Biomass is the main driver of changes in ecosystem process rates during tropical forest succession

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Abstract. Over half of the world's forests are disturbed, and the rate at which ecosystem processes recover after disturbance is important for the services these forests can provide. We analyze the drivers' underlying changes in rates of key ecosystem processes (biomass productivity, litter productivity, actual litter decomposition, and potential litter decomposition) during secondary succession after shifting cultivation in wet tropical forest of Mexico.

We test the importance of three alternative drivers of ecosystem processes: vegetation biomass (vegetation quantity hypothesis), community-weighted trait mean (mass ratio hypothesis), and functional diversity (niche complementarity hypothesis) using structural equation modeling. This allows us to infer the relative importance of different mechanisms underlying ecosystem process recovery.

Ecosystem process rates changed during succession, and the strongest driver was aboveground biomass for each of the processes. Productivity of aboveground stem biomass and leaf litter as well as actual litter decomposition increased with initial standing vegetation biomass, whereas potential litter decomposition decreased with standing biomass. Additionally, biomass productivity was positively affected by community-weighted mean of specific leaf area, and potential decomposition was positively affected by functional divergence, and negatively by community-weighted mean of leaf dry matter content.

Our empirical results show that functional diversity and community-weighted means are of secondary importance for explaining changes in ecosystem process rates during tropical forest succession. Instead, simply, the amount of vegetation in a site is the major driver of changes, perhaps because there is a steep biomass buildup during succession that overrides more subtle effects of community functional properties on ecosystem processes. We recommend future studies in the field of biodiversity and ecosystem functioning to separate the effects of vegetation quality (community-weighted mean trait values and functional diversity) from those of vegetation quantity (biomass) on ecosystem processes and services.

Key words: biodiversity–ecosystem functioning; biomass; community-weighted mean; decomposition; ecosystem functioning; ecosystem processes; functional diversity; functional traits; Mexico; productivity; secondary succession; structural equation modeling.

Introduction

Most of the worlds' tropical forest is naturally regenerated secondary forest (FAO 2010), and the extent and importance of secondary forests will only continue to increase in the future (Letcher and Chazdon 2009). It is thereby vital to understand which functions and services can be provided by secondary forests, and to what extent ecosystem functioning recovers during tropical forest succession. This contributes to understanding the sustainability and maintenance of functions and services in future tropical forest landscapes (Nadrowski et al. 2010, Melo et al. 2013). Ecosystem functioning refers to the joint effects of all processes

that sustain an ecosystem, and ecosystem processes (EPs) can be defined as fluxes of matter and energy over time and space (Reiss et al. 2009). Biodiversity (broadly defined as "the variety of life") is generally accepted to be one of the major drivers of ecosystem functioning (Balvanera et al. 2006), though underlying mechanisms are still highly debated. Functional traits are proposed to provide the most direct link between biodiversity and ecosystem processes (Díaz et al. 2006), the reason for which we consider functional traits to represent biodiversity in this study. Functional traits are defined as those components of an organism's phenotype that determine its effect on ecosystem processes (Petchey and Gaston 2006) as well as its response to environmental factors (Naeem and Wright 2003). We distinguish two complementary ways to quantify the functional trait properties of biodiversity that imply different mechanisms by which biodiversity influences ecosystem processes: functional diversity and community-weighted

functional trait mean. Functional diversity (FD) describes the distribution of species in functional trait space (Mason et al. 2005). FD may have a positive effect on EP rates because highly diverse communities are better able to make optimal use of the available resources leading to increased ecosystem process rates, a mechanism which has been coined the *niche complementarity effect.* Community-weighted means (CWMs) describe the dominant functional trait value of the overall community, by weighting species trait values by the abundance of the species (Lavorel et al. 2007). An effect of CWM on EP rates indicates that the functional traits of the most abundant species in the community are responsible for most fluxes in the ecosystem. This mechanism is described as the *mass ratio effect* (Grime 1998). Whether the direction of the relationship between CWM and EP rates is positive or negative depends on the trait that is used for quantifying functional trait mean; trait values that enhance resource acquisition (high CWM of specific leaf area, high CWM of leaf nutrients) increase EP rates, whereas trait values that enhance resource conservation (high CWM of leaf dry matter contents, high CWM of wood density) decrease such rates (Garnier et al. 2004, Reich 2014).

Empirical progress in *biodiversity–ecosystem functioning* (BEF) research has mainly come from grassland experiments, and showed that both functional diversity and CWM are important for ecosystem processes like primary productivity and decomposition (Tilman et al. 1997, Mouillot et al. 2011) and for ecosystem services like soil carbon sequestration and fodder production (Butterfield and Suding 2013). CWM has been found to be more important than taxonomic diversity in explaining ecosystem processes in temperate grasslands (Mokany et al. 2008), while single-trait functional indices (both in CWM and in FD) were found to be stronger indicators of EPs than multi-trait indices in mediterranean grasslands (Butterfield and Suding 2013). Moreover, increasing evidence shows that different groups of species matter for different ecosystem processes, and that biodiversity matters more when a variety of ecosystem processes is taken into account (Hector and Bagchi 2007, Gamfeldt et al. 2008, Zavaleta et al. 2010, Isbell et al. 2011, Gamfeldt et al. 2013). Few studies have evaluated the link between biodiversity and EPs in forest ecosystems. Forests may fundamentally differ from grasslands, as they are structurally complex and slow growing, thereby providing ample opportunity for niche specialization with large potential effects on ecosystem processes. Earlier work demonstrated that functional diversity positively influenced productivity in temperate and boreal forest (Paquette and Messier 2011, Ruiz-Benito et al. 2014) and carbon stocks in tropical secondary forest (Bu et al. 2014), but negatively influenced carbon stocks in semi-arid forest ecosystems (Conti and Díaz 2013). Highly diverse tropical rain forests are far underrepresented in BEF studies, despite the fact that these face high rates of biodiversity loss due
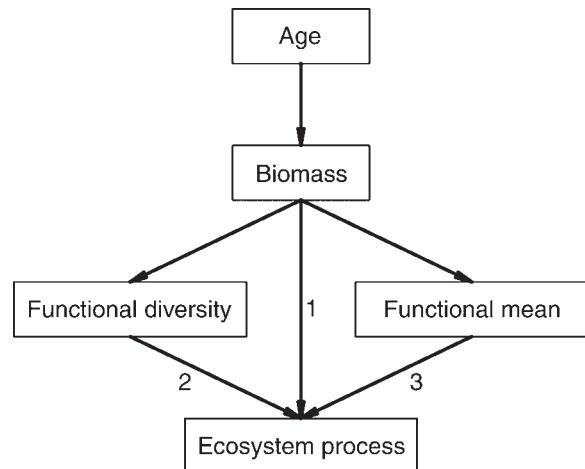

FIG. 1. The conceptual model used to test the link between succession, community functional properties, and ecosystem process rates, and the three alternative hypothetical pathways representing the three key hypotheses tested in this study: (1) vegetarian quantity hypothesis, (2) niche complementarity hypothesis, and (3) mass ratio hypothesis. See also the Appendix: Fig. A1 for a schematic representation of the different facets of the vegetation (quality and quantity), the hypotheses, and what indices are used.

to human activities and despite their importance for ecosystem functioning at the local, regional, and global scales.

In the current study we focus on the drivers of changes in ecosystem process rates in highly diverse tropical forests during secondary succession. We do not only test for effects of functional diversity and functional trait mean (which may be described as "vegetation quality") on EPs, but also for an effect of biomass, proposing that the quality of the vegetation may not matter, but simply their quantity. We coin this the "*vegetation quantity hypothesis.*" (For a schematic overview of the hypotheses addressed in this study see Fig. 1.) For example, positive effects of functional diversity on productivity in boreal and temperate forests were weak compared to the strong positive effect of basal area, which is an indicator of biomass (Paquette and Messier 2011), suggesting that quantity may be more important than quality. Similarly Vilà et al. (2013) found that the effect of species richness on wood production was largely mediated by stand basal area. This "vegetation quantity effect" may be especially relevant in early-successional forests where increases in plant biomass are rapid and may override more subtle changes in biodiversity (Martin et al. 2013).

Here we ask what drives the changes in rates of multiple ecosystem processes during tropical forest succession on abandoned agricultural fields. To this end we study the recovery of biomass, functional diversity, community-weighted mean, and key ecosystem processes in the tropical wet forest of Mexico. We use four ecosystem processes (biomass productivity,

litter productivity, actual decomposition, and potential decomposition) that determine some of the major fluxes of biomass and nutrients over time (Hooper et al. 2005). We focus on secondary forest sites that cover the crucial first three decades of tropical forest succession (e.g., Chazdon 2014). We scale up from species-level functional traits to the community level using three indices (richness, evenness, and divergence [Mason et al. 2005]) and community-weighted means (Garnier et al. 2004, Lavorel et al. 2007). We address the following research question: How do successional changes in biomass, community-weighted mean, and functional diversity affect the recovery of key ecosystem processes? We hypothesize that communities with higher biomass (vegetation quantity hypothesis), higher functional diversity (niche complementarity hypothesis), and community-weighted means towards more acquisitive trait values (mass ratio hypothesis) will have faster ecosystem productivity rates and decomposition rates. We expect that biomass and litter productivity will be mainly influenced by vegetation quantity (biomass), whereas litter decomposition will mainly be influenced by vegetation quality (community-weighted mean and functional diversity).

Methods

Study region

Tropical forest research plots were established close to the village of Loma Bonita, in Marqués de Comillas, Chiapas, southeastern Mexico (16°01′ N, 90°55′ W). Mean annual temperature is 24°C and mean annual precipitation is 3000 mm, with a dry period (<100 mm/month) from February through April (van Breugel et al. 2006, 2007). Small hills and valleys with sandy and clay silt soils of low pH (<5.5) characterize the research area. Fifteen secondary forest plots (permanent sampling plots; 1000 m^2 each) with different fallow ages (<1–29 year) were established on abandoned maize fields. The research plots are located in a landscape of ~1500 ha, within which the distance between plots ranges from 60 m to 11.5 km, where plots of similar age (<2 years difference) were at least 800 m apart (see Appendix: Fig. A3 for a map). Each plot was divided into two 10 × 50 m subplots. In one subplot all individuals with dbh ≥1 cm were taxonomically identified and measured; in the other all individuals with dbh ≥5 cm; this was repeated in annual censuses. Variables measured on each individual were scaled up to plot level according to sampling effort per size class (i.e., sampling effort for $1 \leq dbh \leq 5$ is half the sampling effort for dbh ≥5).

Functional traits

The species that together represent at least 80% of the basal area of the plots were selected for functional trait measurements, as these should accurately describe community functional properties (Garnier et al. 2004, Pakeman and Quested 2007, but also see Pakeman 2014). We therefore measured 80 species that covered on average 92% of the basal area in each plot (range 80–99%). We measured five functional traits per species that are important for the carbon and nutrient balance of plants and thereby for the effect of species on ecosystem-level fluxes of energy and matter. Functional traits were measured on 5–10 individuals per species in the study landscape, not inside the research plots. We followed standardized protocols (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013). For leaf traits, small adult trees (~5 m high) were selected and sun leaves used for trait measurements. Leaves were photographed on a light box, after which leaf area was calculated using pixel-counting software ImageJ (Rasband 2008). Leaves were dried until constant mass and weighed. Specific Leaf Area (SLA, in square meters per kilogram) was calculated as fresh leaf area divided by oven-dried mass, and Leaf Dry Matter Content (LDMC, g/g) as leaf oven-dry mass divided by fresh mass (rehydrated after field collection). To determine leaf nitrogen and phosphorus content (in milligrams per gram), samples were ground to pass a 0.5-mm sieve prior to analysis. Colorimetric determinations were carried out in a Bran-Luebbe AutoAnalyzer III (Technicon Industrial Systems 1977, Norderstedt, Germany) after acid digestion by the macro-Kjeldahl modified method in the case of nitrogen, and after ascorbic acid reduction (Murphy and Riley 1962) in the case of phosphorus. Wood density was based on wood cores, using a 12-inch millimeter increment borer (Suunto, Vantaa, Finland), or stem slices for species where stems did not reach sufficient size (<5 cm dbh). The fresh volume was determined with the water displacement method. Wood density (WD) was calculated as oven-dried mass over fresh volume (grams per cubic centimeter). This measurement was taken in the study area for 66 of the 80 species studied; data on WD for remaining species were taken from comparable studies in Mexican wet forests in Las Margaritas, Puebla (seven species) and Los Tuxlas, Veracruz (seven species). Species' average trait values were used, although we recognize that intraspecific trait variation may play an important role in the acclimation of species adaptation along environmental gradients as well as in their effects on ecosystem processes (Baraloto et al. 2010). However, given the high number of species in tropical forest and the high species turnover during succession (Chazdon et al. 2007), we consider the use of species average trait values meaningful for the purpose of this study.

Site properties

For each plot the time after abandonment was determined based on interviews with landowners. Aboveground biomass (megagrams per hectare) was estimated with allometric formulas developed for secondary forest in Panama and based on dbh and wood density (van Breugel et al. 2011). Where species' wood density values were missing (<20% of total basal area), we used the average wood density value of the

corresponding genus (calculated from our region's data) or else average wood density values across all 80 species considered in this study. To calculate carbon stocks, we multiplied aboveground biomass with the carbon concentration of 0.45 found for a very similar Mexican tropical forest (Hughes et al. 2000). Biomass data used in the analyses came from the year 2010 for nine of the permanent sampling plots and from the year 2012 for six later-established plots. For the biomass productivity only we used the 2009 biomass data for the nine earlier established sites to ensure it corresponded to the initial biomass of the period over which productivity was calculated (2009–2010, see following paragraph). For each of the plots we measured plot-average litter nitrogen and phosphorus content measured for five samples of well-mixed litter from litter traps in each site (see *Ecosystem processes*), using the colorimetric determinations (see *Functional traits*).

Ecosystem processes

The rates of change in four key ecosystem processes were measured in each of the successional sites, which quantified some of the major fluxes in energy and matter that take place in forests. They reflect the buildup of biomass, the litter that is produced, as well as the rates at which this litter decomposes. By including both actual and potential litter decomposition rates we were able to elucidate the effects of just the litter quality (potential) from what really happens in the sites (actual). These EPs are important for the provisioning of several ecosystem services (see Appendix: Table A1).

Biomass production rate.—Biomass production is the difference in aboveground biomass over a one-year interval (megagrams of carbon per hectare per year), and was calculated based on the previously mentioned allometric formulas. For nine of the permanent sampling plots it was calculated for the period 2009–2010 and for six later-established plots for the period 2012–2013.

Litter production rate.—The litter production rate (grams per square meter per day) was estimated by establishing seven litter traps (70 × 100 cm, at a height of 1.3 m) at random locations in each site and collecting the litter for two consecutive months (January–March 2012). Each month the litter was dried and weighed.

Actual litter decomposition rate.—Actual (in situ) leaf litter decomposition rates (percentage mass loss per day) were estimated using the litterbag method. Leaf litter was collected from the litter traps described above. Five litterbags (mesh size of 1 mm) containing an initial dry mass of 2–3 gram of well-mixed litter (leaves only) were incubated in each of the sites from February to April 2012. After two months the remaining litter was dried, carefully brushed clean, and weighed. The litter before incubation was weighed, after which the dry mass was estimated using the site-specific average water content of the litter material. Decomposition is the mass loss as a

percentage of the estimated initial dry mass, expressed per day.

Potential litter decomposition rate.—Potential (ex situ) leaf litter decomposition rates (percentage loss in mass per day) were estimated using the litterbag method in a common garden experiment. Leaf litter was collected from the litter traps described previously. Five litterbags with a mesh size of 1 mm were filled with well-mixed leaf litter of known dry mass (~3 grams) and incubated in a common garden (March to April 2012). During incubation the decomposition bed was irrigated with the average yearly precipitation and after one month the remaining litter was dried, carefully brushed clean, and weighed. The difference between actual and potential litter decomposition is the environment in which the litter mixtures decompose. Actual decomposition was determined by incubating the litter in its natural environment (in situ), thereby reflecting abiotic conditions, decomposer community, and litter material, whereas potential decomposition takes the material into a common garden (ex situ), and variation in decomposition rates is therefore due to the litter characteristics only.

Statistical analysis

Functional traits were scaled from species level to the community level using functional diversity indices and community-weighted means. For functional diversity we used three orthogonal indices: functional richness (convex hull volume encompassing all species in the community), functional evenness (evenness of abundances in trait space) and functional divergence (degree of divergence in abundances in trait space) (Mason et al. 2005). We decided not to include species richness because it tightly correlates to functional richness in our data set (see also Appendix: Table A4), and because functional diversity is suggested to be more important than taxonomic diversity (Tilman 2001, Micheli and Halpern 2005). These multivariate indices were calculated using a selected set of three or four traits that were relevant for a specific process. SLA, leaf N, and WD were used for productivity processes, as these indicate the investment per unit leaf area to capture light, photosynthetic capacity, and volumetric growth capacity (Poorter and Bongers 2006, Poorter et al. 2008). SLA, LDMC, leaf N, and leaf P were used as indicators of decomposition processes, as these indicate leaf toughness, fiber density, nutrient contents, and palatability (Cornelissen and Thompson 1997, Bakker et al. 2011). Community-weighted means are used to approximate plot-level functional trait averages (Garnier et al. 2004, Lavorel et al. 2007). Community-weighted means were based on SLA, leaf N, and WD for productivity processes and on SLA and LDMC for decomposition processes. We chose to measure community-weighted nitrogen and phosphorus directly from the litter because this is a more accurate measure of the substrate's chemical composition than the community-weighted

mean of nutrients measured on green leaves (see also Appendix: Fig. A1 for a schematic representation of the traits used to calculate different indices for the ecosystem processes). Community functional properties were calculated using the R package FD (Laliberté and Shipley 2014). We weighted functional diversity (evenness and divergence) and community-weighted means by a species' relative basal area in the plot. The relative basal area represents the species' relative biomass contribution, which reflects plant performance and adaptation to local conditions and may determine a plant's contribution to ecosystem processes.

Structural equation modeling (SEM, as implemented in the R package Lavaan [Rosseel 2012]) was used to relate site properties, community functional properties, and ecosystem processes. SEM is a statistical method that tests for causal relationships. Our conceptual a priori model (see Fig. 1) is based on existing knowledge of this study system where biomass (van Breugel 2007), functional diversity, and community-weighted means (Lohbeck et al. 2012, 2013) have been shown to change during secondary succession. We tested three alternative pathways that can explain changes in ecosystem processes during succession: the vegetation quantity hypothesis (positive relation between biomass and EP), the niche complementarity hypothesis (positive relation between FD and EP), and the mass ratio hypothesis (positive relation between acquisitive trait values and EP or negative relation between conservative trait values and EP). As our sample size is small ($n = 15$) we were limited to simple model structures (with few variables) and therefore chose to test for different combinations of community functional properties in alternative models. For this same reason, we tested each of the ecosystem processes in separate models, instead of all together. The alternative models include all combinations of functional diversity components (richness, evenness, and divergence) with community-weighted means (based on different individual traits), plus leaving out the functional diversity and community-weighted mean pathways. This produced 16 alternative models for biomass and litter productivity (3 FD components plus leaving out FD [equals 4] times 3 CWMs plus leaving out CWM [equals 4] makes a total of 16 models) and 20 alternative models for actual and potential decomposition (3 FD components plus leaving out FD [equals 4] times 4 CWMs plus leaving out CWM [equals 5] makes a total of 20 models). First, we rejected all models with a significantly poor fit ($P < 0.05$); then, we excluded the models that had no significant links to the EPs we are trying to explain. Subsequently, the best-fitting models were selected based on the lowest AIC (we present test results for the five best models, given our constraints, in Appendix: Table A1). AIC penalizes for model complexity and thereby tests whether the addition of a functional diversity and a community-weighted mean pathway to the model contributes to explaining variation in EPs, despite the increased complexity associated

with additional pathways. In the appendix we presented an additional method based on principal component axes instead of individual indicators for FD and for CWM. Here, PC1 and PC2 are used as compound variables that capture the most important axes of variation in FD and CWM. This reduced the number of alternative models to nine models per EP (Appendix: Table A5 and Fig. A4). All statistical analyses were carried out using R v. 3.0.0 (R Development Core Team 2011).

RESULTS

A best-fitting model, that met our a priori constraints, was found for each of the four ecosystem processes. Results confirm that our conceptual model (in which successional age increases biomass, leading to changes in community functional properties, which in turn affect ecosystem processes; Fig. 1) adequately describes the data, even though not all causal paths were significant (Fig. 2). The single best-fitting model included both a functional diversity component and a community-weighted mean component for each of the ecosystem processes (see Appendix: Table A2). Overall, the selected models explained 25% of biomass productivity, 77% of litter productivity, 24% of actual litter decomposition, and 61% of potential litter decomposition. In all cases aboveground biomass significantly explained changes in EP rates. Aboveground biomass had a positive effect on ecosystem process rates in the case of biomass productivity, litter productivity, and actual decomposition and a negative effect on potential decomposition. Additionally, biomass productivity was positively affected by community-weighted mean specific leaf area (nearly significant, $P = 0.09$). And potential decomposition was positively affected by functional divergence, and negatively affected by community-weighted mean of leaf dry matter content (Fig. 2; Appendix: Fig. A2 and Table A3). For additional information a table with the pairwise correlation coefficients for all variables is given in the appendix (Appendix: Table A4).

DISCUSSION

We assessed drivers of changes in ecosystem process rates during tropical forest succession, and found support for all three alternative hypotheses; the vegetation quantity hypothesis, the niche complementarity hypothesis, and the mass ratio hypothesis. Vegetation quantity (biomass) was an important driver for all the four studied ecosystem processes, while vegetation quality (functional diversity and community-weighted mean) was only of additional importance for biomass productivity and for potential decomposition.

Vegetation quantity overrules the effect of vegetation quality in explaining ecosystem processes

Our model explained 25% of the variation in biomass productivity. Biomass was the only factor contributing significantly to productivity, confirming the "vegetation
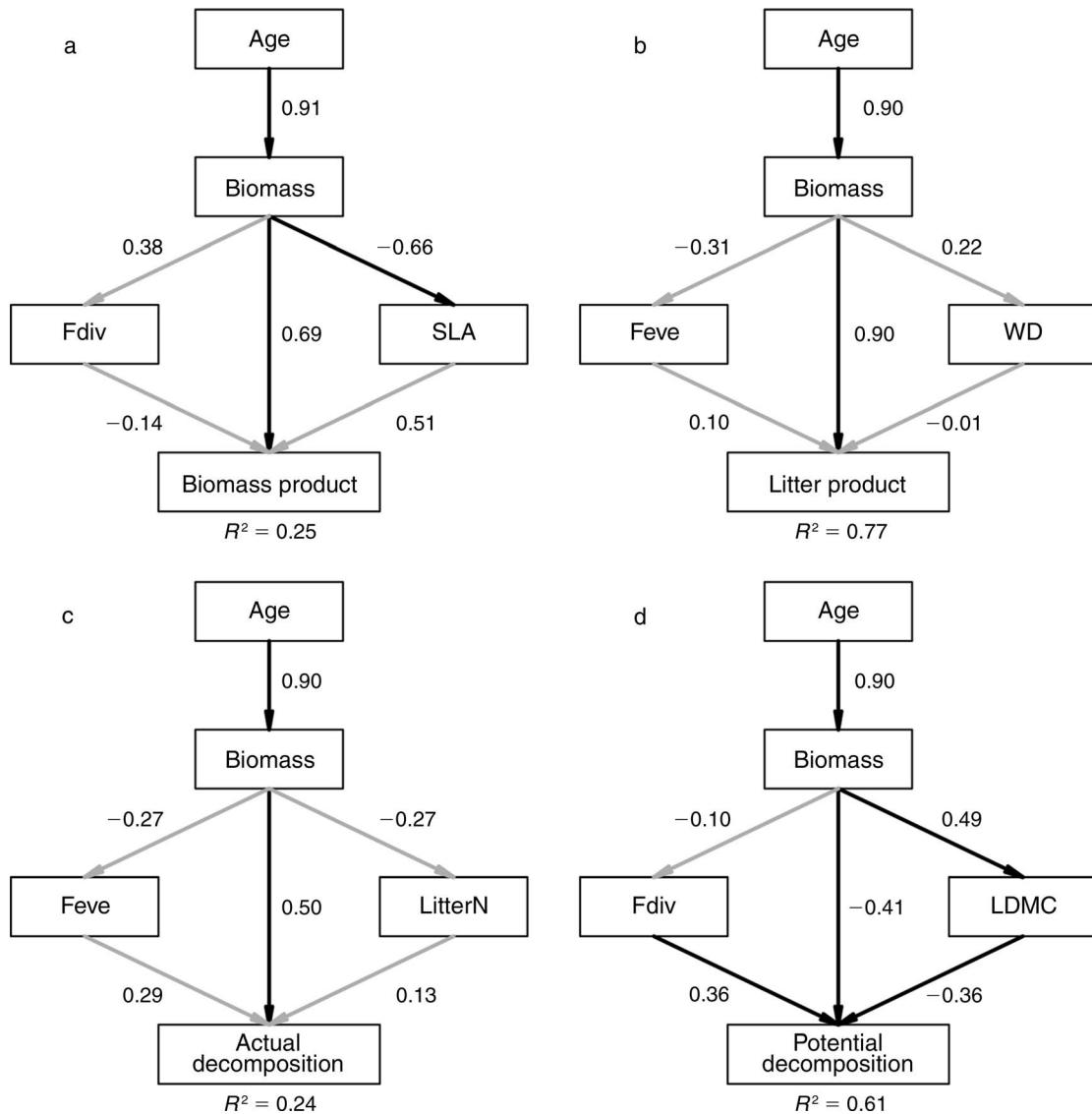
FIG. 2. Best-fitting (see Appendix: Table A2) structural equation models (df = 4) for each of the ecosystem processes studied along a tropical wet forest successional gradient in Chiapas, Mexico. (a) Biomass productivity (Biomass product) was significantly explained by biomass and together with functional divergence (Fdiv) and community-weighted mean specific leaf area (SLA) explained 25% of the variation. (b) Litter productivity (Litter product) was explained by biomass and together with functional evenness (Feve) and community-weighted mean wood density (WD) explained 77%. (c) Actual decomposition (Actual decomposition) was explained by biomass and together with functional evenness (Feve) and litter nitrogen content (LitterN) explained 24% of the variation. (d) Litter potential decomposition (Potential decomposition) was explained by biomass, functional divergence (Fdiv), and community-weighted mean of leaf dry matter content (LDMC) and explained 61%. Black arrows represent significant relations ($P < 0.05$), gray arrows nonsignificant ones. The numbers represent the standardized path-coefficients (for unstandardized path-coefficients see Appendix: Table A3; for process rates as a function of the main explanatory variable see Appendix: Fig. A2).

quantity hypothesis" (Fig. 2a; Appendix: Fig. A2a). Other factors included in the best-fitting model were functional divergence and community-weighted specific leaf area. Although specific leaf area was not statistically significant (see Appendix: Table A3), it has a potentially strong effect on biomass productivity as indicated by its large standardized coefficient (0.51). These results indicate that, as secondary forests increase in biomass,

their absolute annual biomass gain also increases, and at the same time, for communities where the species that dominate have large specific leaf area, the annual biomass gain will be higher. Such a positive relation between forest productivity and initial biomass has been widely found for mature forest systems (Chisholm et al. 2013), but for secondary forest systems no effect was found (Hughes et al. 1999). Patterns are similar to

previous work where the direct effect of basal area on productivity is much larger than the effects of diversity in North American forests (Paquette and Messier 2011), as well as across European forests (Vilà et al. 2013). As secondary forests get older, and contain more biomass, the average size of the trees in a plot also increases. Increasing growth with tree size, at the level of the individual tree (Stephenson et al. 2014), could be one of the underlying mechanisms. Some experimental studies did find diversity effects on productivity, in tropical forest systems (Haggar and Ewel 1997) and in temperate grassland studies (Wilsey and Potvin 2000), but these did not take into account any biomass effects. Niche complementarity as a driver of productivity (and other ecosystem processes) is thought to be primarily important under relatively resource-limiting conditions, when species need to differentiate their resource uptake strategies to be able to coexist. When key resources are unlimited, dominant species (those that most effectively capture resources) may determine biomass productivity (Warren et al. 2009, Paquette and Messier 2011). The positive effect of SLA on productivity may indeed indicate that in the high-light early-successional sites, where high SLA pioneers dominate, productivity is higher than what is expected based on initial biomass only. Along a gradient of tropical forest succession light becomes increasingly limited. One may therefore expect changing drivers of productivity rates from community-weighted mean in early succession when species that most effectively capture light dominate, to functional diversity in late succession when competitively driven niche complementarity starts to shape the community. Previous work at our study site showed that species indeed become increasingly different in their functional strategies during succession, which can be explained by increased resource limitation, and hence, increased resource competition (Lohbeck et al. 2014). This suggests that the niche complementarity effect could become important in later successional stages (cf. Fargione et al. 2007). This is in line with the meta-analysis by Cardinale and co-workers (Cardinale et al. 2007), who concluded that the effect of species diversity on productivity increases due to the increased effect of complementarity as experiments run for a longer time. Our chronosequence is relatively short (up to 29 years of succession), and the sharp increase in vegetation quantity early during succession may overrule more subtle effects of vegetation quality on productivity (Martin et al. 2013). Further research should evaluate how the relative contributions of vegetation quantity and quality to productivity change over longer successional gradients.

Litter production was the ecosystem process for which most variance (77%) was explained. The strongest driver was again aboveground standing biomass, in line with the vegetation quantity hypothesis (Fig. 2b; Appendix: Fig. A2b). When more biomass accumulated in the secondary forests, more litter was produced. The best-fitting model also included functional evenness and wood density, but these factors did not have a significant effect on litter productivity. Other studies also found increases in litter production during succession, but did not evaluate the underlying drivers (Ewel 1976, Yan et al. 2009, Zhang et al. 2013).

The best model explained 24% of the variation in *actual* litter decomposition. The strongest factor increasing decomposition was again aboveground standing biomass, confirming the vegetation quantity hypothesis (Fig. 2c; Appendix: Fig. A2c). The model also included functional evenness and litter nitrogen content, but these did not have a significant effect on actual decomposition, against expectations. A strong positive biomass effect on actual decomposition effect suggests that stands with higher biomass provide better abiotic conditions for decomposition, i.e., less extreme understory temperatures and higher relative humidity (Lebrija-Trejos et al. 2010). This biomass effect overrules any effects of biodiversity and litter quality, suggesting a major role for abiotic conditions (Pérez-Harguindeguy et al. 2007, Ostertag et al. 2008). This is unlike previous studies showing that leaf characteristics exerted a stronger influence on decomposition rates than local environmental conditions (Xuluc-Tolosa et al. 2003, Cornwell et al. 2008, Carreño-Rocabado 2013). In the common garden experiment we did find significant effects of community functional properties. The best model explained 61% of the variation in *potential* decomposition rates. Changes in potential decomposition were attributed to standing biomass (confirming again the vegetation quantity hypothesis), but also by functional divergence and community-weighted mean of leaf dry matter content, thereby also confirming the vegetation quality hypothesis (Fig. 2d; Appendix: Fig. A2d). As explained, actual decomposition (in situ) reflects abiotic conditions, decomposer community, and litter material, whereas potential decomposition (ex situ) should reflect litter characteristics only. Counterintuitively, the aboveground biomass in the plots where the litter came from was still a significant predictor of potential leaf decomposition, having a negative effect. A possible explanation is that the decomposer community in the common garden may be predominantly bacteria based, which is typical for more disturbed sites (Wardle 2004), as the area was previously used for sheep grazing, and to establish the experiment the vegetation had to be removed, causing considerable disturbance to the soil. Such disturbance-related decomposer community may have a food preference for litter of more disturbance-related tree species, having litter quality characteristics that could not be captured by the community functional properties in the model. Potential decomposition is the only ecosystem process that was significantly affected by vegetation quality, perhaps because the more subtle effects of vegetation quality can be better picked up under standardized conditions. Functional divergence had a positive effect on potential

litter decomposition rates. This suggests that a diverse range of decomposer groups was present in the common garden, which by complementary resource use was able to decompose high diverse litter faster than low diverse litter (Gessner et al. 2010, Handa et al. 2014). At the same time, we detected that decomposition rates were negatively related to the average leaf dry matter content of the community. Leaf dry matter content is a defense trait and is widely shown to have a negative effect on decomposition rates (Kazakou et al. 2006, Bakker et al. 2011). Both functional diversity and community-weighted mean LDMC had a significant effect on potential decomposition rate, indicating that both the niche complementarity hypothesis and the mass ratio hypothesis may explain decomposition rates (cf. Handa et al. 2014). In the literature the relative importance of these contrasting hypotheses is under strong debate, where some studies indicate explicit diversity effects on decomposition (Scherer-Lorenzen 2008), whereas other studies found that decomposition rates of litter mixtures rates are driven by the functional characteristics of the average species in the mixture (Garnier et al. 2004, Tardif and Shipley 2013).

Implications for biodiversity ecosystem functioning studies

We found that changes in ecosystem process rates in secondary forests depend mainly on the aboveground biomass of the site. This was also the case when using PCA axes instead of individual indicators for CWM and FD (see Appendix: Fig A4). Vegetation quality characteristics (functional diversity and community-weighted mean) had notable effects only on biomass productivity and in the common garden decomposition experiment. This suggests that biodiversity may not matter as much for these ecosystem processes as often supposed, at least not during the early phase of secondary succession. Though mostly insignificant, both functional diversity and community-weighted mean were maintained in all four best-fitting models. This suggests a role for FD and CWM, but our study does not have sufficient power to be able to conclude they had causal effects. We argue that more detailed studies are needed to better understand the mechanisms linking biodiversity to ecosystem functioning, especially for species-rich tropical forest ecosystems. Experimental studies are urgently needed to clarify such uncertainties, but for many ecosystems, like species-rich tropical rain forest, a proper experimental setup is an overwhelming task. Such experiments have been carried out, and revealed that diversity may not matter, since monoculture and mixed-species assemblages had the same effect on soil fertility (Ewel et al. 1991), were equally productive (Ewel 1999), and equally effective at resource capture in a Costa Rican experiment (Berish and Ewel 1988). In Panama, litter productivity and decomposition were not affected by diversity (Scherer-Lorenzen et al. 2007), but in China diversity promoted nitrogen acquisition and retention (Lang et al. 2014).

Such experiments, though very informative, are still at the low-diversity side of the spectrum, typically using different combinations of up to six species. We emphasize the need for complementary studies based on observational data, and using statistical methods that allow separating different factors underlying changes in ecosystem processes, such as structural equation modeling (e.g., Paquette and Messier 2011, Vilà et al. 2013, Walker et al. 2013). We found that there may be a strong effect of vegetation quantity, which could overrule any effect of vegetation quality (functional diversity and community-weighted mean). To better understand the mechanisms by which biodiversity may relate to functioning we need to disentangle different factors (qualitative from the quantitative vegetation characteristics) contributing to ecosystem functioning (Bengtsson 1998). Doing otherwise, especially in strong change gradients like the secondary succession gradient studied here, a diversity effect may actually be a biomass effect. Such a lack of control for changes in plant biomass is one of the major criticisms to biodiversity–ecosystem functioning studies (Hodgson et al. 1998, Bolam et al. 2002).

Implications for the recovery of tropical forest functioning

We showed that vegetation quantity is the main driver of changes in rates of different ecosystem processes during the first three decades of succession. Our results indicate that optimizing carbon capture (productivity) requires large biomass, so to speed up forest recovery, fast-growing species with high SLA might be planted (Martínez-Garza et al. 2013). The same would account for increasing the litter layer and organic matter content of the upper soil; plant fast-growing species that produce large amounts of leaves. To enhance soil quality through increased decomposition rates, it may be additionally important to plant species that have functional traits that are complementary to each other to increase functional diversity, though avoiding species with high leaf dry matter content. In combination, these results suggest that the recovery of specific ecosystem processes requires specific restoration measures. Combined with clear indications of trade-offs between optimal levels of different ecosystem processes and services (Raudsepp-Hearne et al. 2010), this makes the restoration of ecosystem functioning (being the joined effect of all ecosystem processes) a complex undertaking. Maybe more than realized so far, such restoration requires that the desired levels of ecosystem processes (depending on the stakeholders) are made explicit and that the instruments to achieve the functional restoration goals are adapted to those specific levels.

We show that vegetation quantity overrules the effects of vegetation quality on ecosystem process rates in tropical secondary forests in Mexico. We argue that different components (qualitative and quantitative) of the plant community should be addressed both sepa-

rately and in conjunction to be able to more fully understand the mechanism by which biodiversity affects ecosystem processes.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/14-0472.1.sm