in the field and oven-dry litter mass, and for litter chemical analyses.

COMMUNITY-WEIGHTED MEAN TRAIT VALUES PER LAND USE TYPE

For each plot, the community-weighted mean (CWM) of LNC and SLA were calculated, based on the relative abundance of those species that made up 80% of the basal area (for the mature and secondary forest), or cover (for the agricultural field). Tree basal area scales closely with crown area and is therefore a good indicator of tree cover. The rationale of the 80% cut-off limit is that the most abundant species contribute most to vegetation characteristics and ecosystem processes (Garnier *et al.* 2004). CWM was calculated for each plot as the sum of the relative abundance of the species, multiplied by their species-specific trait value.

STATISTICAL ANALYSES

To evaluate how leaf traits of species were associated, a principal component analysis (PCA) was done with 10 leaf traits and four litter traits, using species ($n = 23$) as data points. A correlation analysis was carried out, to test how leaf and litter traits were correlated with decomposition rate. To evaluate which traits were the best predictors of decomposition rate, a forward and a backward multiple regression analysis were done, using the leaf and litter traits as independent variables. A one-way ANOVA with Tukey HSD post-hoc tests was used to evaluate whether leaf traits and decomposition rates varied between species belonging to different land use types. A one-way ANOVA with Tukey HSD post-hoc tests was used to evaluate whether the CWM differed between land use types. Data were tested for homoscedasticity and leaf area was log₁₀-transformed prior to analysis. All statistical analyses were carried out using SPSS 15.0 (SPSS Inc., Chicago).

Results

ASSOCIATION AMONGST LEAF TRAITS

Associations amongst the 14 leaf and litter traits were analysed with a PCA (Fig. 1a). The first axis explained 46% of the variation, and was positively related to SLA and nutrient

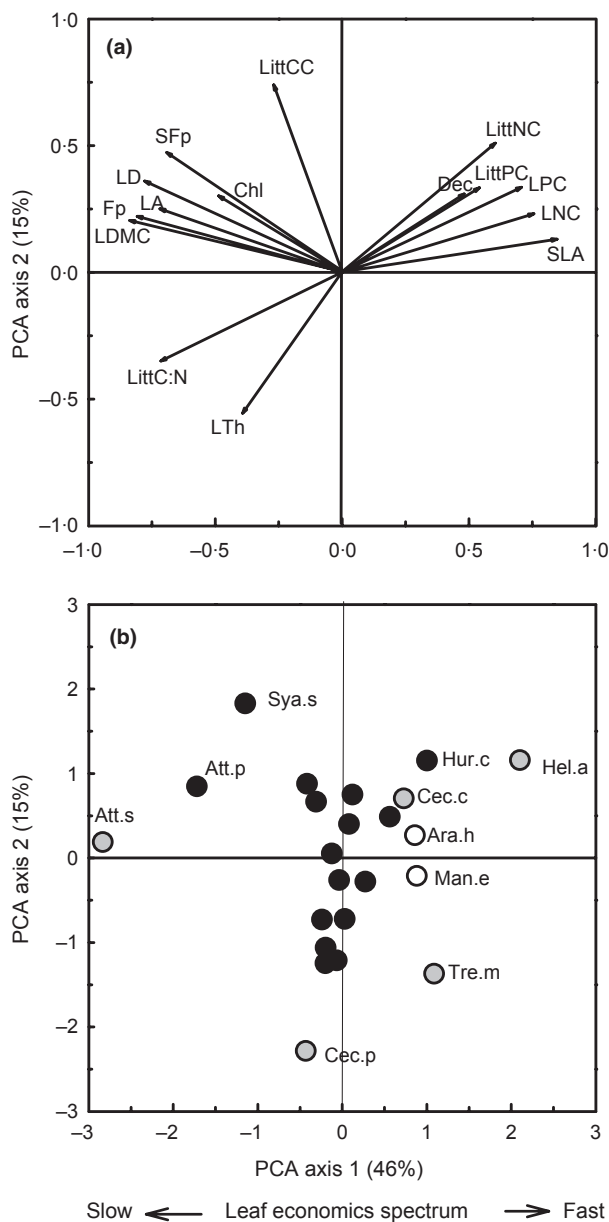


Fig. 1 Principal component analysis of 14 leaf and litter traits of 23 herbaceous and tropical tree species. (a) Loading plots of traits, (b) Species regression scores of mature forest species (black circles), secondary forest species (grey circles), and agricultural field species (open circles). Decomposition after 2 months (Dec) was not included in the analysis but has been plotted in the figure afterwards. Traits included are: LA, leaf area; LTh, leaf thickness; SLA, specific leaf area; LDMC, leaf dry matter content; LD, leaf density; Fp, force to punch; SFp, specific force to punch; Chl, chlorophyll content; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; LittNC, litter nitrogen concentration; LittPC, litter phosphorus concentration; LittCC, litter carbon concentration; LittC:N, litter C:N ratio.

concentrations in leaves and litter and negatively related to leaf density, LDMC, force to punch and leaf area. The second axis explained 15% of the variation and was positively related to litter carbon concentration and negatively related to leaf thickness.

Species are grouped in this multivariate trait space according to their functional types. Pioneer species such as *Heliocarpus* and *Trema*, and agricultural species such as *Arachis* and *Manihot* are found at the right side of the first PCA axis, palm species from the *Attalea* genus are found at the left side, and most mature forest species were found in the middle (Fig. 1b). Pioneer tree species, agricultural species, shade-tolerant tree species and palm species are each grouped together, indicating that these functional groups occupy different positions in the LES.

INTERSPECIFIC VARIATION IN DECOMPOSITION RATE

Species differed significantly in decomposition rate (ANOVA, $F = 30.0$, $P < 0.001$; Fig. 2). After 1 month, average litter mass loss across species was 24%, ranging from 8% for *Pourouma cecropiifolia* to 76% for *Manihot esculenta*. After 2 months, litter mass loss was on average 41%, with *P. cecropiifolia* still being the least decomposed (13%) and the peanut, *Arachis hypogaea*, the most decomposed species (88%, Table 1). Across species, litter mass loss after the first month was strongly correlated with litter mass loss after the second month (Pearson's $r = 0.89$, $n = 23$, $P < 0.001$). Mass loss differed between the two harvests (paired t -test: $t = -9.52$, d.f. = 22, $P < 0.001$) and was always larger after 2 months than after 1 month. For further analysis we will use the decomposition rate after 2 months because interspecific differences were larger at second harvest, thus providing a better resolution.

LEAF TRAITS PREDICTING DECOMPOSITION RATE

Interspecific variation in decomposition rate was significantly associated with the quality of fresh leaves (Table 2). LNC turned out to be the strongest correlate ($r = 0.77$; $n = 23$; $P < 0.001$; Fig. 3a), followed by SLA ($r = 0.57$; $n = 23$; $P < 0.01$; Fig. 3b), species position on the LES ($r = 0.49$; $n = 23$; $P < 0.05$; Fig. 3c) and LDMC ($r = -0.47$; $n = 23$; $P < 0.05$). Decomposition rate was not only related to leaf traits, but also to the regeneration strategy of the species, as indicated by the positive relationship between decomposition rate and CEJuv ($r = 0.50$, $n = 17$, $P < 0.05$; Fig. 3d).

There were no significant correlations between decomposition and concentrations of nutrients or carbon in litter, although litter nitrogen concentration ($r = 0.39$; $P = 0.067$) and litter C:N ratio ($r = -0.39$; $P = 0.07$) almost showed significant correlations. Litter and fresh leaf nutrient concentrations were, however, correlated (r between LNC and litterNC = 0.47; $n = 23$; $P < 0.05$; r between LPC and litterPC = 0.70; $n = 23$, $P < 0.01$). This means that the ranking of the species based on nutrient concentration is largely the same before and after leaf senescence.

Multiple regressions were carried out to analyse which leaf traits are the best independent predictors of decomposition rate. Forward multiple regression indicates that LNC and chlorophyll content explain variation in decomposition rate best ($r^2 = 0.69$; $n = 23$, Decomposition rate =

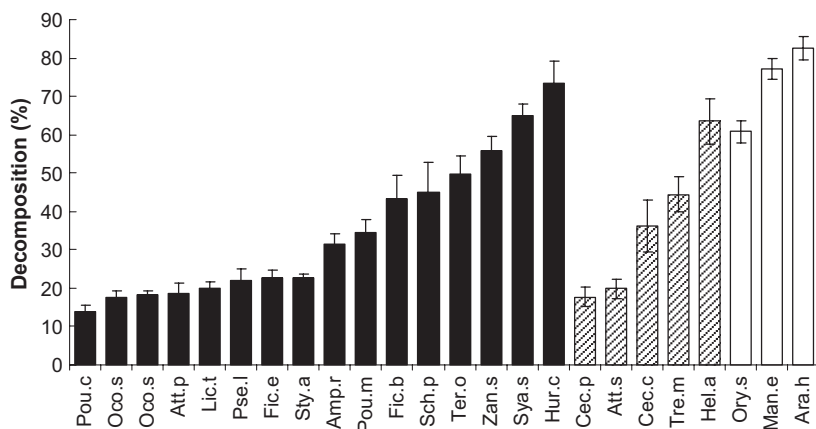


Fig. 2. Decomposition rate of 24 herbaceous and tropical tree species belonging to different land use types in which they are most common: mature forest (black bars), secondary forests (hatched bars), and agricultural field (open bars). Litter weight loss (%) is calculated after 2 months ($N = 8$). Means and SE are shown. Species names are indicated by the first three letters of their genus name and the first letter of their species name (see Table 1).

Table 2. Pearson correlations between 14 leaf and litter traits, the position of a leaf on the leaf economics spectrum, juvenile crown exposure and leaf decomposition after 2 months for 23 plant species from three land use types. Significant correlations are indicated in bold ($P < 0.05$), bold and italics ($P < 0.01$), or bold, italics and underlined ($P < 0.001$). Leaf area was log-transformed prior to analysis

Trait	Trait														Litter				
	Lth	lgLA	LD	SLA	LDMC	Fp	SFp	Chl	LNC	LPC	LitterNC	LitterPC	LitterCC	C:N ratio	LES	CEjuv			
lgLA	0.29																		
LD	-0.09	0.56																	
SLA	-0.49	-0.50	-0.70																
LDMC	0.06	0.59	0.83	-0.74															
Fp	0.34	0.70	0.52	-0.49	0.60														
SFp	-0.08	0.63	0.55	-0.36	0.64		0.86												
Chl	0.29	0.40	0.44	-0.47	0.31		0.44	0.30											
LNC	-0.38	-0.36	-0.61	0.80	-0.66	-0.49	-0.37	-0.10											
LPC	-0.38	-0.35	-0.49	0.67	-0.46	-0.43	-0.28	-0.45	0.57										
LitterNC	-0.30	-0.29	-0.29	0.40	-0.45	-0.41	-0.33	0.04	0.47	0.44									
LitterPC	-0.31	-0.24	-0.26	0.49	-0.34	-0.32	-0.15	-0.28	0.34	0.70	0.37								
LitterCC	-0.18	0.27	0.40	-0.17	0.28	0.33	0.44	0.37	-0.04	0.09	0.21	-0.04							
Litter C : N ratio	0.38	0.44	0.38	-0.48	0.50	0.55	0.44	0.07	-0.54	-0.42	-0.94	-0.34	0.05						
LES	0.39	0.72	0.78	-0.85	0.84	0.81	0.69	0.49	-0.76	-0.71	-0.61	-0.55	0.27	0.71					
CEjuv	0.12	0.53	-0.25	0.31	-0.44	-0.62	-0.60	-0.08	0.35	0.05	0.05	0.32	-0.45	-0.06	-0.35				
Dec	-0.23	-0.12	-0.44	0.57	-0.47	-0.24	-0.16	0.24	0.77	0.44	0.39	0.29	0.05	-0.39	-0.49	0.50			

$-55.3 + 29.4\text{LNC} + 0.58\text{Chl}$), while a backward regression selects both SLA and chlorophyll as the variables that best explain decomposition rate ($r^2 = 0.65$; Decomposition rate = $-71.7 + 0.36\text{SLA} + 1.2\text{Chl}$). As individual traits, LNC and SLA were significantly related to decomposition rate, but chlorophyll content turns out to be a poor predictor of decomposition ($r = 0.24$; $P = 0.27$).

LAND USE, LEAF TRAITS AND DECOMPOSITION RATES

Species belonging to different land use types differed significantly in their LNC (ANOVA, $F = 5.94$; $P = 0.009$, Fig. 4a), with species from agricultural fields having higher LNC than species from mature forest and secondary forest (Tukey HSD, $P < 0.05$). Species from different land use types did not differ significantly in SLA (ANOVA, $F = 2.93$, $P = 0.077$, Fig. 4b) or their position on the LES (ANOVA, $F = 0.99$, $P = 0.393$; Fig. 4c), but they did differ in decomposition rate

(ANOVA, $F = 5.98$, $P = 0.009$); species from agricultural fields decomposed faster than species from secondary and mature forest (Fig. 4d).

Community-weighted mean leaf traits and decomposition rates were also calculated for each land use type, based on the relative dominance of the species making up 80% of the basal area or cover. Both the community-weighted mean LNC (ANOVA, $F = 6.63$, $P = 0.03$) and community-weighted mean SLA (ANOVA, $F = 8.49$, $P = 0.018$) differed significantly among land use types and were lowest in secondary forest, intermediate in mature forest and highest in agricultural fields (Fig. 5).

Discussion

Little is known about decomposition rates of tropical plant species and the potential effects of land use change on decomposition. We first discuss how leaf and litter traits are

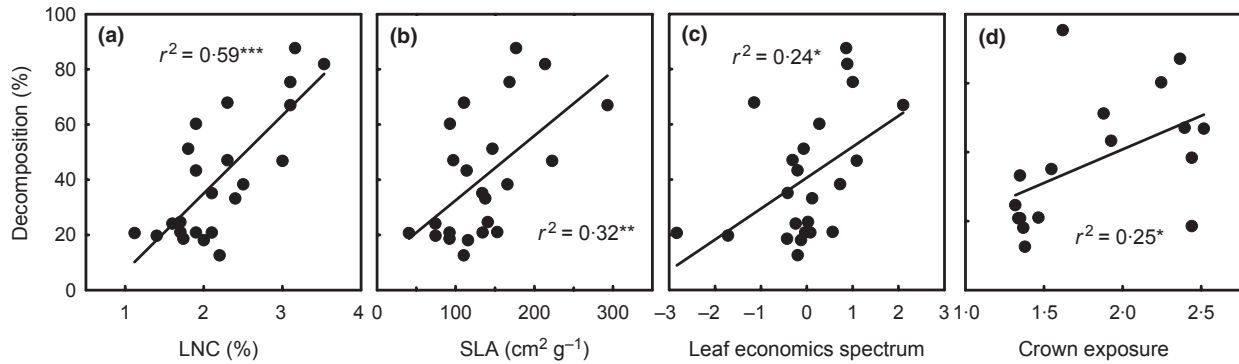


Fig. 3. Litter decomposition rate (leaf litter mass loss after 2 months of incubation) of 23 tropical species as a function of (a) leaf nitrogen concentration (LNC), (b) specific leaf area (SLA), (c) species position on the leaf economics spectrum (LES), and (d) juvenile crown exposure of a 2-m tall sapling of the species. Regression lines, coefficients of determination (r^2) and significance levels are shown.

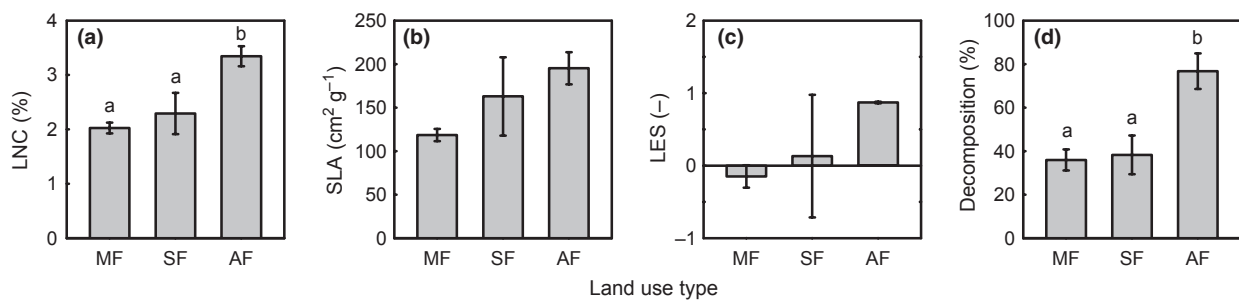


Fig. 4. Traits of species belonging to three different land use types [agricultural fields ($N = 2-3$ species), secondary forests ($N = 5$), and mature forest ($N = 16$)]. (a) Leaf nitrogen concentration (LNC), (b) specific leaf area (SLA), (c) species position on the leaf economics spectrum (LES) and (d) decomposition rate. Bars indicate mean \pm SE. Bars accompanied by a different letter are significantly different (Tukey HSD, $P < 0.05$).

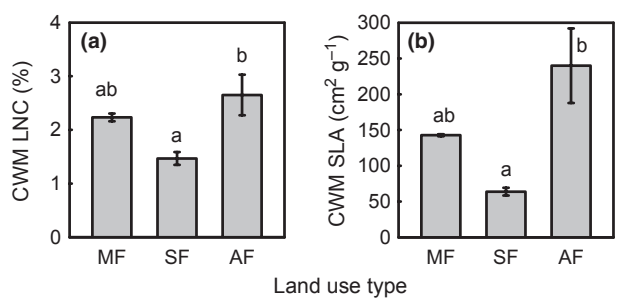


Fig. 5. Community-weighted mean (a) leaf nitrogen concentration (LNC) and (b) specific leaf area (SLA) for plots ($N = 3$) in three different land use types: mature forests (MF), secondary forests (SF) and agricultural fields (AF). Bars indicate mean \pm SE. Bars accompanied by a different letter are significantly different (Tukey HSD, $P < 0.05$).

associated, then evaluate what drives leaf decomposition rate, and conclude how traits and decomposition rates differ for species and communities from different land use types.

ASSOCIATION AMONGST LEAF TRAITS

Nearly half of leaf and litter traits (43 out of 91 possible pairwise combinations) were significantly correlated (Table 2)

and almost half of the variation in leaf and litter traits was explained by the first PCA axis (Fig. 1a). This axis was negatively related to leaf area, density, dry matter content, and toughness, and positively related to SLA and nutrient concentrations in leaves and litter. The first axis therefore represents the LES, with slow, conservative traits to the left, and fast, acquisitive traits to the right. In their analysis of the worldwide economics spectrum, Wright *et al.* (2004) focused on SLA, LNC, LPC and photosynthetic traits. Our current analysis shows that apart from SLA, other leaf defence traits (leaf density, dry matter content and toughness) form an integral part of this LES (cf. Díaz *et al.* 2004; Kitajima & Poorter 2010) and that this fast-slow continuum is mirrored in litter traits (e.g. litter nitrogen concentration, litter C : N ratio, Fig. 1a).

LEAF TRAITS PREDICTING DECOMPOSITION

The multiple regression analysis indicated that of all individual leaf and litter traits, a combination of LNC or SLA with chlorophyll content were the best predictors of decomposition rate. The relation between LNC and SLA and decomposition rate is consistent with previous studies (LNC: Santiago 2007; Cornwell *et al.* 2008; Fortunel *et al.* 2009; SLA: Cornelissen *et al.* 1999; Vaieretti *et al.* 2005; Santiago 2007).

Decomposers prefer nitrogen-rich leaves as nitrogen is an essential and limiting element for their metabolism. They might also prefer high SLA leaves, as decomposers can consume such litter more rapidly and easily, processing less leaf material per unit area or volume. In contrast, accessing C-rich and nutrient-poor material is more difficult, because decomposers need a variety of enzymes (Wieder, Cleveland & Townsend 2009).

Leaf nitrogen concentration was, surprisingly, better at predicting litter decomposition rate than litter nitrogen concentration, probably because a suite of correlated leaf traits affects decomposition rate, and LNC was a better indicator of this suite of correlated traits (as summarized in the LES) than litter nitrogen concentration (Fig. 1). LNC was, also surprisingly, a better predictor than LPC, despite the fact that tropical rainforest soils are thought to be limited in P, and despite the fact that most decomposition studies in lowland tropical forests find LPC to be more important for decomposition than LNC (Vitousek 1984; Aerts 1997; Hobbie & Vitousek 2000; Santiago 2007; Wieder, Cleveland & Townsend 2009). Limitation by nitrogen is not only indicated by the results of our decomposition experiment, but also by the relatively low N : P ratios of fresh leaves (13.7) and litter leaves (12.8). A N : P ratio smaller than 14 is generally a sign of N-limitation whereas a N : P ratio higher than 16 is indicative of P-limitation (Koerselman & Meulman 1996). Moreover, the fact that the N : P ratio declines during senescence, points out that N is preferentially reabsorbed over P. Two factors might explain why nitrogen played a more significant role than phosphorus in our decomposition experiments. Although phosphorus is often the most limiting nutrient in decomposition processes in tropical forests (Cleveland, Townsend & Schmidt 2002), nitrogen seems to be limiting in the forest where we carried out our experiments. The study of Cleveland *et al.* is based on a forest on extremely old, highly weathered soils in Costa Rica, whereas La Chonta forest is located on inceptisol: a soil of relatively new origin and usually fertile. In addition, black anthropogenic forest soils are relatively frequent in La Chonta forest (Paz-Rivera & Putz 2009) and these so-called terra-preta soils are especially rich in phosphorus (Peña-Claros *et al.*, unpublished data). Thus, limitation by nitrogen, as has been frequently found for temperate and high latitude forests, can also be found in tropical forests. A second explanation for the importance of N during decomposition is that nitrogen is most important during early stages of decomposition, whereas P is important later on (Santiago 2007). Decomposers feed preferentially first on nitrogen, but as [N] decreases, they switch to [P] on a certain point. Our experiment might simply not have lasted long enough to detect [P] influences on decomposition.

Specific leaf area, and to a lesser extent LDMC, were also significantly correlated with decomposition rate. SLA and LDMC are highly correlated ($r = -0.74$, $n = 23$, $P < 0.001$), probably because they are both closely related to leaf density. A high percentage of dry matter resulted in a lower decomposition rate (cf. Kazakou *et al.* 2006; Cortez

et al. 2007; Cornwell *et al.* 2008; Kurokawa & Nakashizuka 2008; Fortunel *et al.* 2009).

While chlorophyll content by itself is not correlated with decomposition, it explains in the multiple regression analysis a small additional part of variation in decomposition rate that is not explained by LNC or SLA. The positive effect of chlorophyll on decomposition, which to our knowledge has not been tested before, is surprising. Perhaps a high chlorophyll content is an indirect indicator of the nitrogen or magnesium concentrations in the leaf (as N and Mg are components of chlorophyll, which both directly affect decomposition rate), or an indirect indicator of SLA (as thick leaves with low LA will have a high chlorophyll content per unit leaf area). The effect of chlorophyll content suggests that it would be interesting to include it in decomposition studies, especially because it can readily and quickly be measured with the SPAD metre.

We found a negative, albeit non-significant relationship between force to punch and decomposition rate ($r = -0.24$; $n = 23$; $P = 0.266$). The weak relationship between leaf toughness and decomposability could be explained by a difference in what is measured and how decomposers perceive the plant material. Possibly, microbes are responding to the strength of chemical bonds between atoms, while puncture tests work on a larger scale and respond to the size and orientation of these molecules. For example, in Cornwell *et al.* (2008) mosses are very soft by any method of toughness measurement, but have a very low decomposition rate.

Other studies, which do find a significant negative relationship between leaf toughness and leaf decomposability (Cornelissen *et al.* 1999; Pérez-Harguindeguy *et al.* 2000; Kurokawa & Nakashizuka 2008) attribute this to both a dense leaf and the presence of chemically resistant elements like lignin and cellulose (Cornelissen 1996; Vaieretti *et al.* 2005; Kurokawa & Nakashizuka 2008; Parsons & Congdon 2008). We tried to capture the presence of lignin and cellulose by measuring litter carbon concentration. However, carbon was not significantly related to decomposition rate. A reason could be that only the amount and not the nature of carbon was measured. Thus, the carbon measured could have consisted of small compounds, which do not form a barrier for decomposition, instead of large molecules like lignin and cellulose. Studies in which carbon was found to play a role in decomposition always worked with ratios between carbon and a nutrient (Pérez-Harguindeguy *et al.* 2000; Kurokawa & Nakashizuka 2008), but in our study, ratios were not significantly correlated with decomposition rate either.

Not only individual leaf traits, but also species' position on the LES was positively correlated with decomposition rate ($r = 0.49$; $n = 23$; $P < 0.05$; Fig. 3c), with species with 'fast' acquisitive leaf traits showing higher decomposition rates than species with 'slow' conservative traits. This suggests that selection for a suite of coordinated structural and chemical leaf traits that determine photosynthetic rate, productivity and leaf longevity has strong nutrient cycling consequences. Similar results have been obtained for 35 tropical rainforest species (Santiago 2007) and 108 temperate herbaceous and

woody species from a *Ponderosa* pine forest (Laughlin *et al.* 2010). However, in contrast to our hypothesis, the LES as a multivariate descriptor of leaf traits was a weaker predictor of decomposition rate than individual components of the LES, such as LNC and SLA, and the LES was not selected by the multiple regression analysis. This suggests that individual components of the LES (LNC, SLA) are the real drivers of decomposition rate, rather than the LES itself.

Leaf decomposition rate was also related to the regeneration strategy of the species, albeit indirectly, with regeneration strategy determining leaf traits, which in turn define decomposition rate. Light-demanding pioneer species decomposed faster than long-lived pioneer and shade-tolerant species (Fig. 3d). This means that a plant's strategy determines its entire life cycle: pioneer species, for instance, combine high nutrient uptake rates with fast growth, leaf turnover and litter decomposition rates. Such a positive plant–soil feedback loop might, in the case of pioneer species, enhance soil fertility (Wardle *et al.* 2004) and in this way adults of these acquisitive species may pave the road for a new generation. In other words, systems dominated by pioneer species push themselves to an overall more fertile and productive state (cf. Cornelissen *et al.* 1999; Wardle *et al.* 2004).

LAND USE, LEAF TRAITS AND DECOMPOSITION RATES

Functional parameters of the plant species in each community that are important for decomposition changed with the intensity of land use. The communities of mature and secondary forests consisted of long-lived tree species with low LNC, while in agricultural fields this community had been replaced by assemblages composed of fast-growing herbaceous species with higher LNC (Fig. 4). This reflects disturbance intensity and frequency in the different land use types with land use being least intensive in mature forest and most intensive on agricultural fields. These results are in line with other studies, which found that higher disturbance selects for acquisitive plants with leaf characteristics at the faster end of the growth spectrum (Díaz *et al.* 1999; Garnier *et al.* 2007; Dorrough & Scroggie 2008; Fortunel *et al.* 2009). SLA and position on the LES did not differ significantly between species from different land use types, although they increase gradually from mature forest to agricultural field (Fig. 4b,c), like we expected. One reason can be the relatively low number of species per land use type, another that within mature forest species and secondary forest species there is a large interspecific variation in leaf traits, due to the presence of the palm species *Attalea speciosa*, *Attalea phalerata* and *Syagrus sancona*. If palms are excluded from the analysis, then SLA and LES do differ significantly between land use types (data not shown). Palm species are characterized by tough, long-lived leaves with very low LNC, SLA and extremely low scores on the LES axis (Fig. 1). A palm species like *A. speciosa* becomes very dominant in secondary forest fallows, when these are frequently burned through slash-and-burn activities, because it resists fire, as its apex is well-protected by surrounding leaves, and because it lacks a vascular cambium – an advantage, although

there are, in other parts of the world, other, non-monocot species which are able to succeed in frequently burned environments despite the presence of a vascular cambium (Bond 2008). Herbaceous or woody ferns are known to become dominant in other early successional tropical and sub-tropical forests (Amatangelo & Vitousek 2008, 2009). Species from agricultural fields had a higher average litter decomposition rate than secondary and mature forest species (Fig. 4d). Secondary forests were hypothesized to show a higher decomposition rate than mature forest, but the abundance of palms lead to a lower decomposition rate than expected. This means that the value of secondary forests for increasing fertility can be questioned.

The CWM reflects the characteristics of an 'average' plant in the community. Secondary forests were hypothesized to occupy an intermediate position between mature forests and agricultural fields (in line with Fig. 4), because its communities are thought to consist of rapid growing and photosynthesizing pioneer tree species with high LNC and SLA. However, secondary forests turned out to have the lowest LNC and SLA (Fig. 5), which is again explained by the high abundance of palm species; they make up 55% of total basal area in secondary forests. The palm species *A. speciosa* alone represented 46% of the assembly. It would be interesting to compare this high palm abundance with other secondary forests, to see whether this feature is widespread or typical for the Guarayos region.

This study showed that land use change indirectly affects decomposition rate. The indirect pathway, along which global change influences the functional composition of a community, which in turn changes ecosystem functioning, is known to be more important than the direct pathway, in which changes in abiotic conditions influence processes in the ecosystem (Cornwell *et al.* 2008). The nature of this process has been shown for Mediterranean fields (Kazakou *et al.* 2006; Cortez *et al.* 2007; Fortunel *et al.* 2009), but this is, to our knowledge, the first time that it has been analysed for tropical land use types, which are very important in global carbon and local nutrient cycles.

Conclusions

Tropical tree species show a slow–fast continuum in both the production and breakdown of their leaves. This is due to differences in leaf and litter traits, which range from tough, well-defended leaves to cheap, nutrient-rich and productive leaves. LNC or SLA combined with chlorophyll content per unit leaf area determine leaf decomposition rate of a range of tropical plant species from different land uses. Furthermore, species' position on the LES and regeneration light requirements predict decomposition rate.

Species from different land use types differed not only in their average LNC, but also in decomposition rates. Communities from agricultural fields had higher average LNC and SLA than communities from secondary forests. Given that land use change is happening on a large scale, and results in radical changes in species composition, this study shows that

large consequences for nutrient and carbon cycling are to be expected, both within an ecosystem and globally.

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