Modelling the effects of litter decomposition on tree diversity patterns

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ABSTRACT

Current theories may not fully explain why latitudinal patterns of plant diversity differ between terrestrial and flooded ecosystems. Moreover, the co-occurrence of hyper diverse stands in lowland *tierra firma* (not inundated) forests and almost monospecific stands in mangroves and gallery riparian vegetation within the tropics remains enigmatic. Building on evidence from ecology and agriculture, we present a new model investigating the hypothesis that, besides the general positive feedback of plant growth by nutrients release, litter decomposition builds up an intra-specific negative feedback functionally linked with tree diversity. The model results were compared with extensive published data sets both across and within latitudinal zones. The model predicts correctly the biomass production and decomposition process, as well as the number of tree species, their relative abundance in all environmental conditions providing a novel, putative explanation also for the diversity variations observed within the tropics. The model demonstrates a possible mechanistic link between the carbon cycle and biodiversity patterns, which is interesting in the debate about advancing in the direction of a unifying ecosystem theory.

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1. Introduction

As early recognized (Darwin, 1862), the diversity of terrestrial plant species increases from the poles to the equator ranging from almost monospecific forests at high latitude, to intermediate species richness in temperate climates, to the highly diverse tropic environments (Hawkins et al., 2003; Gillman and Wright, 2006). Interestingly, and in sharp contrast with terrestrial plants, flooded plant communities do not show this latitudinal gradient in species richness (Willig et al., 2003). Floating plants (e.g. *Eichornia crassipes*, *Lemna* spp., *Pistia* spp., etc.), perennial species in wetlands and marshes (*Phragmites australis*, *Spartina* spp., *Typha* spp., etc.), gallery (*Mora* spp., *Tabebuia* spp., etc.) and mangrove forests (*Avicennia* spp., *Nypa fruticans*, *Rhizophora* spp., etc.), seagrass (*Posidonia* spp., *Thalassia* spp., *Zoostera* spp., etc.), seaweed and kelp forests (*Fucus* spp., *Laminaria* spp., *Macrocystis pyrifera*, etc.), both in salt and freshwater, mostly form monospecific stands, irrespectively of the latitudinal level. So, also within the tropics tree diversity can vary from the astonishing floristic richness of the lowland *tierra firma* (not inundated) forests (Gentry, 1988; Givnish, 1999), to the reduced species richness of mangroves

and gallery riparian vegetation (Richards, 1996; ter Steege et al., 2000).

Plant ecologists have taken into account a plethora of processes in the attempt to explain this enormous variability of species diversity (Palmer, 1994). These have included equilibrium mechanisms through niche partitioning (Tilman, 1994) and non-equilibrium coexistence dynamics (Huston, 1994) related to disturbance (Connell, 1978), predation and biotic interactions (Janzen, 1970; Wills et al., 1997), fluctuations of environmental conditions (Chesson, 2000), and balance between immigration/speciation and extinction (McArthur and Wilson, 1967; Hubbell, 2001). However, none of such proposed mechanisms is able to explain all observed patterns of tree diversity in a satisfactory way (Willig et al., 2003).

Species-specific negative plant-soil feedback, i.e. the rise in the soil of negative conditions for plant vegetative and reproductive performances induced by the plants themselves, has been described for many plant species (Mazzoleni et al., 2007; Kulmatisky et al., 2008). This effect can both be intra- and interspecific (Oremus and Otten, 1981; van der Putten et al., 1993; Bever, 1994; Singh et al., 1999; Kiers et al., 2000; Packer and Clay, 2000; Klironomos, 2002; Kardol et al., 2007; Mazzoleni et al., 2007) and has been related to depletion of soil nutrients (Ehrenfeld et al., 2005), build up of soilborne pathogens (van der Putten et al., 1993; Packer and Clay, 2000), shifts of microbial communities (Bever, 1994; Klironomos, 2002; Kardol et al., 2007), and phytotoxicity

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of decaying plant litter (Webb et al., 1967; Singh et al., 1999; Armstrong and Armstrong, 2001). Much evidence of such negative feedback has been reported for primary succession (van der Putten et al., 1993), secondary succession and temperate grasslands (Bever, 1994; Klironomos, 2002; Kardol et al., 2007), temperate (Streng et al., 1989; Packer and Clay, 2000) and tropical forests (Webb et al., 1967; Kiers et al., 2000; Hood et al., 2004).

Modelling studies demonstrated that intra-specific negative feedback, by creating unsuitable conditions for conspecifics but not for others species, can allow species coexistence through reciprocal indirect facilitation (Bonanomi et al., 2005; Callaway, 2007), thus also increasing community diversity (Bever et al., 1997). Indeed, field evidence confirms these model outcomes (van der Putten et al., 1993; Bever, 1994; Bonanomi et al., 2008). However, to be considered an explanatory mechanism of the latitudinal gradient of biodiversity, the strength of this feedback should consistently vary with latitude (Reynolds et al., 2003). So far, no models have explored the impact of intra-specific negative plant-soil feedback on species diversity along environmental gradients.

Autotoxicity resulting from litter decomposition is wide spread in agriculture (Singh et al., 1999 for a review), and evidence of such autotoxicity also comes from ecological studies (Webb et al., 1967; Armstrong and Armstrong, 2001; Perry et al., 2005; Bonanomi et al., 2008). Indeed, the rise of intra-specific negative plant-soil feedback after repeated monoculture was already well-known in agriculture since ancient time (Columella: *De Re Rustica*, 50 A.D.), with the practice of crop rotation being specifically developed to avoid such "soil sickness" (Zucconi, 2003). In this agricultural context, it is quite clear that negative intra-specific plant-soil feedbacks can rise because of both soilborne pathogens and autotoxicity produced by soil organic matter. On the other hand, in the field of plant ecology, most research concentrated on pathogens and microbes rather than intra-specific phytotoxicity.

Therefore, we think that the ecological implications of autotoxicity merits further exploration, also in consideration of the logical relationships between litter toxicity, decomposition rates and climatic conditions. Based on this concept, a hypothetical model was discussed in a previous paper, to provide a putative explanation for the tree diversity patterns at both global and local scales (Mazzoleni et al., 2007). According to this model, the biogeochemical organic matter cycle is linked with both nutrients and autotoxicity dynamics in decomposing litter. Here, we further develop this idea and present and validate a new mathematical model to explore the effects of litter decomposition on basic ecosystem processes (primary productivity) and species diversity. The model is based on the co-occurrence of intra-specific negative plant-soil feedback by autotoxicity and both inter- and intra-specific positive plant-soil feedback by nutrients.

2. Methods

2.1. Model rationale

In the model, litter decomposition rate, which varies with latitude (Olson, 1963; Gholz et al., 2000; Berg and McClaugherty, 2003), is the main driver of the build up of positive as well as negative feedbacks on plant growth (Fig. 1). Inter- and intra-specific positive plant-soil feedback, beneficial for all species, is due to nutrient release during litter decomposition (Berg and McClaugherty, 2003). In contrast, intra-specific negative plant-soil feedback is a consequence of autotoxicity, enhanced by the activity of soilborne pathogens (Blok and Bollen, 1993; Bonanomi et al., 2007b). This latter mechanism works as follows. During decomposition of plant residues, tissue degradation and microbial activity produce phytotoxic materials (Singh et al., 1999; Bonanomi et
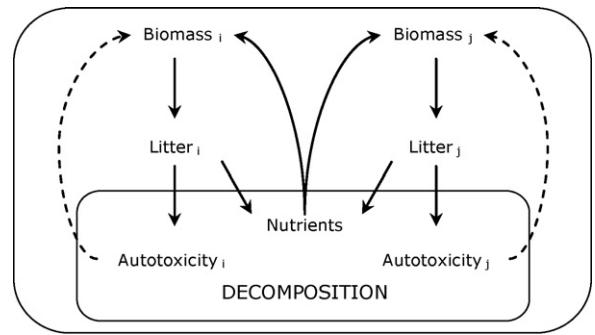

Fig. 1. Schematic representation of the litter decomposition feedbacks. Continuous and dashed lines indicate positive and negative effects respectively. Plant biomass is positively affected by nutrients, constituting an inter- and intra-specific positive feedback and negatively influenced by autotoxicity generated during litter decomposition, involving an intra-specific negative feedback.

al., 2006) with direct harmful effects on plants. These are further exacerbated by pathogens in two ways. First, because plant resistance to pathogens attack is reduced by the phytotoxic conditions (Patrick and Toussoun, 1965; Bonanomi et al., 2007a), and second because the decaying organic matter, by providing the substrate for saprophytic growth of soilborne pathogens, enhances the pathogenicity of pathogens (Hoitink and Boehm, 1999; Bonanomi et al., 2010).

Being species-specific, we assume that phytotoxicity is predominantly produced by the decomposition of conspecific litter (Bonanomi et al., 2008), hence the term autotoxicity (Fig. 1). Although evidence showed that intra-specific autotoxicity due to litter decomposition could indeed be stronger than inter-specific phytotoxicity (Webb et al., 1967; Armstrong and Armstrong, 2001; Perry et al., 2005), the generality of this assumption remains to be tested experimentally. This idea might appear an evolutionary paradox. Instead, the reasoning could be reversed provided autotoxicity is intrinsic of all living organisms, requiring continuous and effective removal of their own metabolic products from living tissues (Mazzoleni et al., 2007). However, by this modelling exercise, and based on the principle of parsimony, we seek to investigate theoretically whether this assumption might provide a putative explanation for observed tree diversity patterns that remain unexplained so far. So, in our model, species which suffer because of their own litter residuals, will receive a benefit by litter diversity because of nutrient release, reducing the negative feedback effects according to the relative abundances of the different species. The diversity of decomposition substrate is also of major importance for the stabilization of the decomposed organic matter and the relative reduction of its autotoxicity (Zucconi, 2003).

The link with climatic conditions is related to the known increase of litter-decaying rate with temperature. In our model, autotoxicity increases with litter decomposition rate but it is reduced in time by decay processes (Bonanomi et al., 2006). Independent of climatic conditions, however, negative feedback can be released either by the removal of autotoxic material with flowing water, or because of substrate renewal by newly accreted soil (van der Putten et al., 1993).

2.2. Model description

The model is a set of ordinary differential equations describing the dynamics of four state variables: biomass (B; kg$_C$ dm^{-2}), litter (L; kg$_C$ dm^{-2}), nutrients (N; kg$_N$ dm^{-2}), and autotoxicity (A; kg$_C$ dm^{-2}).

Plant growth and the rate of litter decomposition depend on environmental conditions that change with latitude. This dependence is mimicked by one single variable E reflecting

Table 1
List of model parameters, state and auxiliary variables.

Symbol	Interpretation	Unit	Assigned value	Reference
B	Biomass	$kg_C \, dm^{-2}$	$0.01/n \, (t=0)$	–
L	Litter	$kg_C \, dm^{-2}$	$0.001/n \, (t=0)$	–
N	Nutrient	$kg_N \, dm^{-2}$	$0.3 \, (t=0)$	–
A	Toxic products by decomposition	$kg_C \, dm^{-2}$	$0.01/n \, (t=0)$	–
i	Species index	–	$1, \dots, n$	–
n	Number of species	–	1, 2,5, 10, 25, 50, 100, 200, 300, 400	–
E	Environment	–	Between 0 and 1	–
B_{total}	Total biomass	$kg_C \, dm^{-2}$	–	–
B_{max}	Max biomass	$kg_C \, dm^{-2}$	1	Vogt et al. (1986)
g	Growth rate	$dm^2 \, kg_N^{-1} \, year^{-1}$	Between 0.9 and 0.5	Calibrated
d	Death rate	$year^{-1}$	0.05	Calibrated
s	Parameter determining A effect	$dm^2 \, kg_C^{-1} \, year^{-1}$	0 or 10	Calibrated
k	Decomposition parameter	$year^{-1}$	1	Calibrated
dec	Litter decomposition	$year^{-1} \, kg_C \, dm^{-2}$	–	–
u	Plant uptake parameter	$dm^2 \, kg_C^{-1} \, year^{-1}$	0.001	Calibrated
r	Decay parameter of A	$year^{-1}$	1	Calibrated
h	Exponential of A effect power law	–	4	Calibrated
p	Exponential of dec power law	–	2.5	Olson (1963), Gholz et al. (2000), and Berg and McClaugherty (2003)
q	Exponential of A decay power law	–	2.5	Olson (1963), Gholz et al. (2000), and Berg and McClaugherty (2003)
W	Washing or escape effects	–	Between 0 and 1	–

the environment and represented by a dimensionless real value between 0 and 1. Hereby 0 means that at least one limiting factor (e.g. temperature or water) prevents growth and decomposition, while 1 is interpreted as the environment being optimal. Then E is also a surrogate of latitude where 0 represents polar and 1 equatorial conditions. If environmental conditions are optimal ($E = 1$), plant growth is still limited by nutrients and a crowding effect (e.g. light).

Biomass change is a function of plant growth and mortality. Plant growth is a linear function of environment E and nutrients. Plant mortality is due to a constant loss fraction d ($year^{-1}$), equal for all species, and changed into litter. An extra loss is induced by autotoxicity A. So, we can write:

$$\frac{dB_i}{dt} = g_i \cdot B_i \cdot N \cdot E \cdot \left(1 - \frac{B_{total}}{B_{max}}\right) - (d + A_i \cdot s \cdot E^h) \cdot B_i \quad (1)$$

where t is time (year), i the species index, g_i a growth parameter ($dm^2 \, kg_N^{-1} \, year^{-1}$), B_{total} the sum of all species biomass ($\sum_{i=1}^{n} B_i$; $kg_C \, dm^{-2}$), B_{max} is the maximum biomass of all species (system carry capacity) ($kg_C \, dm^{-2}$), A_i is autotoxicity, and s ($dm^2 \, kg_C^{-1} \, year^{-1}$) determines the extra loss of biomass due to autotoxicity $A_i \cdot s$ ($year^{-1}$). The negative feedback due to autotoxicity A is enhanced by favourable environment, and by the effects of pathogens (Blok and Bollen, 1993; Bonanomi et al., 2007b) The latter was parameterized by setting the exponent of the environment $h > 1$. For simplicity, species differ for the growth parameters g_i only.

Litter (produced by either plant mortality, leaf and root turnover) is decomposed according to a parameter k ($year^{-1}$), equal for all species, and a power law of the environment. So, we can write:

$$\frac{dL_i}{dt} = (d + A_i \cdot s \cdot E^h) \cdot B_i - k \cdot E^p \cdot L_i \quad (2)$$

The decomposition rate of litter of a species is then $k \cdot E^p \cdot L_i = dec_i$.

Litter decomposition of all species produces nutrients necessary for plant growth. The nutrient cycle is considered closed and common to all species, i.e. nutrients produced by the litter decomposition of any species can be taken up by all plants (Fig. 1). So, we

can write:

$$\frac{dN}{dt} = \sum_{i=1}^{n} k \cdot E^p \cdot L_i \cdot \frac{u}{g_i} - \sum_{i=1}^{n} u \cdot B_i \cdot N \cdot E \cdot \left(1 - \frac{B_{total}}{B_{max}}\right) \quad (3)$$

where u is a plant uptake parameter ($dm^2 \, kg_C^{-1} \, year^{-1}$), and n is total species number. The term g_i/u is the C/N ratio of plant material (kg_C/kg_N).

Autotoxicity increases with decomposition dec_i and is reduced in time, like for litter, by a decay rate $r \cdot E^q$. Then:

$$\frac{dA_i}{dt} = dec_i \cdot (1 - w) - r \cdot E^q \cdot A_i \quad (4)$$

where w is toxicity removal by washing or escaping, i.e. the litter toxicity can be either decreased by water flushing of phytotoxic materials or avoided through substrate renewal by newly accreted soil. r ($year^{-1}$) is a A_i decay parameter.

The interpretation of the model might not be restricted to litter decomposition; we speculate that incorporating intra-specific negative feedback by soil pathogens as a state variable would produce similar outcomes, if such feedback is stronger than inter-specific negative feedback. Indeed, soil communities are similarly affected by flooding (Newhall, 1955; Stoves, 1979; Katan, 2000), however, their direct link with latitudinal gradient is less straightforward than for litter decomposition. The model parameters description is reported in Table 1. The references for data used for model validation are reported in Electronic supplementary material, Tables S1 and S2.

2.3. Model calibrations

The values of major model parameters were defined either based on published reference ($p = q = 2.5$; Olson, 1963; Gholz et al., 2000; Berg and McClaugherty, 2003) or by adjusting their levels ($k = r = 1$, $h = 4$, $s = 10$, g_i between 0.9 and 0.5) to best fitting of litter production and accumulated litter with published data (Fig. 2). In particular, the assignment of g_i values to the different species was done by a parametric distribution curve of ranked growth rates, calibrated by an iterative non linear programming procedure of least-squares curve fitting based on Levenberg and Marquardt algorithm by Matlab software (Mathworks, 2007).
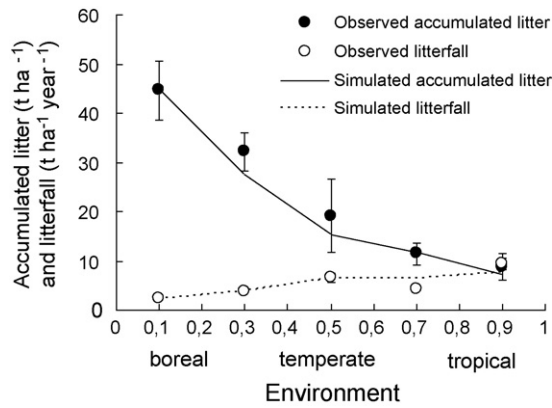
Fig. 2. Trends of ecosystem variables along a climatic gradient showing simulated *vs* observed (Vogt et al., 1986) accumulated litter (t ha^{-1}) and litterfall (t ha^{-1} year^{-1}) from boreal to tropical conditions.

2.4. Simulation experiments

Model analysis has been performed through a series of numerical simulations:

(i) The changes of main ecosystem variables (total number of coexisting species, total living biomass, accumulated litter and litterfall) have been assessed along a climatic gradient. This was done by simulating the growth of competing species (initial species pool: $n = 400$) under different environments ($E = 0$, 0.1, ..., 0.9, 1) until the equilibrium condition was reached, i.e. when the number of coexisting species during the simulations remained unchanged for 1000 years. The initial living biomass was settled for all species at 0.2×10^{-4} kg dm^{-2} and a species was considered as living if its biomass was above 0.1×10^{-8} kg dm^{-2}.

(ii) The effects of interactions between species diversity and soil negative feedback on ecosystem productivity were tested. Simulations were done with different values of initial species pool ($n = 1, 2, 5, 10, 25, 50, 100, 200, 300, 400$) and with different weight (s) of negative feedback (either 0 or 10) and run until the equilibrium was reached under different environmental conditions ($E = 0, 0.1, ..., 0.9, 1$).

(iii) The relative abundance of the coexisting species has been assessed for ever-wet tropical ($E = 1$), tropical ($E = 0.8$), temperate ($E = 0.5$) and boreal ($E = 0.3$) environmental conditions. This analysis was done by running simulation with an initial species pool of 500 species with the same setting of biomasses as in the first exercise.

(iv) To verify the effects of flooding on the number of coexisting species simulations were done for three environmental conditions (tropical $E = 0.8$, temperate $E = 0.5$ and boreal $E = 0.3$) with or without removal of the decomposition products ($w = 0, 1$).

2.5. Model validation with field data

Published field data of species-rank abundance of forests from different environments have been compared with simulation results. Model fitting was evaluated by testing the significance of linear regression between simulated and observed data. Specifically, we used data from: two sites with one plot each for ever-wet tropics (Pitman et al., 2002); averages of 50, 31, 6 and 4 plots, respectively, for four different sites of seasonal tropics in Central America (Condit et al., 2002); averages of 14, 8 and 1 sites of temperate forests from Europe, North America and Japan, respectively; averages 5, 5 and 1 site of boreal forests from Europe, North America and Siberia, respectively. When species cover was

recorded by Braun-Blanquet scale (Braun-Blanquet, 1928), data have been transformed in % values as follows: 5 = 90%; 4 = 60%; 3 = 30%; 2 = 15%; 1 = 5%; + = 1%. Full reference list is reported in Electronic supplementary material, Table S1.

The simulated number of coexisting tree species in flooded and unflooded forest in three different environments (tropical, temperate and boreal) has been compared with available field data. The number of coexisting species in different environments has been averaged as follows: unflooded tropical forests – 35 sites from Central and South America, Asia, Africa and Australia; flooded tropical forests – 14 sites from Central and South America, Asia, Africa and Australia; unflooded temperate forests – 24 sites from Europe, US and Japan; flooded temperate forests – 18 sites from Europe; unflooded boreal forests – 10 sites from Europe, North America and Siberia; flooded boreal forests – 14 sites from Europe and North America. Full reference list is reported in Electronic supplementary material, Table S2. The size of plots used to record species richness was ranging between ∼0.01 ha in boreal and temperate systems and ∼1 ha in tropical unflooded forests. All data for tropical forests were based on forest inventories (∼1 ha plots) while Braun-Blanquet phytosociological cover data have been used only for temperate and boreal forests, where no problem of species richness underestimation is expected (Table S1). In the published papers, these sizes were considered adequate to assess the species richness of the studied forests.

3. Results

3.1. Primary productivity and litter decomposition

Model calibration led a satisfactory prediction of basic ecosystem variables with litter fall steadily increasing from boreal to tropical environments, and accumulated litter reaching maximal levels in boreal forest and progressively decreasing in temperate and tropical systems (Fig. 2). These results are consistent with well established evidences from a range of ecosystems (Vogt et al., 1986), and also with recent observations that productivity and litter fall of moist tropical forests significantly increase with temperature whereas standing litter and soil organic matter decrease under the same conditions (Raich et al., 2006). Without negative feedback, biomass depends only on environmental conditions with maximal levels unrelated to the initial species pool (Fig. 3). In contrast,
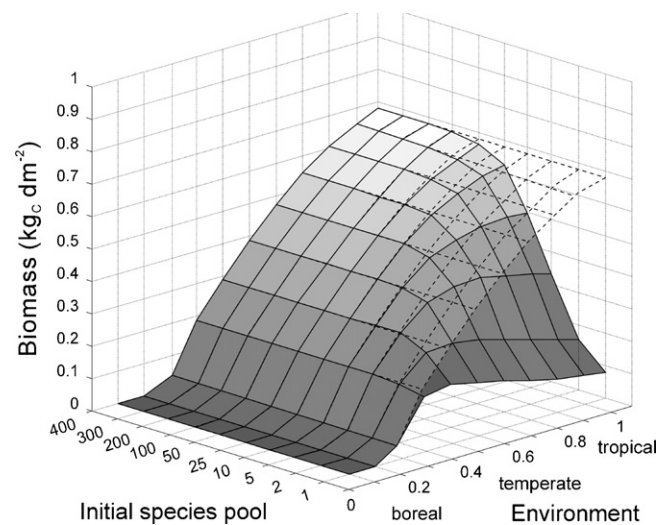

Fig. 3. Community biomass for different environments and initial species pools. Grey shaded surface represents model results with high levels of negative feedback, whereas the transparent dashed projection shows the model output in absence of negative feedback effects.
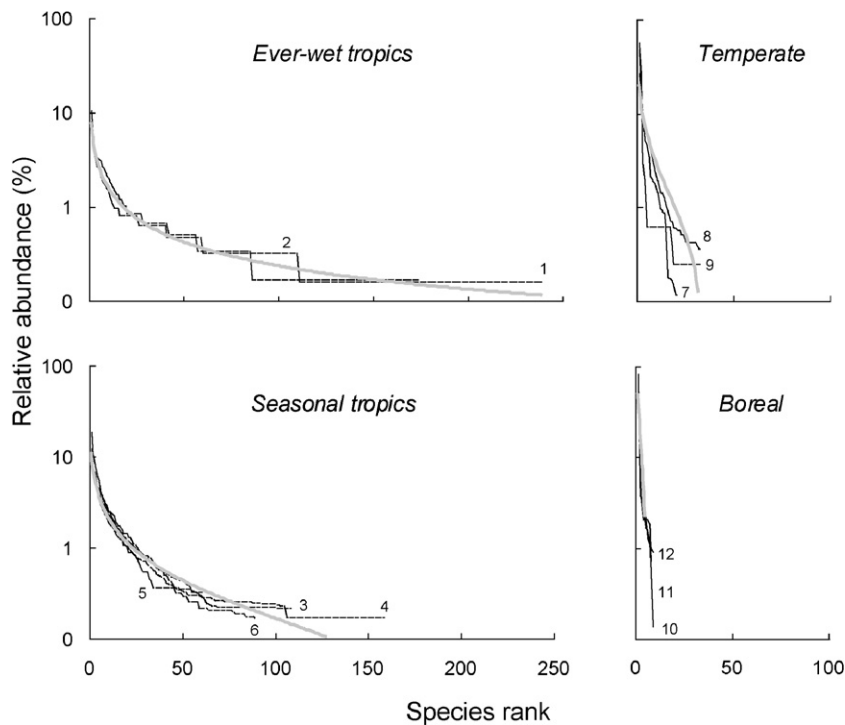
Fig. 4. Species-rank abundance curves of forest systems. Observed (dashed lines) and simulated (thick grey lines) abundances of ranked species for different environmental conditions. (1) Ecuador ($n = 1$); (2) Peru ($n = 1$); (3) BCI ($n = 50$); (4) P ($n = 31$); (5) C ($n = 4$); (6) S ($n = 6$); (7) Europe ($n = 8$); (8) US ($n = 14$); (9) Japan ($n = 1$); (10) Europe ($n = 5$); (11) US ($n = 5$); (12) Siberia ($n = 1$). References for the observed data are reported in Electronic supplementary material, Table S1.

with negative feedback, the model predicts that in tropical environments ecosystem biomass production is positively affected by the available species pool (Fig. 3). The validity of our model regarding these basic ecosystem processes (primary productivity and organic matter decomposition) in relation to temperature and moisture, provides the necessary framework to further explore their relationship with species diversity.

3.2. Species richness and diversity

The occurrence of both positive and negative feedback in the simulations produces a sharp increase of species richness from boreal to tropical environments (Fig. 4). In contrast, only the presence of positive feedback leads to competitive exclusion independent of climatic conditions, although the rate of this process progressively decreases with latitude (data not shown).

Concerning species diversity, field data from boreal to tropical environments show species-rank abundance progressively shifting from geometric to log-normal distributions characterized by a long tale of rare species (Hubbell, 2001). Our model simulations correctly reproduced both the number of coexisting species and the patterns of relative abundance in different environments across latitudinal gradients (Fig. 4). This constitutes a consistent validation of the model because the highly fitting outputs with real data were obtained without any empirical adjustment of the model (Fig. 5). In the model, the systematic removal of negative feedback, which for instance occur in flooded or buried environment, led to the dominance of few species in the community in all latitudes (Fig. 6).

4. Discussion

The prevailing scientific consensus relates plant species richness and productivity to resource availability in relation to disturbance, biotic interactions and environmental gradients. However, these frameworks fail in predicting species richness at community scale in relation to temperature (i.e. latitudinal and altitudinal gradients), rainfall level, soil fertility and, therefore, to ecosystem productivity (Willig et al., 2003). Our model, by focusing on 'resource-waste' (negative feedback) rather than 'resource-only' dynamics (positive feedback) provides a putative explanation for the high species diversity of environments where litter decomposition is rapid, and for the high species dominance in communities where litter decomposition is slow or negative feedback (litter phytotoxicity and soilborne pathogens) is removed from the nutrient cycle pathway (Fig. 6).

Our model also provides a possible explanation for the long debated richness-productivity relationship (Waide et al., 1999; Gillman and Wright, 2006). The simulated high and low productivity in temperate and tropical environment at low species diversity (Fig. 3) is consistent with the occurrence of monospecific stand in temperate climate and the often reported failures of monospecific forestry plantation in the tropics. This result suggests that biodiversity is a prerequisite for high biomass especially in ecosystems where litter decomposition is rapid. In these conditions high biomass production is only compatible with low diversity, if the products of litter decomposition are removed from the substrate, but nutrients are still available, such as under nutrient-rich conditions in flooded systems where nutrients remains decoupled from litter decomposition. In other words, ecosystem productivity is dependent on high species richness where the nutrient cycle is closed and rapid. Differently, it will progressively be less dependent on plant diversity as the litter-decaying rate declines and/or plant nutrition is decoupled, either in space or time, from the litter decomposition of conspecifics.

This is the case for flooded communities regularly flushed with nutrient-rich water, such as wetlands, floating plant communities, freshwater riparian forests, mangrove forests, seagrass and seaweed beds, and kelp forests in salt water. In all these systems, nutrition and productivity are primarily related to the concentration of nutrients in water and/or in newly accreted soil, and no impact by species-specific negative feedback should be expected.
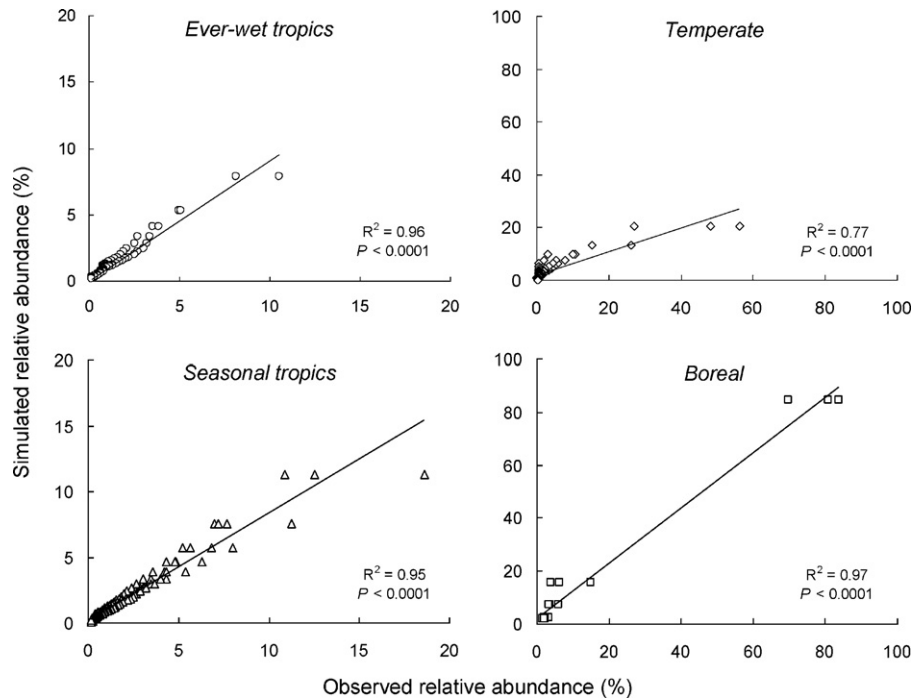
Fig. 5. Comparison of simulated *vs* observed species-rank data in different environments and linear regression results (coefficient of determination and associated *P*-value).

This is our hypothetical explanation for the occurrence of stable monospecific stands of mangroves and riparian forests adjacent to the extremely diverse *terra firme* tropical forests. So far, this pattern has been explained by the stress hypothesis (Terborgh, 1973) claiming that more species can adapt and coexist in benign environments. However, stressful environments are those where biomass production is constrained (Grime, 1977; Lortie and Callaway, 2006), which is not the case for productive mangroves and riparian forests. Therefore, unlike our explanation, the stress hypothesis appears to be inconsistent with the case of mangroves and riparian forests, commonly exhibiting low diversity associated with high productivity (Lugo and Snedaker, 1974; Richards, 1996). Indeed, our model seems the only one capable of conciliating high ecosystem productivity with both high and low species diversity.

Litter decomposition rate (k, year^{-1}) varies from a maximum of 5 in ever-wet tropical forest, to less than 0.015 in sub-alpine coniferous forests (Olson, 1963; Gholz et al., 2000; Raich et al., 2006; Cornwell et al., 2008). Relating this variation to negative plant-soil feedback provides a possible explanation for the latitudinal

and altitudinal distributions of plant richness. The model predicts that hot-spots of tree diversity will occur where litter decomposition is rapid and for a closed nutrient cycle. The occurrence of root mats above mineral soil surface can be considered an indirect evidence of a closed nutrient cycle and rapid decomposition (Jordan, 1982), because it reflects the need of plants to extract nutrients from decomposing litter. Consistently with model predictions, a strong positive correlation between the percent of thin roots in the top soil and tree diversity can be observed in published data on tropical forests (Electronic supplementary material, Fig. S1). Our model also suggests that under such conditions a positive correlation should be found at world scale between litter decomposition rate and tree diversity. As can also be inferred from our model, a lower k (slower decomposition), e.g. because of litter characteristics, would lead to monodominance under equatorial conditions, with relatively high productivity and the build up of a thick litter layer, which is again consistent with observations (Torti et al., 2001).

Prevailing ecological theories relate the latitudinal gradient of tree species richness to the amount of energy and productivity (Wright, 1983), the balance between immigration and extinction (Hubbell, 2001), the level of disturbance (Connell, 1978), and the biotic interactions producing negative intra-specific density-dependent effects (Wills et al., 1997). None of these theories is able to explain tree diversity patterns on both global and local scales (Table 2). For instance, co-occurrence of hyper diverse and almost monospecific stands within the tropics remains enigmatic (Willig et al., 2003), while the intra-specific negative feedback hypothesis by autotoxicity (Mazzoleni et al., 2007) might provide a possible framework for these patterns. Negative intra-specific density dependence has been reported as an important mechanism for maintaining tree diversity both in the tropics (Wills et al., 1997; Harms et al., 2000) and in temperate forests (Hille Ris Lambers et al., 2002). The negative effect of increasing density of conspecifics has been related to enhanced occurrence of predators (Janzen, 1970), soilborne pathogens (Hood et al., 2004; Wills et al., 1997), allelopathy and intra-specific competition. In comparison with such causal factors, negative plant-soil feedback seems the only one capable to
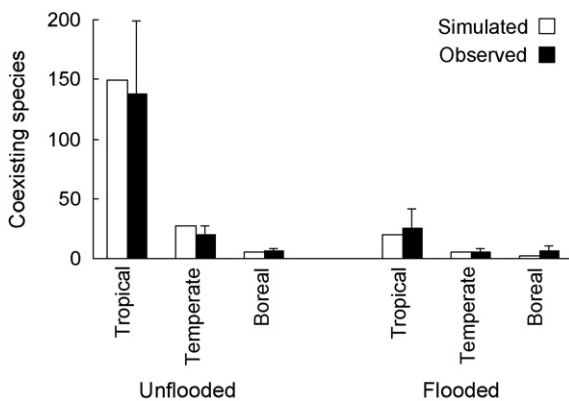

Fig. 6. Number of coexisting species in flooded and unflooded forest in tropical, temperate and boreal environments. References for the observed data are reported in Electronic supplementary material, Table S2.

Table 2
Comparative summary of theories on species coexistence.

Theory	Ecological process and range of variation	Strength	Weakness
Intermediate disturbance hypothesis (Connell, 1978)	Gap formation (1–10 m²/ha/year) or turnover rate (1–5%)	The average turnover rate significantly increases from temperate to tropical forests (Stephenson and van Mantgem, 2005)	No evidence of optimal disturbance rates of gap formation in tropical hyper diverse forests (i.e. turnover rates do not change between tropical forests with different species richness: Pitman et al., 2002) Despite the general trend of decreasing average turnover rates with latitude, the values of many tropical forests fall well within the range of temperate environments (Stephenson and van Mantgem, 2005)
Species-energy hypothesis (Wright, 1983)	NPP or litter fall (<1–37 t/ha/year)	NPP and litterfall consistently increase from boreal to temperate to tropical if water is not limiting (Vogt et al., 1986; Raich et al., 2006)	This hypothesis is not consistent with the occurrence of both high NPP with low diversity and low NPP with high diversity (Richards, 1996; Waide et al., 1999)
Negative intra-specific density-dependent processes (Wills et al., 1997)	Predation by animals (Janzen, 1970) and soilborne pathogens (Reynolds et al., 2003)	Negative intra-specific density dependence is pervasive in tropical forests and is strongly species specific, affecting mainly conspecific (Wills et al., 1997; Harms et al., 2000)	Negative intra-specific density dependence occur with similar frequency both in temperate and tropical forests (Hille Ris Lambers et al., 2002) Species-specificity is low for herbivorous insects (Novotny et al., 2002) and almost unknown for soilborne pathogens in tropical forests Lack of information on the impact of soilborne pathogens across the latitudinal gradient
Neutral theory (Hubbell, 2001)	Immigration and extinction balance	Good fitting with observed diversity abundance data (Hubbell, 2001; Volkov et al., 2005)	Parameters for model simulations (e.g. speciation and immigration rates) are largely immeasurable (Abrams, 2001) Calibration of model parameters is not connected to their underlying ecological mechanisms The assumption of competition equivalence is not supported by empirical evidences
Species-specific litter toxicity (Mazzoleni et al., 2007)	Negative intra-specific density-dependent effects are produced by litter phytotoxicity (Bonanomi et al., 2006) in synergy with soilborne pathogens (Bonanomi et al., 2007a)	Negative intra-specific density dependence is pervasive in tropical forest and is strongly species specific affecting mainly conspecific (Wills et al., 1997; Harms et al., 2000) Litter decomposition rate (k) dramatically increases from boreal to tropical forest (from 0.01 to 5) if water is not limiting (Olson, 1963; Raich et al., 2006; Cornwell et al., 2008) Phytotoxicity of fresh plant litter is widespread and consistently declines during decomposition (Bonanomi et al., 2006)	Negative intra-specific density dependence occur with similar frequency both in temperate and tropical forests (Hille Ris Lambers et al., 2002) No experiment test for the species-specificity of litter phytotoxicity in tropical forests Lack of information on the impact of phytotoxicity and soilborne pathogens across the latitudinal gradient

explain the consistent variations of negative intra-specific density dependence with latitude (Table 2).

We left out inter-specific negative plant-soil feedbacks in our model as a simplification according to the principle of parsimony. The inclusion of such negative feedbacks would alter our model outcomes, if the strength of those feedbacks could outbalance the strengths of the other positive and negative feedbacks. Further experimental and modelling studies are now urgently needed to unravel the relative importance of those feedbacks and their emergent effects.

In conclusion, based on our reasoning and the seemingly good model outcomes, we suggest that focusing on 'resource-waste' rather than 'resource-only' dynamics indeed provides a hypothetical explanation for species diversity patterns. As a matter of fact, unlike other theories (Abrams, 2001), the functional and mechanistic factors of species-specific negative feedback related to litter decomposition can be explicitly quantified and experimentally verified. We think that the integration of this new model with the intermediate disturbance hypothesis and the immigration/extinction balance theory (McArthur and Wilson, 1967; Hubbell, 2001) may contribute to a solid and improved theoretical framework for understanding global tree diversity.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2010.08.007.

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