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MR SYLVAIN MIKAËL SCHMITT (Orcid ID : 0000-0001-7759-7106)

DR ISABELLE MARÉCHAUX (Orcid ID : 0000-0002-5401-0197)

DR JEROME CHAVE (Orcid ID : 0000-0002-7766-1347)

DR BRUNO HÉRAULT (Orcid ID : 0000-0002-6950-7286)

Functional diversity improves tropical forest resilience: insights from a long-term virtual experiment

Sylvain Schmitt [*,1,2], Isabelle Maréchaux[3], Jerome Chave [4], Fabian Jörg Fischer[4], Camille Piponiot[5], Stéphane Traissac[6], Bruno Herault [*,7,8]

[1] CNRS, UMR EcoFoG (Agroparistech, Inra, Université des Antilles, Université de la Guyane, Cirad), Campus Agronomique, 97310 Kourou, French Guiana

[2] UMR BIOGECO, Université de Bordeaux, 69 route d'Arcachon, F-33612 Cestas cedex France

[3] AMAP, INRA, Univ Montpellier, IRD, CIRAD, CNRS, F-34000 Montpellier, France

[4] Laboratoire Evolution et Diversité Biologique, UMR5174, CNRS, Université Paul Sabatier, IRD, Toulouse Cedex 9, France

[5] Université de la Guyane, UMR EcoFoG (Agroparistech, CNRS, Inra, Université des Antilles, Cirad), Kourou, French Guiana

[6] AgroParistech, UMR EcoFoG (CNRS, Inra, Université des Antilles, Université de la Guyane, Cirad), Campus Agronomique, 97310 Kourou, French Guiana

[7] Cirad, Univ Montpellier, UR Forests & Societies, Montpellier, France

[8] Institut National Polytechnique Félix Houphouët-Boigny (INP-HB), BP 1093, Yamoussoukro, Ivory Coast

[*] **Corresponding authors:** sylvain.schmitt@agroparistech.fr ; bruno.herault@cirad.fr

Abstract

1. Human activities modify the disturbance regimes of tropical forests. Since tropical forests host high biological diversity, understanding the role of biodiversity in ecosystem recovery pathways and the underlying ecological mechanisms is crucial to predict the fate of tropical ecosystems. Studies relying on regularly-censused forest plots rarely include disturbed forests, are not long enough to assess long-term forest dynamics and often lack repeatability.

2. We used an individual-based model of tropical forest growth to assess the effect of species and functional diversity on long-term ecosystem recovery from disturbance. We manipulated the number of species and functional assemblages across a large number of simulations and simulated different levels of disturbance. To investigate the ecological mechanisms that underlie the effect of biodiversity on forest functioning along recovery pathways, we partitioned the net effect of biodiversity on ecosystem properties into complementarity and selection effects over time.

3. We found that functional diversity improved tropical forest resilience after a disturbance. The complementarity effect dominated soon after the disturbance but was progressively surpassed by a selection effect as more competitive species dominated the forest community. This pattern increased with the intensity of the disturbance.

4. *Synthesis*. We found that the mechanisms through which biodiversity influences forest functioning depend on the ecosystem state, shifting from a dominant complementarity effect in recently disturbed systems to a selection effect in systems disturbed a long time ago. Our results thus suggest that the time since the last disturbance is a key to understanding biodiversity-ecosystem functioning relationships in tropical forests and can help reconcile previous contrasting results obtained with snapshots of ecosystem state in empirical studies.

Keywords

Recovery; Disturbance; Complementarity effect; Selection effect; Biodiversity-ecosystem functioning; Individual-based model; Simulation

Introduction

Disturbance regimes in tropical forests are being altered by human activities (Davidson et al., 2012; Lewis, Edwards, & Galbraith, 2015). The main type of disturbance across the tropics is forest logging, encompassing selective timber harvesting in old-growth forests and wood fuel harvesting mainly in secondary forests (Pearson, Brown, Murray, & Sidman, 2017). In addition to direct human impacts, global change is modifying regional climates with, for instance, an increase in the frequency and intensity of drought events and associated fires (Davidson et al., 2012) and of convective storms (Negrón-Juárez et al., 2018), both resulting in increased tree mortality rates and forest biomass loss (Phillips et al., 2009; Ibanez et al., 2019).

Even without deforestation, such human-induced disturbances can result in degraded forests in which ecological processes underlying forest dynamics are significantly altered (Ghazoul et al., 2015). Deforestation has attracted worldwide attention, while the consequences of degradation for tropical forest functioning have received far less emphasis (Putz & Redford, 2010; Simula, 2009). However, forest degradation concerns ten times the amount of forest deforested (Herold et al., 2011). Forest degradation can trigger severe biodiversity loss (Burivalova, Şekercioğlu, & Koh, 2014), and is estimated to account for 2.1 billion of tons of carbon dioxide emissions per year, or 25% of the greenhouse gas emissions related to deforestation and forest degradation worldwide (Pearson, Brown, Murray, & Sidman, 2017). Understanding the drivers of tropical forest resilience, i.e. the forests' ability to resist and recover from disturbances (Gunderson, 2010), is thus important to predict their fate under ongoing global change.

Forest recovery from disturbance can be influenced by various factors. For example, the intensity of the disturbance has been found to largely determine the recovery time of ecosystems, including the recovery of biomass, biodiversity, and tree species composition (de Avila et al., 2015; Burivalova et al., 2014; Rutishauser et al., 2015). Forest composition is also known to influence post-disturbance trajectories, as tree species respond differently to disturbances depending on their functional properties (Hérault et al., 2011). Indeed, a functional shift from resource-acquisitive traits (e.g. high nutrient content and photosynthetic

capacity) to resource-conservative traits (e.g. high leaf toughness and wood density) has been evidenced along chronosequences of secondary forest succession in the wet tropics (Craven, Hall, Berlyn, Ashton, & van Breugel, 2015; Poorter et al., 2019; Norden, Chazdon, Chao, Jiang & Vílchez-Alvarado, 2009). Soil nutrients and dispersal limitation also appear to strongly drive community reassembly and dynamics in early succession before light limitation surpass edaphic constraints (van Breugel et al., 2013; van Breugel, Craven, Lai, Baillon, Turner & Hall, 2019), imposing a stricter filter on functional diversity (Craven, Hall, Berlyn, Ashton, & van Breugel, 2018).

Another factor that can influence forest resilience to disturbances is forest diversity itself (Cadotte, Carscadden, & Mirotchnick, 2011; Ives & Carpenter, 2007; Loreau & Mazancourt, 2013). Two mechanisms have been suggested to underlie the effect of biodiversity on ecosystem functioning (Loreau & Hector, 2001). The complementarity effect results from niche partitioning and facilitation, leading to more efficient use of available resources at the community level. The selection effect describes how more diverse communities have a higher probability of including functionally efficient species. Previous theoretical work (Loreau, 2010), experiments (Cardinale et al., 2009; Cardinale et al., 2007; Huang et al., 2018; Niklaus, Baruffol, He, Ma, & Schmid, 2017), and observations along natural gradients (Chisholm et al., 2013; Liang et al., 2016; Paquette & Messier, 2011; Poorter et al., 2017) produced contrasting results regarding the relative importance of complementarity and selection effects. Their relative importance can also vary with succession. Fargione et al. (2007) and Huang et al. (2018) found an increasing effect of complementarity in 10-year and 8-year long grassland and forest biodiversity experiments, respectively. On the contrary, Holzwarth, Rüger & Wirth (2015) found an increasing selection effect in a simulated temperate forest succession.

Secondary forest successional trajectories can be difficult to predict (Norden et al., 2015), presumably due to land-use history and legacy effects (Arroyo-Rodriguez et al., 2017, N'Guessan et al., 2019). The long-term effects of biodiversity on ecosystem recovery and their underlying mechanisms in tropical forests remain under-documented (van der Sande et al., 2017). Studies relying on forest stand inventories often lack repeatability (Poorter et al., 2017; Schnitzer &

Carson, 2016), rarely include disturbed forests (Sist et al., 2015), and are not long enough to assess long-term effects (Hérault & Piponiot, 2018). Forest simulators have proved useful to investigate the effect of biodiversity on forest functioning through virtual biodiversity experiments (Bohn & Huth, 2017; Maréchaux & Chave, 2017; Morin, Fahse, Mazancourt, Scherer-Lorenzen, & Bugmann, 2014; Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011; Sakschewski et al., 2016). However, the problem of representing biodiversity beyond a few plant functional types has long been an impediment to applying this approach to species-rich tropical forests (Kazmierczak, Wiegand, & Huth, 2014; Köhler & Huth, 1998; Purves & Pacala, 2008).

In the present study, we explore the effect of species and functional diversity on long-term tropical forest recovery from disturbances of different levels of intensity using a simulation approach. We take advantage of recent advances in the forest simulator TROLL (Chave, 1999), an individual-based and spatially-explicit model of tropical forest that can simulate high levels of diversity through species-specific parameterization relying on plant functional traits (Maréchaux & Chave, 2017). We manipulated the number of species and functional identity across a large number of simulations and quantified the net effect of biodiversity on forest properties along recovery pathways. To investigate the underlying ecological mechanisms in greater detail, we partitioned the net effect into complementarity and selection effects. We specifically addressed the following questions: (1) Does tree diversity influence forest recovery from disturbances? (2) If so, which facets of pre-disturbance diversity (taxonomic vs. functional) drive this effect? (3) How does the intensity of the disturbance affect forest recovery? (4) What is the relative importance of complementarity and selection effects along post-disturbance trajectories? We hypothesized that: (i) more diverse forests recover more rapidly from a disturbance event due to higher productivity (Liang et al., 2016; but see Dormann et al., 2019); (ii) functional diversity is more directly linked to forest recovery than species diversity, as it represents forest assembly and function better (Cadotte, Carscadden, & Mirotchnick, 2011); (iii) forest recovery time increases with an increase in disturbance intensity (Rutishauser et al., 2015); and (iv) biodiversity effects vary along post-disturbance trajectories

(Holzwarth, Rüger & Wirth, 2015), with a stronger effect of complementarity soon after the disturbance, as more heterogeneous local conditions can foster niche partitioning (Craven, Hall, Berlyn, Ashton, & van Breugel, 2018), subsequently surpassed by a stronger selection effect as typically observed in mature forests (Chiang et al., 2016).

Material and Methods

TROLL Model

TROLL is an individual-based and spatially explicit model of forest dynamics that uses species-specific functional traits to parameterize tree physiological function and demographic processes. A detailed description of the model is given in Maréchaux & Chave (2017) and is only summarized here. In TROLL, the life cycle (recruitment, growth, seed production, and death) is simulated for individual trees > 1 cm dbh (diameter at breast height). The light environment in which trees grow is computed within a $1\ m^3$ voxel grid. Each tree is flagged with a species label inherited from the mother tree through the seed. Each species label is associated with a number of species-specific functional traits (Table 1) from which ecophysiological and demographic processes are simulated using relationships taken from the literature. These functional traits can be directly obtained from field measurements. Overall, the model data requirement at the species level and its outputs at the individual level reflect current trait collection efforts and field inventories, respectively. For all our simulations and analyses, we used a parameterization for 163 species based on a comprehensive set of functional trait data gathered from a distributed network of intensively-monitored old-growth forest plots in French Guiana (Baraloto et al., 2010), like in Maréchaux & Chave (2017). This species pool is representative of the functional composition of a Guyanese forest community that typically shelters many late-successional species and few pioneer species (see Fig. 6 in Maréchaux & Chave, 2017).

Seedlings below the 1 cm size class are not modeled on an individual basis but are part of a seed/seedling pool. This simulated pool is supplied at each monthly time step by seed dispersal from simulated mature trees inside the simulated plot and by a low external seed rain (50 seeds

per hectare) with a species composition similar to that of an old-growth forest. This generates a local seed bank in every square meter of the ground. A maximum of one seed/seedling per square meter is randomly drawn from this local seed bank, and if enough light is available locally for the selected species to thrive, a tree of that species is recruited. Once established, the tree is defined by its age, dbh, height (h), crown radius (CR), crown depth (CD) and leaf area (LA). Tree geometry is calculated using allometric relationships.

Carbon assimilation is computed every half hour of one representative day per month using the Farquhar, von Caemmerer, and Berry model of photosynthesis (Farquhar, Caemmerer, & Berry, 1980). Photosynthetic capacities and leaf respiration rate are computed from species-specific leaf nitrogen (N) and phosphorus (P) concentration, and leaf mass per area (LMA; Atkin et al., 2015; Domingues et al., 2010). The net amount of assimilated carbon allocated to growth is then partitioned among the different plant organs using empirical factors. The fraction allocated to woody growth is converted into increments of stem volume using species-specific wood density, while the fraction allocated to leaves is converted into leaf area increments using LMA. Leaf demography is simulated using species-specific leaf lifespan derived from LMA. Here we did not use the same relationship between LMA and leaf lifespan as in Maréchaux & Chave (2017), as we found that it underestimated leaf lifespan in low LMA species. We consequently designed a new leaf lifespan allometry, specific to tropical tree species that is used throughout this study (see Appendix S1). Natural tree deaths are stochastic events and their rate is negatively correlated with wood density in TROLL, as observed pan-tropically (Kraft & Ackerly, 2010; Poorter et al., 2008; Wright et al., 2010) and locally (Aubry-Kientz, Hérault, Ayotte-Trépanier, Baraloto, & Rossi, 2013). Additionally, trees can die due to carbon starvation or treefall. Below-ground processes, herbaceous plants, epiphytes and lianas are not simulated.

The source code is written in C++, version 2.3.1 used in this study is available at https://github.com/TROLL-code/TROLL. The simulated forest dynamics were validated against observations of both forest composition (e.g. species relative abundance, trait distribution), functioning (e.g. gross primary productivity), and structure (e.g. tree density, plot biomass, tree

size distribution) made in secondary and mature forest sites in French Guiana (Maréchaux & Chave, 2017).

Implementing a mechanistic disturbance module in an individual-based model is challenging since disturbances are diverse in tropical forests and can affect individual tree or species depending on specific features (De Laender et al., 2016). For instance, species-specific wood density and tree diameter are key species features in selective logging whereas species hydraulic strategies will influence drought-induced tree mortality (Garcia-Valdés, Bugmann & Morin, 2018; Anderegg et al., 2016). Although tree mortality rates appear to be increasing in tropical forests, the underlying causes remain poorly understood, and predicting tree mortality based on physiological principles and functional traits remains a formidable challenge (Anderegg et al., 2016; McDowell et al., 2018; Aleixo et al., 2019). For the sake of parsimony, we implemented a module of random disturbance in the TROLL model. In so doing, we studied the effect of disturbance intensity without directionally impacting forest structure and composition.

The module works as follows: at a given iteration $disturb_{iter}$, individual trees are randomly picked, independently of particular individual or species-specific properties. Selected individuals are then removed without triggering a treefall to control disturbed biomass volume. The operation is repeated until the cumulative basal area of removed trees reaches the targeted threshold ($disturb_{intensity}$). We acknowledge that this module depicts a particular type of random disturbance, but this is a first test case to explore the response of forest biodiversity on tropical forest resilience to disturbance. Future versions of TROLL could build on this random disturbance module to include more mechanistic details and explore the effect of different disturbance types (for more details, see the Discussion section).

Simulation experiment

To assess the role of biodiversity in forest recovery from disturbance, we simulated forest trajectories with different levels of disturbance intensity ($disturb_{intensity}$) and tree community compositions. For each simulation, we first simulated forest regeneration from bare soil for 600 years (pre-disturbance step). We then simulated the disturbance described above ($disturb_{iter}$),

and then let the simulated forest community recover freely from the disturbance for a further 600 years (post-disturbance step). Disturbance intensity ($disturb_{intensity}$) was fixed at 0% (control), 25%, 50% or 75% of basal area loss. For each level of disturbance intensity, we ran 60 simulations differing in the original number of species (species richness $SR \in \{5,25,125\}$) and in floristic composition. For each level of species richness, we first created 1000 virtual communities by randomly picking the desired number of species among the pool of 163 parameterized species. Then, among the 1000 communities, we selected 20 with a wide range of functional trait convex hull volumes CVH (Cornwell, Schwilk, & Ackerly, 2006) but with a community mean (CM) close to the one of the regional species pool ($CM_{LMA} = 115 \pm 19\ g.m^{-2}$, $CM_{wsg} = 0.73 \pm 0.07\ g.cm^{-3}$, $CM_{dmax} = 0.37 \pm 0.1\ m$, $CM_{hmax} = 40 \pm 11\ m$, Baraloto et al., 2010) in order to control for average functional composition. This led to 240 simulations with different community composition and disturbance intensity (3 SR * 20 CVH * 4 levels of disturbance intensity).

Analysis

Quantifying simulated community diversity

Species and functional diversities were assessed for each simulation just before the disturbance, i.e. at the end of the pre-disturbance simulation step, with species richness (SR) and functional diversity indices ($FDiv$, the volume of the functional space occupied by the community; $FEve$, the regularity of the distribution of abundance in this volume; Villéger, 2008) using the FD R package (Laliberté & Legendre, 2010). To compute these indices, we used the traits listed in Table 1, which are related to the main independent economics spectra identified in Neotropical forests (Baraloto et al., 2010). Initial species pools resulted in a wide range of values of functional diversity indices after 600 years of pre-disturbance simulation ($FDiv$ ranged from 0.4 to 1.0 and $FEve$ from 0.1 to 0.8).

Ecosystem recovery from disturbance

Simulated tropical forests were characterized in terms of changes in ecosystem properties regarding (i) forest structure (aboveground biomass, AGB in $Mg\ C.ha^{-1}$; basal area, BA in $m^2.ha^{-1}$; total number of stems, N; number of stems above 10 cm dbh, $N10$; number of stems above 30 cm dbh, $N30$), and (ii) forest functioning (gross primary productivity, GPP in $MgC.ha^{-1}$; net primary productivity, NPP in $MgC.ha^{-1}$; tree autotrophic day-time respiration, $Rday$ in $MgC.ha^{-1}$; tree autotrophic night-time respiration, $Rnight$ in $MgC.ha^{-1}$).

The recovery of the simulated forest at time t regarding a given property X, $R_x(t)$, was defined relative to an undisturbed baseline:

$$R_x(t) = \frac{X_D(t)}{X_C(t)} \qquad (1)$$

where $X_D(t)$ and $X_C(t)$ are the values of ecosystem property X at time t in the disturbed simulation ($disturb_{intensity} = 25\%, 50\%, 75\%$) and in the control simulation ($disturb_{intensity} = 0\%$), respectively (Fig. 1). Note that the variability among replicated simulations with the same set up, due to demographic stochasticity in the model, is low enough to assume that a given simulation is representative of the community properties and dynamics for an initial species pool and disturbance intensity (Maréchaux & Chave, 2017).

When $R_x(t)$ approaches $R_{eq} = 1$, the disturbed and control systems are considered equivalent, indicating perfect recovery of X. We then calculated the Euclidean distance to this state of perfect recovery as $d_x(t) = \sqrt{(\text{R}_{eq} - R[X(t)])\text{^2}}$ (Fig. 1). To capture the temporal dimension of resilience, we integrated $d_x(t)$ over time, which quantifies the cumulative difference between disturbed and control runs, as illustrated by the grey area in Fig. 1. We finally computed the inverse of this area as an index of ecosystem resilience, hereafter denoted I_R, so that a higher I_R reflects greater resilience:

$$I_R(X) = \left(\int_{t = disturb_{iter}}^{t = disturb_{iter} + 600} d_x(t).dt\right)^{-1} \quad (2)$$

Distance to equilibrium d_x and resilience index I_R were calculated in a multi-dimensional space for the two sets of ecosystem property values: (i) forest structure (AGB, BA, N, $N10$, and $N30$) and (ii) forest functioning (GPP, NPP, $Rday$, and $Rnight$).

Biodiversity effect

We tested the influence of three factors on the resilience index I_R: pre-disturbance species richness (SR), functional evenness ($FEve$) and functional diversity ($FDiv$) as follows:

$$\log(I_R) \sim N\left(\Theta_{SR} + \Theta_{FEve} \times Feve + \Theta_{FDiv} \times Fdiv; \sigma^2\right)$$

where Θ_{SR} is a vector of three parameters corresponding to the three levels of species richness, Θ_{FEve} and Θ_{FDiv} model the effect of, respectively, $Feve$ and $Fdiv$ on $\log(I_R)$ under a normal law of variance σ^2. The analysis was conducted twice for each level of disturbance (25%, 50% and 75% of basal area loss): once with forest structure properties and once with forest functioning properties. We used the Akaike information criterion (AIC) to select the final, most parsimonious models. The ecosystem resilience index I_R was log-transformed to improve the normality of the residuals.

For each ecosystem property X, we investigated the effect of biodiversity and its variation along post-disturbance trajectories. The net effect of biodiversity (NE) on ecosystem property X is defined as the difference between the ecosystem property X of the simulated mixed-species community and the one expected under the null hypothesis. The latter would mean that there is no effect of biodiversity, i.e. that ecosystem property X for the mixed-species community equals the abundance-weighted sum of that in monocultures (Loreau & Hector, 2001). To this end, we simulated a monoculture of each of the 163 species and for each level of disturbance leading to 652 simulations of monocultures.

We then partitioned this net biodiversity effect into complementarity and selection effects using the partitioning procedure of Loreau & Hector (2001):

$$NE = CE + SE \quad (3)$$

$$CE = SR * \overline{\Delta RX\ M} \quad (3a)$$

$$SE = SR * cov(\Delta RX, M) \quad (3b)$$

where SR represents the total number of species, M is the vector of X for the 163 simulated monocultures, and ΔRX is as follows:

$$\Delta RX_{sp} = \frac{X_{sp}(mixture)}{X_{sp}(monoculture)} - P_{sp} \quad (4)$$

where X_{sp} is the value X for the species sp either in mixture $X_{sp}(mixture)$ or in monoculture $X_{sp}(monoculture)$. P_{sp} is the relative abundance of the species in the mixture. In the absence of disturbance, biodiversity net effect NE can vary over time due to stochasticity. To correctly assess selection and complementarity effects, we normalized NE by the value NE_C calculated for the control simulation ($disturb_{intensity} = 0\%$) to measure the recovery of the net biodiversity effect $R(NE)$:

$$R(NE) = \frac{NE}{NE_C} = \frac{SE}{NE_C} + \frac{CE}{NE_C} \quad (5)$$

Results

Biodiversity effect on forest resilience

As species richness (SR) increased from 5 to 125 species, mean functional diversity varied from 0.76 ± 0.18 to 0.96 ± 0.02 and mean functional evenness ($FEve$) varied from 0.46 ± 0.24 to 0.64 ± 0.02. In the models testing the influence of taxonomic and functional diversities on the resilience index I_R, species richness (SR) was never retained by the AIC selection procedure,

whatever the disturbance intensity. Both functional diversity ($FDiv$) and functional evenness ($FEve$) were positively related with I_R, i.e. forest resilience increased with both functional diversity and functional evenness (Fig. 2 and Table 2). Similar results were obtained for all disturbance levels, with higher significance for higher disturbance intensity. The model R^2 was higher for forest functioning (from 0.27 to 0.51) than for forest structure (from 0.18 to 0.27) variables. While $FDiv$ was the most significant variable in forest structure models, $FEve$ was the most significant variable in forest functioning models (Table 2).

Post-disturbance trajectories of the biodiversity effect

The net effect of biodiversity on each ecosystem property was quantified (Table 3) and partitioned into selection and complementarity effects. The net effect was positive for most ecosystem variables, apart for the number of stems above 10 cm dbh and the net primary productivity for which the average net effects were negative, albeit weak. We found that the complementarity effect of biodiversity on aboveground biomass increased sharply just after disturbance and remained the dominant effect of biodiversity during the first decades after which it progressively vanished (Fig. 3). When we increased the disturbance intensity, the effect of complementarity showed a steeper increase after disturbance and dominated even longer. On the other hand, the selection effect decreased sharply immediately after the disturbance, and only gradually came to play a more important role, dominating the net biodiversity effect about one century after disturbance. At high disturbance intensity, the net effect of biodiversity on aboveground biomass was still lower than the control 600 years after disturbance (Fig. 3). We found similar results, but with an amplified signal, for basal area (BA) and stem abundance (N, see Appendix S3). Finally, forest primary productivity and respiration (GPP, NPP, R_{day} and R_{night}) recovered within a few years with a dominant complementarity effect.

Discussion

Using an individual-based and trait-based model of tropical forest, we assessed the effects of species and functional diversity on long-term forest recovery from different disturbance levels by manipulating the number of species and functional assemblages across a large number of simulations. To investigate the ecological mechanisms that underlie the effect of biodiversity on forest functioning along recovery pathways, we further partitioned the net effect of biodiversity on ecosystem properties into complementarity and selection effects. We found that functional diversity improved tropical forest resilience in our simulations. Complementarity was the dominant effect of biodiversity on ecosystem properties shortly after disturbance but was progressively surpassed by a selection effect, as more competitive species dominated the forest community, a pattern that increased with disturbance intensity. Overall, our results suggest that the time since the last disturbance is a key to understanding the ecological mechanisms that underlie the relationships between biodiversity and ecosystem functioning in tropical forests. This helps reconcile the contrasting results obtained previously with snapshots of ecosystem state in empirical studies.

Functional diversity accelerates tropical forest resilience

Our results provide strong evidence for a significant positive relationship between functional diversity and forest resilience. In particular, the volume of the functional space occupied by the community (Villéger, Mason, & Mouillot, 2008), and its evenness, both of which turned out to be major predictors of forest resilience. This may be due to (i) an increased range of species niches that enable post-disturbance successional pathways to unfold rapidly, and (ii) functional dissimilarity reducing competition strength (Loreau & Mazancourt, 2013). Our results thus support Díaz & Cabido (2001), who pointed to the under-evaluated importance of plant functional diversity in ecosystem processes, and Zhang, Chen, & Reich (2012) who highlighted the role of evenness in the productivity of forest ecosystems. The effect of functional diversity increased with increased disturbance intensity, although forest recovery trajectories were longer for more intense disturbances, in agreement with the results of previous short-term

empirical (Hérault & Piponiot, 2018) or long-term simulation studies (Hiltner et al., 2018) in the area. Decreased resilience with increased disturbance intensity may result from a more extreme shift of the forest functional composition toward an early-successional composition (Carreño-Rocabado et al., 2012) that would impede recovery (Qie et al., 2019). Our model simulations provide new evidence that the high diversity of functional traits in tropical forests can reinforce their resilience under the predicted increase in disturbances in the context of global change.

The mechanisms underlying the effect of biodiversity on forest functioning shift along a successional trajectory

We found that complementarity among species was the prevailing effect of biodiversity on forest functioning for several decades after a disturbance. This is a direct consequence of the appearance of gaps and increasingly heterogeneous light availability, the main limiting resource in dense tropical forests. Species are known to vary widely in their demographic response to light availability depending on their functional strategy (Hérault, Ouallet, Blanc, Wagner, & Baraloto, 2010; Rüger, Huth, Hubbell, & Condit, 2009). Pioneer species with productive leaf tissue and light wood tend to rapidly occupy gaps after they open, hence creating a shaded environment where late successional species with more conservative leaf tissue can establish later (Craven, Hall, Berlyn, Ashton, & van Breugel, 2015). By inducing a higher diversity of shade tolerance and growth response to light in the species pool, species richness fosters forest response to disturbances (Morin et al., 2011). This complementarity effect decreases over time while the selection effect progressively takes over. The reduced complementarity effect can be attributed to the increased abundance of the most competitive late-successional species in a stable canopy with more homogenous light availability (Holzwarth, Rüger & Wirth, 2015).

Implications of modelling choices and generalizability of the results

In this study, we used an individual-based forest simulator to jointly simulate biodiversity and ecosystem functioning, and explored the effect of biodiversity on forest resilience over centuries, a timeframe that remains out of reach of most experimental approaches.

Like any modelling approach, our study has its simplifications and assumptions. Our simulations did not account for the secondary effects of disturbances on community structure, such as damage to surrounding trees or secondary treefalls. This should result in larger disturbance gaps and hence increase the spatial scale at which biodiversity impacts forest resilience (Chisholm et al., 2013; Sullivan et al., 2017). However, it should not modify our main results, as our analyses were conducted at the plot scale (16 ha). Similarly, we assumed that our simulated plots were surrounded by old-growth forests resulting in a continuous seed rain of late-successional species. Yet forest fragmentation can strongly influence forest recovery pathways (Arroyo-Rodriguez et al., 2017), reducing selection and enhancing complementarity effects when dispersal is limited (Leibold, Chase & Ernest, 2017).

In our simulations, light was the only resource whose variability was explicitly accounted for (Maréchaux & Chave, 2017). Our analysis thus simulated a situation where aboveground competition for light is greater than the effect of belowground competition for water and nutrients, a reasonable assumption in humid tropical forests, even in early successional stages (van Breugel, Breugel, Jansen, Martínez-Ramos, & Bongers, 2012). However, competition for water may become stronger if drought intensity and frequency increase in the tropics (Duffy, Brando, Asner, & Field, 2015). The same remark applies to nutrient competition given increased human-induced nutrient imbalances (Peñuelas et al., 2013). Species richness has been shown to stabilize ecosystem growth and mortality in tropical plantations undergoing increasing hydric stress (Hutchison, Gravel, Guichard, Potvin, 2018). We would expect a stronger role of complementarity through hydrological and edaphic niche partitioning under more heterogeneous water availability (Baltzer, Thomas, Nilus, & Burslem, 2005; Jucker et al., 2018; Silvertown, 2004), and more generally under more heterogeneous environmental conditions. However, under long-term drier-conditions, we would expect selection to have a stronger effect, as more drought-tolerant taxa progressively become more dominant (Sakschewski et al., 2016, Esquivel-Muelbert et al., 2019). Here, we used traits identified as key predictors of ecological functions in Neotropical forests (Baraloto et al., 2010), but other traits, e.g. hydraulic traits such as vulnerability to cavitation or leaf water potential at turgor loss point, play an important role

in resilience to specific disturbances such as drought (Maréchaux et al., 2018; Santiago et al., 2019). We hope to include these other facets of functional diversity in future contributions, as more data are becoming available for these physiological traits.

More generally, we simulated random disturbances, and our findings could differ for other types of disturbances (Radchuck et al., 2019). For instance, selective logging typically targets a few species, which could favor complementarity over selection if dominant species are repeatedly chosen. Repeated disturbances such as periodic harvesting, one of the main causes of degradation in tropical forests, would also increase the prevalence of early recovery stages during which complementarity plays the main role. Other natural disturbances do affect tropical forests, including droughts, which can impact larger trees (Bennett, McDowell, Allen & Anderson-Teixeira, 2015; but see Enquist & Enquist, 2011 or Fauset et al., 2012), fire, which typically impacts smaller trees (Cochrane & Schulze, 1999), pests, which can impact a single species (Novotny et al. 2002, 2005), or wind-related disturbances, to which softer-wood species can be more vulnerable (Curran, Gersbach, Edwards, & Krockenberger, 2008; but see Jackson et al., 2019). Previous studies suggested that tree diversity fosters forest resilience to such disturbances (Sakschewski et al., 2016; Guyot, Castagneyrol, Vialatte, Deconchat & Jactel, 2016; d'Hôte, 2016), in agreement with our findings for random disturbances. However, whether our results concerning long-term recovery trajectories would be the same under these other types of disturbances and their interactions remain to be tested. Ongoing development of the model and improved knowledge of the mechanisms underlying tree vulnerability to various disturbances will allow us to test such hypotheses in future contributions.

Looking at temporal dynamics can unify biodiversity-ecosystem functioning studies

Previous biodiversity-ecosystem functioning studies yielded contrasting results on the relative importance of the different biodiversity effects in tropical forests. While the complementarity effect was identified as the dominant effect in some studies (Huang et al., 2018; Niklaus et al., 2017), the selection effect was identified in others (Tobner et al., 2016; Bauters et al., 2015;

Maréchaux & Chave, 2017; Finegan et al., 2015; Lohbeck, Bongers, Martinez-Ramos, & Poorter, 2016; de Avila et al., 2018). Our results suggest that the mechanisms through which biodiversity influences forest functioning depend to a great extent on the state of the ecosystem and its history of disturbances, with a complementarity effect dominating in recently (i.e. a few decades) disturbed ecosystems and a selection effect surpassing complementarity in systems disturbed a long time ago. In agreement with our results, Huang et al. (2018), Niklaus et al. (2017) and Poorter et al. (2017) did find a stronger complementarity effect in recently disturbed forest sites (8- to 32-year-old plantations or logged plots). On the contrary, other studies of forests disturbed a long time ago and of undisturbed forests showed a dominant selection effect (77-year-old planted forest, Bauters et al., 2015; undisturbed forests, Finegan et al., 2015; 500-year-old simulated forest, Maréchaux & Chave, 2017). The dominant selection effect observed in plantations by Tobner et al. (2016) or in secondary forests by Lohbeck et al. (2016) could be explained by the recent ecosystem conversion from agricultural fields and fallows, respectively, resulting in the absence of high tree diversity at this stage (see Appendix S2).

Taken together, our results pave the way for a unifying framework to reconcile the apparent contradictions among previous studies, and call for an accurate description of the history of ecosystem disturbances, in agreement with the increasingly recognized importance of legacy effects in shaping forest dynamics and composition (Chazdon et al., 2003; Arroyo-Rodriguez et al., 2017; Levis et al., 2017; Odonne et al., 2019). This opens the way for improved prediction of ecosystem resilience in a context of increasing disturbances and the biodiversity crisis.

Supporting Information

- Appendix S1: Leaf lifespan model
- Appendix S2: Biodiversity trajectories
- Appendix S3: Post-disturbance trajectories of ecosystem variables
- Appendix S4: Variation of forest resilience with taxonomic and functional diversity for different levels of disturbance intensity.

Acknowledgements

Authors' contributions

SS, BH, ST, CP, and IM conceived the study, designed the methodology and analysed model outputs; IM, JC and FF developed the initial model code and ensured its transferability; SS, IM and BH led the writing of the manuscript. All the authors contributed to the drafts and gave their final approval for publication.

Data availability

TROLL source code is written in C++ and version 2.3.1 used in this study is available at https://github.com/TROLL-code/TROLL. Species traits used in the simulation experiment are derived from the BRIDGE dataset (Baraloto et al., 2010) available on TRY (Kattge et al., 2011).

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Table captions

Table 1 Species-specific parameters used in TROLL from Maréchaux & Chave (2017). The data originate from the BRIDGE (Baraloto et al., 2010) and TRY (Kattge et al., 2011) datasets.

Table 2 Effects of functional diversity on forest resilience. Results of the linear models testing the effect of functional diversity indices ($FDiv$ and $FEve$) on the resilience index (I_R) for forest structure and functioning and for each level of disturbance intensity *($disturb_{intensity}$ in % of total basal area)*. To meet the assumption of normality I_R was log-transformed. Values of $FDiv$ and $FEve$ are model coefficients. Significant $P - values$ are in bold. ns, non-significant; p < 0.1; * p < 0.05; ** p < 0.01; *** p < 0.001.

Table 3 Mean and standard deviation of the biodiversity net effect across simulations before the disturbance event (i.e. after 600 years of establishment) for different ecosystem variables.

Figure captions

Figure 1 Definition of the recovery function R and the resilience index I_R shown for aboveground biomass dynamics for a simulation with $disturb_{intensity} = 50\%$.

Figure 2 Variation of forest resilience with taxonomic and functional diversity at different levels of disturbance intensity. Resilience index I_R is represented versus functional diversity ($FDiv$) for different levels of disturbance ($disturb_{intensity}$ = 25%, 50% and 75% of total basal area); the shape of the symbols varies with species richness. The intensity of the color of the symbols refers to functional evenness ($FEve$). Left column: I_R computed for forest structure variables; right column: I_R computed for forest functioning variables. Solid lines and grey areas show fitted relationships with their mean and variance of the form $I_R \sim N(\Theta_{FDiv} \times Fdiv;\sigma^2)$. For a clearer illustration of the variation of I_R with $FEve$, see Appendix S4.

Figure 3 Post-disturbance trajectories of complementarity and selection effects on aboveground biomass at increasing levels of disturbance (disturb$_{intensity}$ = 25%, 50% and 75%

of basal area loss). The net biodiversity (NE, in red), complementarity (CE in green) and selection (SE in blue) effects were normalized by the net effect of biodiversity in the control simulation (disturb$_{intensity}$ = 0%). Solid lines represents the mean value whereas shaded areas represent the range of values across the 20 simulations with a species richness (SR) of 125. The time axis has been square-root transformed to highlight dynamics in the first decades.

Table 1 Species-specific parameters used in TROLL from Maréchaux & Chave (2017). The data originate from the BRIDGE (Baraloto et al., 2010) and TRY (Kattge et al., 2011) datasets.

Abbreviation	Description	Units of measure
LMA	leaf mass per area	$g.m^{-2}$
N_m	leaf nitrogen content per dry mass	$mg.g^{-1}$
P_m	leaf phosphorus content per dry mass	$mg.g^{-1}$
wsg	wood specific gravity	$g.cm^{-3}$
dbh_{thresh}	diameter at breast height threshold	m
h_{lim}	asymptotic height	m
a_h	parameter of the tree height-dbh allometry	m

Table 2 Effects of functional diversity on forest resilience. Results of the linear models testing the effect of functional diversity indices (FDiv and FEve) on the resilience index (I_R) for forest structure and functioning and for each level of disturbance intensity ($disturb_{intensity}$ in % of total basal area). To meet the assumption of normality I_R was log-transformed. Values of FDiv and FEve are model coefficients. Significant P − values are in bold. ns, non-significant; p < 0.1; * p < 0.05; ** p < 0.01; *** p < 0.001.

$\log (I_R)$	$disturb_{intensity}$	FDiv	FEve	R^2
structure	25	**0.29 ****	0.13 n.s.	0.18
structure	50	**0.68 ****	0.07 n.s.	0.27
structure	75	**0.7 ****	**0.36 ****	0.24
functioning	25	**0.72 ****	**1.06 *****	0.51
functioning	50	**0.98 ****	**0.95 ****	0.30
functioning	75	**0.8 ***	**1.33 *****	0.27

Table 3 Mean and standard deviation of the biodiversity net effect across simulations before the disturbance event (i.e. after 600 years of establishment) for different ecosystem variables.

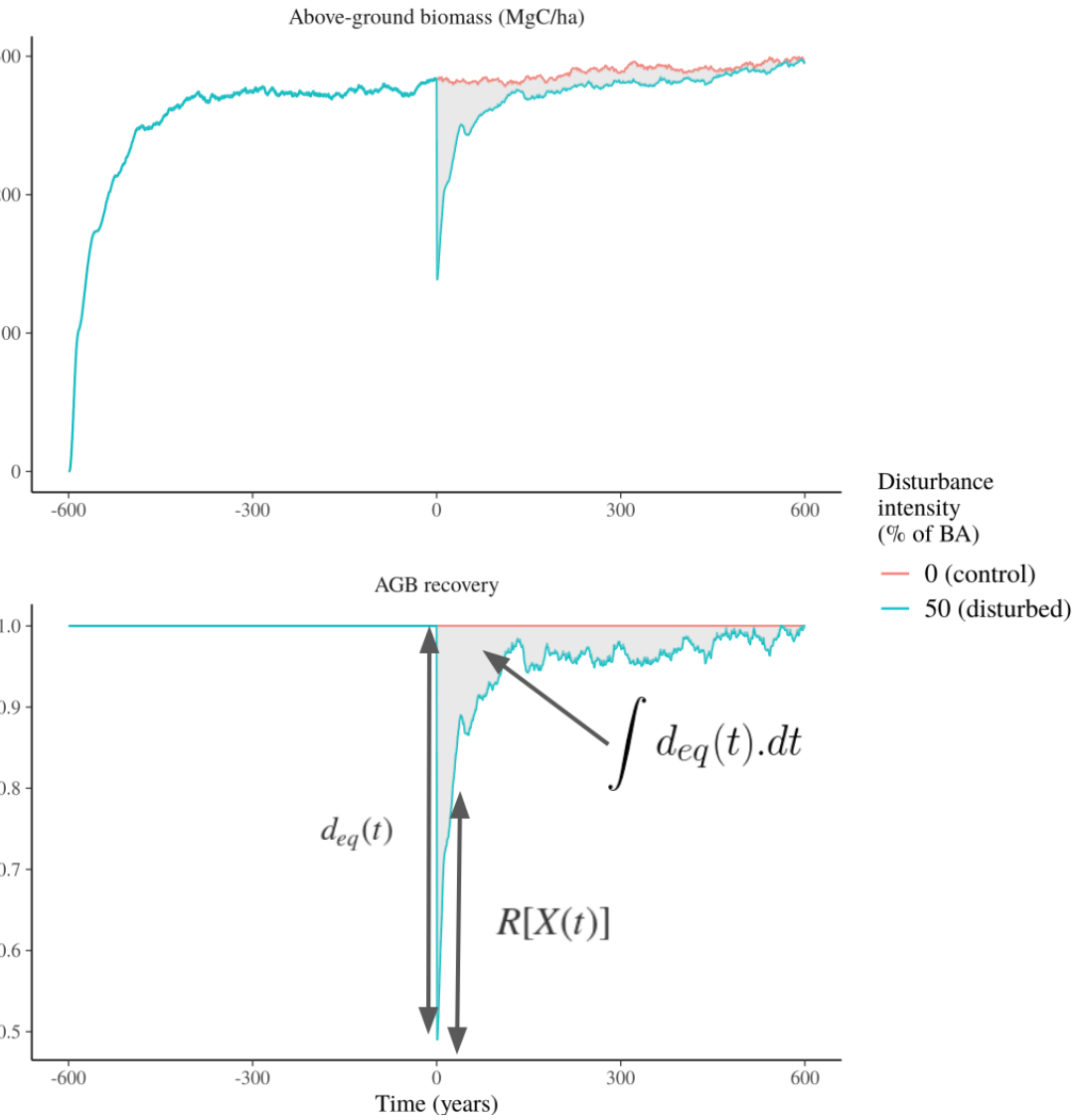| Ecosystem property	Net effect	Unit of measure
aboveground biomass	32.72 ± 17.84	$MgC.ha^{-1}$
basal area	1.63 ± 0.74	$m^2.ha^{-1}$
number of stems	103.88 ± 231.62	$n.ha^{-1}$
number of stems above 10 cm dbh	-6.82 ± 13	$n.ha^{-1}$
growth primary production	0.15 ± 0.05	$MgC.ha^{-1}.yr^{-1}$
net primary production	-0.04 ± 0.04	$MgC.ha^{-1}.yr^{-1}$
autotrophic respiration during the day	0.05 ± 0.02	$MgC.ha^{-1}.yr^{-1}$
autotrophic respiration during the night	0.07 ± 0.03	$MgC.ha^{-1}.yr^{-1}$

Figure 1 Definition of the recovery function R and the resilience index I_R shown for aboveground biomass dynamics for a simulation with $disturb_{intensity} = 50\%$.
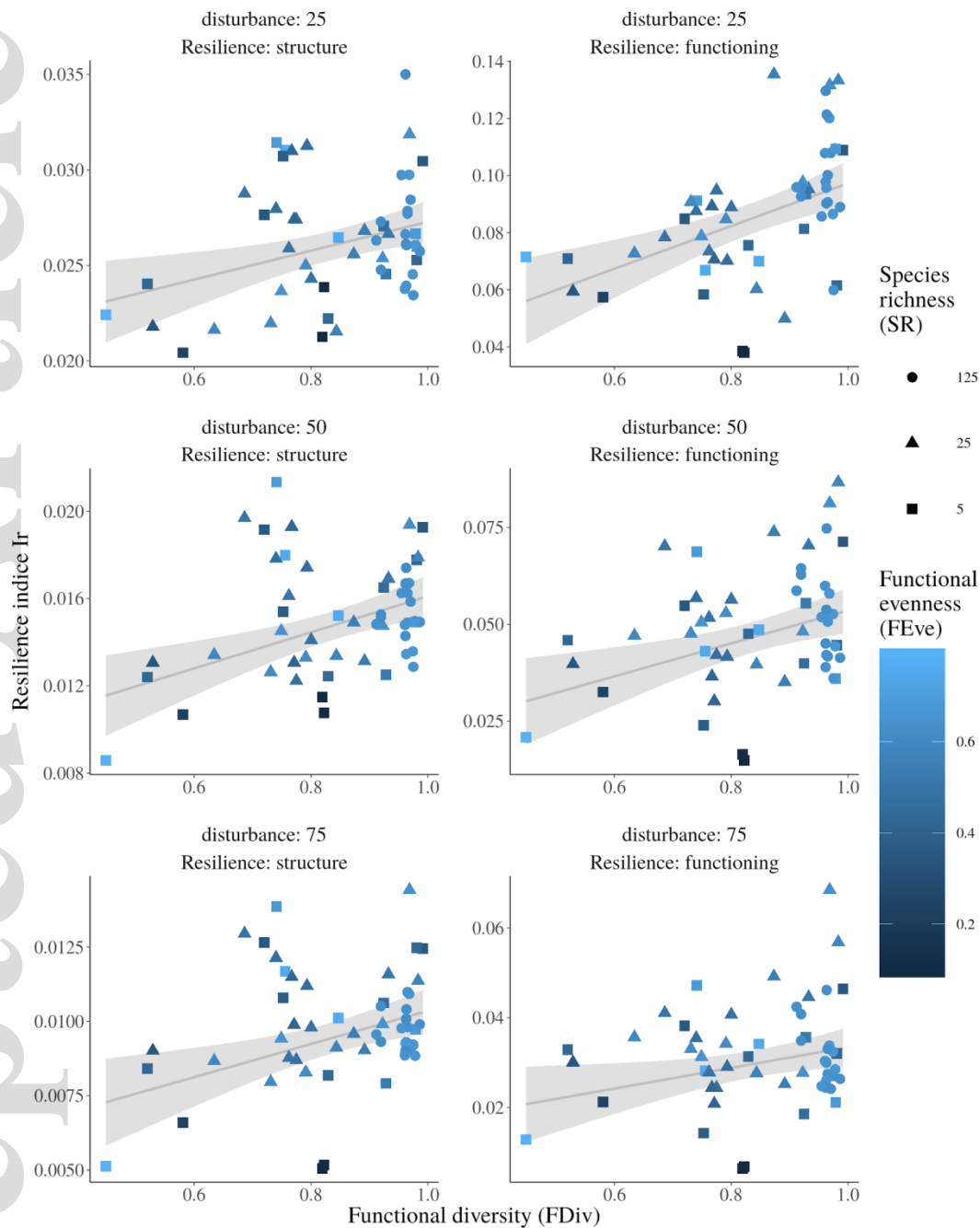
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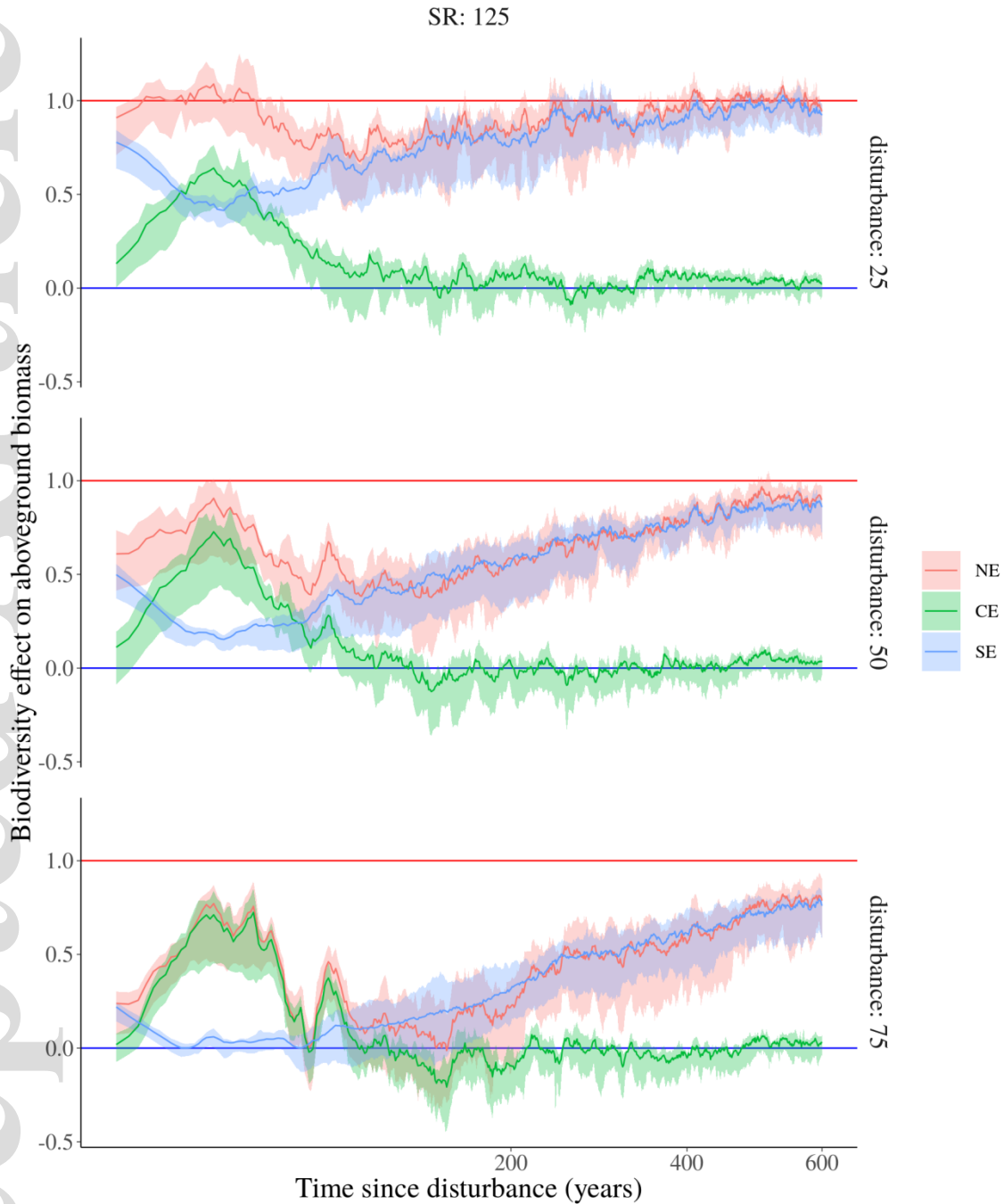
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