Title: Directed Species Loss Reduces Community Productivity in a Subtropical Forest Biodiversity Experiment

Short title: Non-random diversity–productivity relationships

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ABSTRACT

Unprecedented species loss in diverse forests indicates the urgent need to test its consequences for ecosystem functioning. However, experimental evaluation based on realistic extinction scenarios is lacking. Using species interaction networks, we introduce an approach to separate effects of node loss (reduced species number) from effects of link loss or compensation (reduced or increased interspecific interactions) on ecosystem functioning along directed extinction scenarios. By simulating random and non-random extinction scenarios in an experimental subtropical Chinese forest, we find that species loss is detrimental for stand volume in all scenarios, and that these effects strengthen with age. However, the magnitude of these effects depends on the type of attribute on which the directed species loss is based, with preferential loss of evolutionarily distinct species and those from small families having stronger effects than those that are regionally rare or have high specific leaf area. These impacts were due to both node loss and link loss or compensation. At high species richness (reductions from 16 to 8 species), strong stand volume reduction only occurred in directed but not random extinction. Our results imply that directed species loss can severely hamper productivity already in diverse young forests.

MAIN TEXT

Concerns over the accelerating loss of species [1-3] have led to more than 600 experiments studying how biodiversity affects ecosystem functioning [4]. These experiments have shown that species loss generally reduces plant community productivity and its temporal stability [4]. Most experiments simulated the random, trait-independent loss of species; less than 2% implemented designed non-random extinction scenarios (Supplementary Table 1). However, random loss of species may be atypical in nature. For example, species loss may depend on species attributes (e.g. body size, rarity, and sensitivities to environmental change), which may be related to phylogeny [1,5-8]. Forests account for 75% of terrestrial gross primary production globally [9] and their biodiversity is threatened by environmental change and deforestation [2,10]. Yet, no experiment has been conducted so far to test impacts of directed tree species loss on ecosystem functioning (Supplementary Table 1; but see two forest studies based on simulation [11,12]).

Effects of directed species loss on ecosystem functioning may differ in two ways from effects of random species loss. First, directed loss of species could lead to directed shifts in average attribute values of post-extinction communities, which could in turn affect ecosystem processes [13,14]. For example, severe drought may lead to the loss of species with high specific leaf area (SLA) due to their intolerance to water deficit [15], which in turn may reduce productivity due to the loss of species with fast growth rate[16]. If lost species (representing lost nodes in species interaction networks; Fig. 1) had higher or lower contribution to ecosystem functioning than remaining species, effects of node loss on ecosystem functioning may be negative or positive, respectively (Fig. 1 and Supplementary Table 2). However, random species loss by definition should, on average, not lead to directed shifts in community-weighted mean attribute values of post-extinction communities.

Second, directed species loss often removes species with extreme attributes [1,5,8] or high evolutionary distinctiveness [6,7], which in turn may increase species similarity in attributes or phylogeny of post-extinction communities. Species similarity is often associated with species interactions which correspond to links in species interaction networks (Fig. 1). For example, competition may be more severe among species similar in attributes or phylogeny due to high niche overlap [17]. However, random species loss, on average, should not lead to a change in mean pairwise species similarity in post-extinction communities [18].

Species loss could change species interactions and links in at least two ways: losing interspecific interactions associated with lost species (link loss) and increasing frequency of interactions between remaining species (link compensation; Fig. 1). If lost links are dominated by processes associated with niche partitioning or facilitation, post-extinction communities without these links may have lower ecosystem functioning than pre-extinction communities (Fig. 1 and Supplementary Table 2). If lost links are dominated by strong interspecific competition, post-extinction communities lacking these links may become more productive than pre-extinction communities (Supplementary Table 2). Remaining species may maintain total community density (i.e., number of individuals per area) by increasing their own individual densities (i.e., full numerical compensation) after species loss [12,19]. The increased individual densities of remaining species could increase the frequency of interactions between remaining species (Fig. 1). If remaining links are enriched for niche partitioning or facilitation, post-extinction communities may be more productive than pre-extinction communities (Supplementary Table 2). If remaining links are dominated by strong interspecific competition, post-extinction communities may have lower ecosystem functioning than pre-extinction communities (Fig. 1 and Supplementary Table 2).

In this study, we assessed the impacts of random and directed species loss on productivity over seven years in a subtropical forest biodiversity experiment in China. The part of the experiment we use here consists of a total of 469 plots that harbored 1 to 16 tree species on an area of 0.067 ha (Chinese land area unit of 1 mu). We used a pool of 40 tree species to simulate both random and non-random extinction scenarios at two sites [20,21] (Extended Data Fig. 1). Each site had a pool of 24 species. For the random species loss scenario, we randomly sampled three pools of 16 species from the 24 species present at each site (Extended Data Fig. 1). These pools were then randomly divided into halves and this procedure repeated, yielding nested, non-overlapping subsets of 8, 4, 2 and 1 species. In this design, the average species attribute value of two lower-richness halves equal that of the corresponding pre-extinction community with twice the species richness. Also, each species has the same extinction probability across richness levels. For the scenarios of designed non-random species loss, richness gradients were derived from species pools with decreasing local rarity or specific leaf area (SLA) [20] (Extended Data Fig. 1). Total community planting density was constant, reflecting the above-mentioned full numerical compensation of lost by remaining species (substitutive design).

In the designed random scenario, the average difference in the community weighted mean (CWM, weighted by planted abundance) attribute values between a pre-extinction community (e.g., a four-species community [A, B, C, D] with the letters designating the species) and its two post-extinction communities (e.g., [A, B] and [C, D]) should be zero, i.e. neutral. However, for each extinction step descended from a given pre-extinction community (e.g., [A, B, C, D] →[A, B]), CWM differences could range from non-neutral to neutral (Extended Data Fig. 2). Therefore, in order to consider the full range of attribute shifts due to species loss, we combined communities from both the designed non-random and random extinction scenarios and constructed new extinction sequences of directed species loss from the entire set of 469 plots. We did not assess differences between the designed non-random and random extinction scenarios, because the latter were based on incomplete species attribute information at the time we designed the experiment.

We derived four new types of effectively non-random extinction scenarios, in which species with the following attributes went extinct first (Table 1): species with high SLA (as measured in the experiment), evolutionary distinctiveness (ED), regional rarity or from small clades (small family sizes). These four attributes are known to correlate with extinction risk, represent a wide spectrum of extinction mechanisms and have been widely studied in previous research (Table 1). Richness gradients in the new extinction scenarios were created from extinction steps where the remaining species were those with lower extinction risk based on the particular attribute (Extended Data Figs. 3 and 4). We assessed the difference between the new effectively non-random scenarios with the designed random scenarios. Species attribute compositions in the designed random scenarios were associated with similar extinction risks across richness levels (Extended Data Fig. 4).

In all plots selected for the different extinction scenarios, we measured the height and basal diameter of the surviving trees in the16 central planting positions and calculated the stand volume per plot as the aggregated volumes of these trees using allometric equations derived from trees harvested near the experimental site [21]. This stand volume and its annual increment were used as productivity measures. Stand-volume increment is the short-term productivity in a specific year. Stand volume is the long-term productivity accrued since planting of the tree communities and one of the critical determinants of short-term productivity due to the size-dependent metabolic constraint [22]. We compared the impacts of species loss on forest productivity along five types of extinction scenarios, which were classified as random or directed by the four species attributes.

To explore the mechanisms driving the impacts of directed species loss on productivity, we developed a partitioning method to decompose the net extinction effect into a node-loss (monoculture difference between remaining and lost species), a link-loss (reduced species interactions associated with lost species or nodes) and a link-compensation (increased frequency of species interactions between remaining species or nodes) effect (Fig. 1 and Supplementary Table 2; *Decomposing the net effects of species loss on stand volume* in METHODS). Species interactions could have positive (niche partitioning or facilitation), negative (competition) or neutral contributions to mixture productivity (Fig. 1). We focused the partitioning analysis on stand volume, our measure of longer-term accumulated productivity across years. The objectives of this study are to (1) assess the impacts of multiple scenarios of species loss on forest productivity, (2) disentangle the mechanisms driving the impacts of directed species loss on forest productivity, and (3) compare the impacts of directed with those of random species loss on forest productivity.

RESULTS

Effects of species loss on productivity

We found negative effects of species loss on stand volume for all random and directed extinction scenarios (Figs. 2 and 3). Halving of species richness reduced stand volume of seven-year-old mixtures by 2.87, 1.56, 5.22, 0.78 and 4.19 $\mathrm{m^3 ha^{-1}}$ on average for the random extinction scenario or those directed by specific leaf area (SLA), evolutionary distinctiveness (ED), regional rarity and inverse of taxon size (small family size), respectively. The negative effects of species loss were statistically insignificant or weak at the beginning of the experiment but became strong and significant as stands developed. This resulted in a temporal strengthening of the trends that we found (Fig. 3, Supplementary Table 3). The random and directed extinction scenarios had comparable effects in general, with differences that depended on the specific attribute driving species loss (Figs. 2 and 3). Species loss directed by ED and inverse of taxon size had stronger effects, while species loss directed by SLA and regional rarity had weaker effects than random species loss.

We found similar results for the effects of species loss on stand-volume increment (short-term productivity). The effects were weak at the beginning of the experiment but became strongly negative for all the five extinction scenarios as our forest stands developed (Extended Data Figs. 5 and 6, Supplementary Table 3). Species loss directed by ED had the strongest effects, while species loss directed by regional rarity had the weakest effects. However, the differences in species loss effects between extinction scenarios were less evident on stand-volume increment than on stand volume. Nevertheless, in the latest year of measurements, halving species richness reduced community stand-volume increments of mixtures by 1.63, 1.26, 1.96, 0.74 and 1.75 $m^3 ha^{-1} year^{-1}$ on average for the random extinction scenario or those directed by SLA, ED, regional rarity and inverse of taxon size.

Stand volume was significantly higher in communities containing species with higher SLA or ED or from smaller clades in the corresponding extinction scenarios directed by SLA, ED or inverse of taxon size across richness levels (Supplementary Table 4), indicating that attributes directing species loss were important in driving the species loss effects on productivity in these three scenarios. However, for the scenario directed by regional rarity, the community mean value of species regional rarity did not have a significant impact on stand volume (Supplementary Table 4).

Mean pairwise similarities between species in post-extinction communities for SLA and ED decreased faster as richness decreased in the extinction scenarios directed by SLA and ED, respectively, than in the random extinction scenario (Extended Data Fig. 7). Stand volumes were higher in communities with species more dissimilar in SLA and ED along the extinction scenarios directed by SLA and ED, respectively (Supplementary Table 4), indicating the importance of interspecific interactions in mediating species loss effects in these two extinction scenarios. We do not present species similarities for regional rarity or taxon size, because species differences in regional rarity or taxon size do not have a clear biological meaning with regard to their effects on ecosystem functioning.

Decomposing the net effect of species loss on stand volume

We developed a partitioning method to decompose the net effect of directed species loss into additive contributions from node loss, link loss and link compensation (see worked examples for the partitioning in Supplementary Table 2). We applied the partitioning to the two extinction scenarios directed by SLA and ED, for which we had good replication (12 plots at least for each richness level of each scenario, Extended Data Fig. 8). We also calculated the net effects of extinction steps in the random scenario. The effects of species loss in nested community pairs (i.e., extinction steps) on stand volume varied greatly, depending on the richness level of the pre-extinction community and the type of extinction scenario (Fig. 4).

The negative net effects of species loss became more prominent as forest stands developed for all the three scenarios investigated (random, SLA and ED) (Figs. 4 and 5), consistent with the results obtained from direct regression of stand volume against species richness [19] (Figs. 2 and 3). However, the temporal patterns across richness levels of pre-extinction communities differed between the random and non-random (directed by SLA and ED) scenarios. For the random extinction scenario, the temporal strengthening of net effects was statistically significant at lower species richness levels (extinction steps 8→4, 4→2 and 2→1 species) but not at the highest species richness level (step 16→8 species) (Fig. 4 and Extended Data Fig. 9). The pattern reversed in the scenarios directed by SLA and ED, with stronger temporal strengthening at the higher species richness levels (steps 16→8, 8→4 and 4→2 species) than at the lowest richness level (step 2→1 species) (Fig. 4 and Extended Data Fig. 9). The net effects of species loss in in the latest age of seven years also showed the richness-dependent reversal between the random and non-random extinction scenarios (Fig. 5). For the random scenario, the net effects were significantly negative and strong at the lower species richness levels (steps 8→4, 4→2 and 2→1 species), but statistically insignificant and weak at the highest species richness level (step 16→8 species). However, for the non-random scenarios directed by SLA and ED, the net effects were significantly negative and strong for all species richness levels except the lowest one (step 2→1 species).

The relative importance of the three additive components of extinction effects varied among species richness levels of pre-extinction communities. The node-loss effects were important in 8-species communities (step 8→4 species), while the effects of link loss were important in16-species communities (step 16→8 species; Fig. 5).

Node loss had negative impacts on stand volume in general for both SLA- and ED-directed extinction scenarios (Figs. 4 and 5), indicating that lost species (high SLA and ED) had a higher contribution to stand volume than remaining species (low SLA and ED). The negative node-loss effects strengthened as forests developed (Fig. 4 and Extended Data Fig. 9). The temporal strengthening was strongest in 8-species communities (step 8→4 species). The node-loss effects at the latest age were strongest and significantly negative in 8-species communities for both directed scenarios (Fig. 5).

The effects of link loss on stand volume also tended to strengthen with stand age for extinction scenarios directed by SLA and ED, but the temporal trends were significant only in 16- and 8-species communities (steps 16→8 and 8→4 species) (Fig. 4 and Extended Data Fig. 9). At the latest age, the effects of link loss were significantly negative at the highest richness level (step 16→8 species; Fig. 5), indicating that the loss of interspecific interactions reduced stand volume. The negative effects of link loss weakened with decreasing richness of pre-extinction communities (Fig. 5).

The effects of link compensation on stand volume showed a more complicated pattern across time and richness levels. As forest stands developed, the negative effects of link compensation became more prominent in 4-species communities (step 4→2 species) for both SLA- and ED-directed extinction scenarios (Fig. 4 and Extended Data Fig. 9). However, in 16-species communities (step 16→8 species), the positive effects of link compensation became more prominent (Fig. 4 and Extended Data Fig. 9). In the oldest communities, link compensation increased the reduction of stand volume in 4-species communities (step 4→2 species), but buffered it in 16-species communities (step 16→8 species; Fig. 5).

DISSCUSSION

Predicting how realistic extinction scenarios will affect forest-ecosystem functioning is of vital importance for both biodiversity conservation and forest management in the face of global deforestation [2,10]. In this study, we found that the detrimental effects of species loss occurred early or later in the extinction sequences, depending on the attributes of species loss. Directed species loss from communities with the highest richness level (step 16→8 species) had strong negative impacts on stand volume, while random species loss from communities with the same richness level had weak impacts. Our results have potentially far-reaching implications for biodiversity conservation in species-rich forests confronting realistic species loss.

Overall, the magnitude of reduction in forest productivity was not always less severe with random than with directed species loss. On average, halving species richness reduced stand volume of seven-year-old mixtures by 2.87 (95% CI: [1.34, 5.03]) and 3.03 (95% CI: [0.29, 6.33]) $\mathrm{m}^3\mathrm{ha}^{-1}$ for the random and directed extinction scenarios, respectively. This indicates that biodiversity experiments based on random species loss can still provide valuable information about the general trends of ecosystem functioning under species loss driven by multiple species attributes or events.

The productivity loss varied between directed extinction scenarios, depending on the specific attribute on which the species loss was based. Stand-volume reductions caused by a loss of 50% of the evolutionary distinct species (5.22 $\mathrm{m}^3\mathrm{ha}^{-1}$, 95%CI: [3.71, 6.86]) were over six times higher than when 50% of the regionally rare species were lost (0.78 $\mathrm{m}^3\mathrm{ha}^{-1}$, 95% CI: [0.13, 2.08]). These findings are in line with theoretical simulations of species loss based on multiple species attributes that showed divergent patterns [12,14,19,23]. This suggests that biodiversity experiments based on random extinctions can both overestimate or underestimate the impacts of non-random, directed species loss, depending on the specific attribute conferring high extinction risk. The difference in species loss effects between random and directed extinction scenarios was less evident when we analyzed yearly stand-volume increments rather than stand volume accumulated over the years. This suggests that differential impacts of species loss only become evident when small effects on short-term productivity can accumulate over time.

We predicted that the magnitude of the effects of directed species loss can be influenced by two factors: (1) a positive or negative correlation between the contribution of a species attribute to ecosystem productivity and to extinction risk and (2) increased or decreased species similarities in attributes or interactions between species in post-extinction communities. We found positive relationships between stand volume and the CWMs of SLA and ED, and negative node-loss effects for extinction steps directed by SLA and ED. However, CWM of regional rarity had a weak and insignificant effect on stand volume, which may be one of the reasons for the weak effect of species loss on stand volume in the scenario directed by regional rarity. Species-attribute correlations with ecosystem functioning and extinction risk may vary in different ecosystems and for different ecosystem functions. For example, local rarity-driven species loss was found to increase invasion success in grasslands [24] and reduce the rates of nitrogen use in coastal seaweeds [25], but to have no detectable effects on productivity in grasslands [26]. Therefore, to improve prediction reliability about the impacts of directed species loss, we need to better understand the relationships between species attributes and extinction risk and the subsequent effects on ecosystem functions of interest [13,14].

Extending previous studies, we tested how directed extinction scenarios affected forest productivity by changing interspecific interactions. We found that species similarities in SLA and ED decreased faster with decreasing richness in the extinction scenarios directed by SLA and ED as compared with the random scenario where the CWM of SLA or ED were not reduced along extinction steps. This difference could be large in hyper-diverse ecosystems such as tropical and subtropical forests, given their high species redundancies with respect to traits and evolutionary histories [7,27]. This implies that directed species loss from species-rich communities can severely hamper ecosystem functioning if species similarity is correlated with interspecific interactions [17,28]. In contrast, random loss of the first few species from species-rich communities should have minor impacts on ecosystem functions due to the mentioned species redundancies [29]. We found that the net effects of directed species loss (based on SLA and ED) on stand volume were strong at the highest richness level (step 16→8 species), while the net effects of random species loss were weak at the same richness level. For these two scenarios of directed species loss, the effects of link loss strengthened with the richness of pre-extinction communities. These results suggest that directed loss of species from species-rich young forests could reduce productivity and losing interspecific interactions associated with lost species might be one of the causes. The results also highlight the importance of species interactions besides the response–effect relationships of species attributes in driving the impacts of species loss on ecosystem functioning [13,14].

One common approach to infer the impacts of directed species loss is to regress productivity against CWM or trait diversity across richness levels. This approach is helpful because variation in CWM or trait diversity can be both the result of directed species loss and the cause of productivity variation. However, our results demonstrate that (1) it is crucial to focus on sequences of nested communities, not just the overall average relationship obtained from regression; (2) functioning loss may systematically occur early or late in the extinction series, depending on the attributes of the species loss. Considering the slope of the overall relationship in a regression analysis would mask these important aspects.

We note that our results are from early-stage forest stands (< 10 years-old) and that species interactions may change during succession, which may further modify the effects of species loss on ecosystem functioning [30]. For example, the observed positive relationship between stand volume and CWM of SLA (and the negative node-loss effect in the SLA-directed extinction scenario) may be only evident at the early forest stages but may decrease at the late successional stages when pioneer species with high SLA are becoming less abundant and species with low SLA reach dominance. However, it is also possible that differences between non-random and random extinction scenarios become even larger over time, if the temporal trend observed in the current study continues over time [31]. Our on-going long-term experiment will give us the chance to investigate such future changes potentially compounded by successional dynamics, continued biomass accumulation and uncertain climatic events.

Although hundreds of studies on the relationships between biodiversity and ecosystem functioning have been conducted, we argue that the question on how realistic species loss would impact ecosystem functioning is still far from being resolved due to the rarity of empirical studies addressing realistic species loss. Our study demonstrates that biodiversity–ecosystem functioning (BEF) relationships under realistic species loss can deviate from BEF relationships under random species loss, the extinction scenario that has been established as de-facto standard in experimental biodiversity research. Specifically, our results suggest that directed species loss could hamper ecosystem functioning already at high levels of species richness, where random species loss would mainly reduce species redundancy with little effect on ecosystem functioning. Our partitioning approach revealed that changed species interactions were crucial in directed species loss. The new method is helpful in linking empirical (regression-based) BEF relationships to species interaction networks, thereby bridging these areas of research. It could also be applied to other large-scale biodiversity experiments in retrospect or in future analyses.

Table 1 | Species attribute-directed extinction scenarios

Species attribute	Extinction scenario	Data source and calculation
SLA (specific leaf area)	Species with larger SLA are more sensitive to some environmental stresses (e.g., drought) [15,32], and thus have higher extinction risk.	Measured at the experimental sites [33].
ED (evolutionary distinctiveness)	Species distinct in evolutionary history may have unique traits, niches and habitat requirements [34], and thus are at higher risk of extinction.	Calculated with the phylogeny [31] of the 40 species present in the experiment using the method from [35,36]. Species with larger ED have fewer relatives locally.
Regional rarity	Rare species are more prone to extinction due to their narrow distribution range and high vulnerability to habitat fragmentation and reduction [8].	Number of counties in China with species presences using the specimen records from China National Specimen Information Infrastructure [37]. Species rare regionally are present in lower numbers of counties.
Inverse of taxon size	Species of species-poor angiosperm families are at higher risk of extinction [6].	Inverse of the number of species within the corresponding family, using the records from The Plant List [38].

METHODS

Study site and original experimental design

The BEF-China experiment was established in Jiangxi Province, subtropical China (29°08′–29°11′N, 117°90′–117°93′E). The mean annual temperature and precipitation are 16.7 °C and 1,800 mm, respectively [39]. Using a total of 40 native broad-leaf tree species, we manipulated species richness along both random and non-random extinction scenarios (Extended Data Fig. 1) to study their effects on ecosystem functioning [20]. To gain generality and increase statistical power, the experimental communities were derived from multiple, partly overlapping pools of 18 tree species each. The corresponding plots were established at two different sites of approximately 20 ha each (A and B, established in 2009 and 2010, respectively) [20,21]. In brief, we implemented a broken-stick design [20] to create the random extinction scenarios. First, we randomly sampled three minimally overlapping pools of 16 species from a set of 24 species per site (Extended Data Fig. 1). These were then randomly split into halves, resulting in nested, non-overlapping subsets of 8, 4, 2 and 1 species. The design makes the average attribute value of two lower-richness halves equal to that of the corresponding pre-extinction community with twice the species and each species has the same presence probability across richness levels. Species composition was replicated for one of the three 16-species pools per site (Extended Data Fig. 1). We established the plots with two sizes: 0.067 ha (equivalent to the Chinese area unit of 1 mu) and 0.267 ha (4 mu, only for the two pools with replicates). We conducted all the analyses at the scale of 1 mu as our previous study did not detect a scale-dependency of diversity effects in this experiment [21]. Therefore, to keep the description simple, we refer to all 1-mu partitions within the 4-mu plots as plots as well.

We also designed non-random scenarios, where we did not split species pools randomly but rather based on preliminary data for two species attributes: specific leaf area (SLA) and local rarity (species with higher SLA and local rarity going extinct first). Richness gradients were derived from species pools with decreasing SLA or rarity [20] (Extended Data Fig. 1). Attribute data of some species were missing at the time of setting up the experiment, thus part of the attribute information was based on the knowledge of local experts. In the present study, we have now replaced the preliminary data for the two attributes with newly collated complete data (Table 1), which led to a re-definition of the extinction steps in these scenarios where species pools were not split randomly (see below).

We assumed full numerical compensation after extinction [12,19] according to the substitutive design commonly used in biodiversity experiments [40]. That is, remaining species can fully compensate densities of extinct species with equal probability and maintain total community density. Thus, all 1-mu plots have the same tree density (20×20 trees). Species have equal density and are distributed randomly across the regular 20×20 planting positions of grids in each mixture. All designed extinction scenarios contained plots of 1, 2, 4, 8 and 16 species.

We measured height and basal diameter of the surviving trees in the 16 central planting positions in site-A plot from 2009–2015 and in site-B plots from 2010–2016 [21]. We calculated tree volume proxies using the volume formula for cylinders: $\text{volume proxy} = \pi(basal\ radius)^2 height$. Then we adjusted the volume proxies with size-specific form factors, estimated from 119 harvested trees near the experimental sites [21]. Finally, we aggregated the volumes of the 16 central trees to obtain stand-level tree volume. This stand-level tree volume and its annual increment were used as productivity measures. In this study, we used the plots from both the designed random (373 1-mu plots, excluding 13 1-mu plots due to unsuccessful establishment of plants at the beginning of the experiment) and non-random (96 1-mu plots) extinction scenarios [51] from 2009–2016. The plot data of the designed random extinction scenarios from 2013–2016 were from a previous study [21,41], while the other data (the plots of the designed non-random extinction scenarios for all years and the plots of the designed random extinction scenarios from 2009 to 2012) are new and original in this study.

Re-assigning plots to effectively non-random scenarios of directed species loss

The design of nested community compositions allowed us to explore each extinction step from a pre-extinction community (e.g., community composed by species A and B) to its corresponding post-extinction communities (e.g., communities composed by species A or B, separately). The non-random degree of some steps from the designed random scenario were sometimes even higher than those from the designed non-random scenarios (Extended Data Fig. 2). That is, extinction steps within designed random scenarios could be non-random with regard to the differences in attribute composition. Therefore, we re-assigned plots from both the designed random and non-random scenarios to new effectively non-random extinction scenarios for the purpose of the present study.

The effectively non-random scenarios of directed species loss were created in the following way, based on four species attributes that were measured in the experiment or collected from well-recognized databases (Table 1): SLA (measured in the experiment), evolutionary distinctiveness (ED), regional rarity and inverse of taxon size (from small family). Species with large SLA, high ED, regional rarity or from small clades (from small family) were considered more extinction-prone than species with opposite attribute values (Table 1). We log-transformed SLA and taxon size because their original distributions were right-skewed. We did not directly assess the designed non-random extinction scenarios because they were based on in-complete data on species attributes at the time we designed the experiment.

Species-richness gradients in the new scenarios of directed species loss were created based on an attribute-based filtering rule applied to the 469 plots. We illustrate the rule using regional rarity as an example (Extended Data Fig. 3). We selected 16, 8, 4 and 2 species from sets of 24, 20, 16 and 12 species of least regional rarity at each site. We kept the monoculture of the more common species in each two-species mixture. In this way, communities at lower richness levels contained species that are more common, or rare species lost first at higher-richness levels (Extended Data Fig. 4). For the scenario based on the inverse of taxon size, we filtered species from different families by their family sizes, and species from the same family by their genus sizes. The filtering rule produced apparent gradients in mean attribute values and extinction risks across richness levels (Extended Data Fig. 4). Each richness level from each extinction scenario contained at least 12 plots (red bars in Extended Data Fig. 8).

Effects of species loss on productivity

We constructed hierarchical Bayesian models to assess the effects of species richness on stand-level tree volume (Figs. 2 and 3). At the first hierarchical level, we modeled stand volume ($y_{i,j}$) of plot *i* at age *j* as a normal distribution with an age-specific standard deviation (σ_j) and a mean as a function of age-specific intercept ($\varphi_{0,j}$), site ($site_i$), log-transformed designed species richness ($logSR_i$) and random effects of plot ($plot_i$) and community composition ($comm_i$):

$$y_{i,j} = Normal\left(\varphi_{0,j} + \varphi_1 site_i + \varphi_{2,j} logSR_i + plot_i + comm_i, \sigma_j\right) \quad (1).$$

Age is the year since planting of tree seedlings in plots. We did not log-transform stand volume because the log-transformation may exaggerate biodiversity effects due to the inequality of arithmetic and geometric means. For example, consider that a mixture AB has productivity equal to 300 and the two corresponding monocultures yield 200 (A) and 400 (B), respectively. The biodiversity effect derived from the untransformed values is zero (300 – (200+400)/2), while the biodiversity effect derived from the log-transformed values is positive (log(300)–[log(200)+log(400)]/2 = 0.059). At the second hierarchical level, we modeled the age-specific intercept ($\varphi_{0,j}$) and the richness effect ($\varphi_{2,j}$; i.e., the inverse of the species loss effect) as a linear function of age:

$$\varphi_{0,j} = N\left(\beta_{0,0} + \beta_{0,1} age_j, \sigma_{\alpha_0}\right) \quad (2),$$

$$\varphi_{2,j} = N\left(\beta_{2,0} + \beta_{2,1} age_j, \sigma_{\alpha_2}\right) \quad (3).$$

The random-effects terms were assumed to follow normal distributions with mean zero. There are two parameters of particular interest: the age-specific effect of species richness ($\varphi_{2,j}$) and its change across ages ($\beta_{2,1}$; Figs. 2 and 3, Supplementary Table 3). We standardized $logSR_i$ and age_j (mean zero and unit standard deviation) before running the models for faster convergence and easier interpretation of parameters. We back-transformed the parameters associated with these two variables for presentation of results. We set diffuse priors for the parameters. We repeated the analysis for stand-volume increment with the above model (equations 1–3; Extended Data Figs. 5 and 6). We also performed an alternative analysis with stand volume, in which we constrained the data and parameters associated with stand volume ($y_{i,j}$ and $\varphi_{0,j}$) to be positive, because stand volume should be theoretically positive. The alternative models produced qualitatively similar results (Extended Data Fig. 10). We ran the models with and without positive constraints on stand volume in rstan 2.19.2 [42] and rjags 4-6 [43], respectively.

We also assessed the effects of CWM attributes and mean pairwise species dissimilarities (similar to functional diversity) within communities on stand volume at the latest age (Supplementary Table 4), because directed species loss could change both CWMs or dissimilarities. CWMs were used as a measure encapsulating effects of the species' functional identity, while species dissimilarities were associated with species interactions and niche differentiation. We calculated species dissimilarities only for SLA and ED because species differences in regional rarity or taxon size did not have clear biological meaning with respect to plant species interactions. Species dissimilarities in SLA and ED were calculated as mean pairwise trait and phylogenetic distances, respectively. Phylogenetic distance was calculated as the cophenetic distance in a phylogeny [31]. Mean pairwise species dissimilarity within a community was calculated as functional dispersion (FDis) [18] for SLA, or mean pairwise phylogenetic distance (MPD)

[44] for ED. Both FDis and MPD are measures independent of species richness [18,45]. We constructed linear mixed-effects models in asreml-R [46] to assess the effects of CWMs and species dissimilarities on stand volume at the latest age separately. Site and CWM or dissimilarity metric were set as fixed-effects terms while community composition was set as a random-effects term. To facilitate the comparisons across models, we standardized both CWMs and dissimilarity metrics (with mean zero and unit standard deviation).

Decomposing the net effect of species loss on stand volume

We developed a method to decompose the net effect of species loss into a node-loss effect, a link-loss effect and a link-compensation effect (Fig. 1 and Supplementary Table 2). First, we selected pairs of species compositions of which one was a subset of the other, representing one step in a nested extinction series (e.g., from 4- to 2-species mixtures). We normalized each attribute to have extinction probability spanning from 0.01 to 0.99 [12] (i.e., $\frac{attribute_{species}-\min(attribute)}{\max(attribute)-\min(attribute)} = \frac{P_{species}-0.01}{0.99-0.01}$) and calculated the species coextinction probability as the geometric mean of extinction probability of all species present in a community ($P_{community} = \sqrt[n]{P_{species-1}P_{species-2} \dots P_{species-n}}$). We selected nested community pairs if species coextinction probability of the higher-richness community (P_{high}) was at least 10% more likely than that of the corresponding lower-richness community (P_{low}; $\frac{P_{high}-P_{low}}{P_{low}} > 10\%$). In this way, we could assure that each community pair mimicked an extinction step directed by the specific attribute considered.

For each selected community pair or extinction step (i.e., from a n-species to a ${}^{n}\!/_{2}$-species community with $\mathrm{n} \rightarrow {}^{n}\!/_{2}$, $\mathrm{n} \geq 2$ and n being an even number), we decomposed the net effect of species loss on stand volume into three components. The net effect is defined as the yield difference between post- (mix$\left(SP_1, \dots SP_{n/2}\right)$; post-extinction community is monoculture when $\mathrm{n} = 2$) and pre-extinction (mix$(SP_1, \dots SP_n)$) communities:

$$\text{net effect}\left(\mathrm{n} \rightarrow {}^{n}\!/_{2}\right) = \text{mix}\left(SP_1, \dots SP_{n/2}\right) - \text{mix}(SP_1, \dots SP_n) \qquad (4).$$

Note that our definition of net effect is different from that in additive partitioning [47], where the net biodiversity effect is the difference between the observed yield of a mixture and the sum of the expected yields from corresponding monocultures. However, our partitioning method uses the same core assumption that the observed yield of an n-species mixture (mix$(SP_1, \dots SP_n)$) is the sum of expected yields from corresponding monocultures ($\frac{1}{n}\sum_i^n mono(SP_i)$) and effects of pairwise species interactions ($(\frac{1}{n})^2 \sum_{i,j\ (i\neq j)}^n \delta_{ij}$) [47,48]:

$$\text{mix}(SP_1, \dots SP_n) = \frac{1}{n}\sum_{i=1}^{n} mono(SP_i) + \left(\frac{1}{n}\right)^2 \sum_{i,j\ (i\neq j)}^{n} \delta_{ij} \qquad (5),$$

where δ_{ij} represents the effect of interspecific interaction between species *i* and *j*. We assume each species has an equal initial density and shares the same area in a community. Thus, each species has the same relative density ${}^{1}\!/_{n}$. The second term on the right side of equation 5 is equal to the net biodiversity effect in additive partitioning (see Supplementary Table 2) [47]. The net biodiversity effect is (1) zero when intraspecific competition is equal to interspecific competition on average (i.e., $\sum_{i,j\ (i\neq j)}^{n} \delta_{ij} = 0$), (2) positive when the pairwise species interactions are dominated by niche partitioning (i.e., intraspecific competition > interspecific competition) or facilitation (i.e., $\sum_{i,j\ (i\neq j)}^{n} \delta_{ij} > 0$) or (3) negative when species competition dominates the community (i.e., intraspecific competition < interspecific competition; $\sum_{i,j\ (i\neq j)}^{n} \delta_{ij} < 0$). Besides pairwise species interactions, higher-order interactions among species may also affect community yield, which is not considered in our approach.

The node-loss effect is the functional difference with regards to monoculture yields between species remaining in the post-extinction community $(1, 2, \ldots {}^{n}/_{2})$ and species lost by extinction $({}^{n}/_{2} + 1, {}^{n}/_{2} + 2, \ldots \mathrm{n})$:

$$\text{node loss}\left(\mathrm{n} \to {}^{n}/_{2}\right) = \frac{1}{n}\sum_{i=1}^{{}^{n}/_{2}} mono(SP_i) - \frac{1}{n}\sum_{i={}^{n}/_{2}+1}^{n} mono(SP_i) \qquad (6).$$

A negative node-loss effect indicates higher yield contributions by species lost than remaining.

The link-compensation effect (link comp. $\left(\mathrm{n} \to {}^{n}/_{2}\right)$) represents the effect of increased interaction frequency between remaining species on yield due to density compensation after species extinction (e.g., the relative density of remaining species increases from ${}^{1}/_{\mathrm{n}}$ to ${}^{2}/_{\mathrm{n}}$). We assumed that the average strength of species interactions (δ_{ij}) were constant between post- and pre-extinction communities. The effect of link compensation can be calculated as the sum of two components:

$$\text{link comp.}\left(\mathrm{n} \rightarrow {}^{n}\!/_{2}\right) = \left(\left(\frac{2}{n}\right)^{2} - \left(\frac{1}{n}\right)^{2}\right) \sum_{S\left({}^{n}\!/_{2}\right)} \delta_{ij} =$$

$$\frac{3}{2}\left\{\begin{array}{c} \left[\text{net effect}\left(\mathrm{n} \rightarrow {}^{n}\!/_{2}\right) - \text{node loss}\left(\mathrm{n} \rightarrow {}^{n}\!/_{2}\right)\right] + \\ \left[\text{mix}(SP_1, \dots SP_n) - \frac{1}{2}\text{mix}\left(SP_1, \dots SP_{{}^{n}\!/_{2}}\right) - \frac{1}{n}\sum_{{}^{n}\!/_{2}+1}^{n} mono(SP_i)\right] \end{array}\right\} \qquad (7),$$

where the first component represents the sum of link-loss and link-compensation effects, and the second component is the opposite of the sum of the link-loss effect and ${}^{1}\!/_{3}$ of the link-compensation effect. $S\left({}^{n}\!/_{2}\right)$ represents the set of pairwise interspecific interactions composed by species 1 to ${}^{n}\!/_{2}$. When $\mathrm{n} = 2$, the link-compensation effect is zero because there would be only one remaining species in the post-extinction community. The full derivation can be found in the *Supplementary Information* and worked examples in Supplementary Table 2. A positive effect of link compensation indicates that remaining links have positive contribution (e.g., through niche partitioning or facilitation) on yield on average (i.e., $\sum_{S\left({}^{n}\!/_{2}\right)} \delta_{ij} > 0$).

The link-loss effect represents the effect of lost interspecific interactions between lost species and between remaining and lost species on yield and can be calculated as the difference between the net effect and the sum of node and link-compensation effects (see the *Supplementary Information* for the full derivation). A negative effect of link loss indicates that lost links had positive contributions (e.g., through niche partitioning or facilitation) on yield. In summary, we can calculate the net extinction effect and its three additive components from the productivity of pre-extinction community, post-extinction community and corresponding monocultures based on the equations 4, 6 and 7, without the need to estimate the coefficients of pairwise interspecific interactions. In Supplementary Table 2 we provide worked examples for our new partitioning approach and its comparison with the approach by Loreau and Hector [47].

We decomposed the net effect of species loss for each community pair and took the average values for the pairs having the same higher-richness plot. We conducted the partitioning analyses only for SLA- and ED-directed extinction scenarios, because there were too few pairs reaching the 10% threshold for the scenarios directed by regional rarity or inverse of taxon size (Extended Data Fig. 8). We calculated the net effect of species loss for the random extinction scenario as the opposite of average yield difference between a pre-extinction mixture and its corresponding two halves. Note that some plots that were used in directed extinction scenario for one attribute might have been used in non-random extinction scenarios for other attributes.

We constructed a second set of hierarchical Bayesian models to assess the temporal trends of different components of species loss effects (Fig. 4 and Extended Data Fig. 9):

$$z_{i,j} = Normal\left(\theta_{0,j} + \theta_1 site_i + \theta_{2,j} age_i + plot_i + comm_i, \sigma\right) \qquad (8),$$

where $z_{i,j}$ is a specific effect of species loss of pre-extinction plot *i* in extinction step *j* (e.g., from 4 to 2 species); $\theta_{0,j}$ and $\theta_{2,j}$ are intercept and slope of age for extinction step j, respectively; $plot_i$ and $comm_i$ are random effects of plot and community composition, respectively; and σ is the process error. $\theta_{2,j}$ is of particular interest as it represents the change of species loss effect across the ages for a specific extinction step *j* (Fig. 4 and Extended Data Fig. 9). We standardized age_j (mean zero and unit standard deviation) before running the models for faster convergence and easier interpretation of parameters. We back-transformed the parameters associated with this variable for presentation of results. The random-effects terms were assumed to follow normal distributions with mean zero. Although a model with age-dependent errors may describe the underlying processes in our system more accurately, we found that we were unable to generate reliable parameter estimates and predictions with such a model (Supplementary Table 5), and therefore chose a more parsimonious parameterization with a homogeneous model error (σ). The values of $\theta_{0,j}$ and $\theta_{2,j}$ were modeled as fixed instead of random terms because the number of extinction steps was low (three for the link-compensation effect and four for the others). We repeated this model for net effects, node-loss effects, link-compensation effects and link-loss effects.

To compare species loss effects among different extinction steps at different ages (Fig. 5), we fitted a simplified model of equation 8, where we freed the assumption of linear change of species loss effects through age:

$$z_{i,j,k} = Normal\left(\theta_{0,j,k} + \theta_1 site_i + plot_i + comm_i, \sigma\right) \qquad (9),$$

where $\theta_{0,j,k}$ represents the average effect of species loss for extinction step *j* at age *k* (Fig. 5) and was modeled as a fixed term. We ran the Bayesian models associated with equations 8 and 9 in rjags 4-6 [43].

We used R 3.3.1 [49] for all analyses. We ran Bayesian models with three parallel chains. We assessed parameter convergence both visually and by Gelman and Rubin’s convergence diagnostics (with a cutoff value of 1.05) [50].

Author Contribution: Y.C. and Y.H. are co-first authors. Y.C. and B.S. conceived the study, Y.C. and A.T.C. developed the analytical procedure and Y.C. performed the analyses with contributions by Y.H. and B.S.; H.B., N.C., Y.C., K.M., Y.H., P.A.N. and B.S. contributed to the data collection. All authors discussed analysis results and helped writing the paper.

Data Availability: The data supporting the findings of this study are available in the Figshare digital repository [51].

Code Availability: The JAGS and Stan codes of Bayesian models are available in the Figshare digital repository [52].

Competing Interest: The authors declare no competing interest.

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FIGURE LEGENDS:

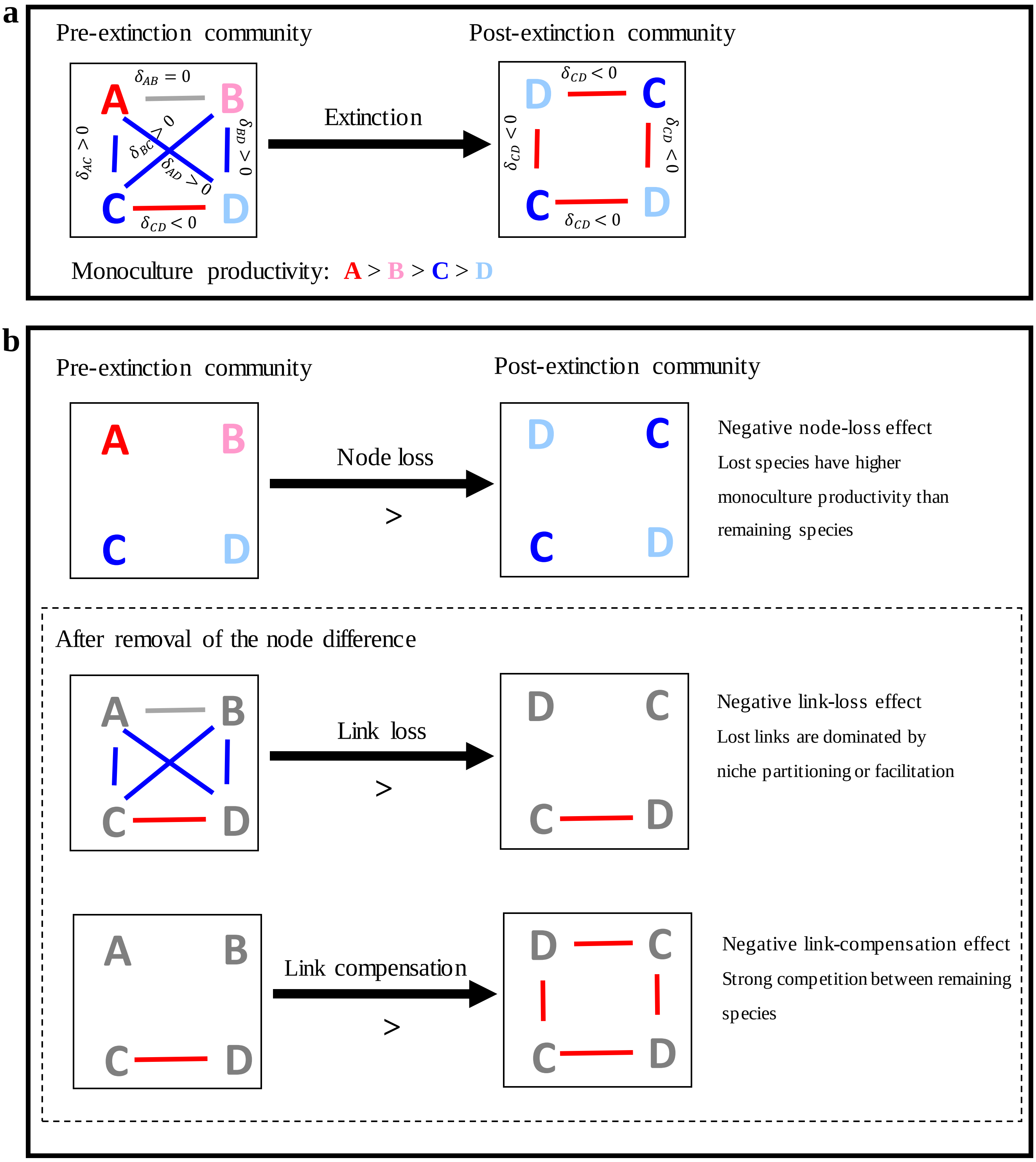
Figure 1 | Conceptual diagram showing the processes affecting community productivity after loss of species A and B from a community of four species A–D. a: species interactions (links) connect the four species (nodes) within the community as a network. Extinction causes the loss of two nodes (A and B) and five links (blue and grey lines), while the density compensation by the remaining species (C and D) increases the frequency of interaction between the remaining species (red lines; link compensation). Species links can have negative (red lines; $\delta < 0$ due to interspecific competition), positive (blue lines; $\delta > 0$ due to niche partitioning or facilitation) or neutral (grey line; $\delta = 0$ when intraspecific competition = interspecific competition) contributions to community productivity compared with corresponding monocultures. b: partitioning of the net extinction effect from panel a into three components. The node-loss effect considers only the difference relating to monoculture yields between lost and remaining species. If lost species (A and B) have higher monoculture productivity than remaining species (C and D), the pre-extinction community yields more than the post-extinction community (indicated by “>”) and the effect of node loss is negative. We can derive the effects of link loss and compensation after removing the node-loss effect (greyed species symbols). If the lost links (blue and grey lines) are dominated by niche partitioning or facilitation, the pre-extinction community is more productive than the post-extinction community (“>”) and the effect of link loss is negative. If there is strong competition between remaining species (red lines), the pre-extinction community is more productive than the post-extinction community (“>”) and the effect of link compensation is negative (for further examples see Supplementary Table 2).

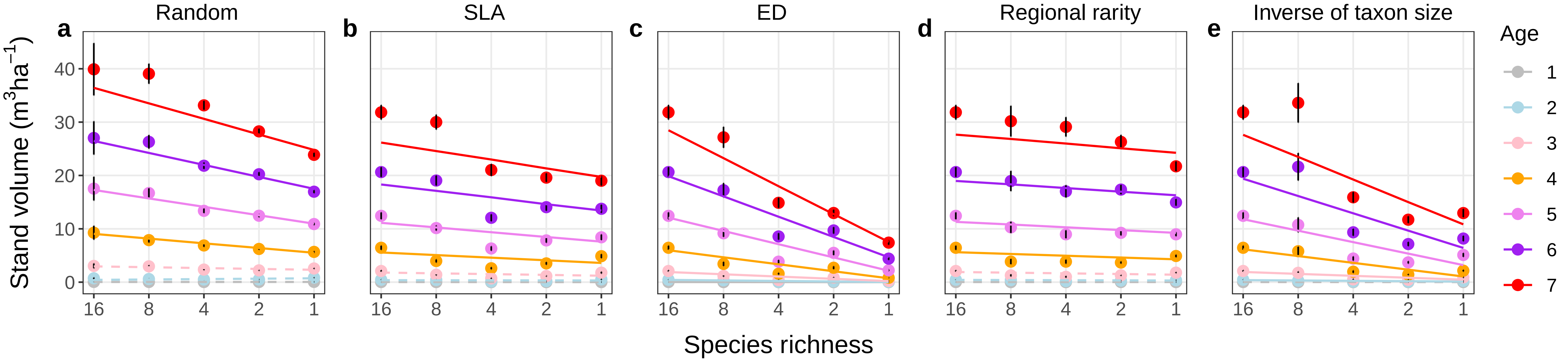
Figure 2 | Effects of species loss on stand volume across forest ages along five types of extinction scenarios. Species loss is random (a) or directed by specific leaf area (SLA; b), evolutionary distinctiveness (ED; c), regional rarity (d) or inverse of taxon size (from small family, e). Points and vertical lines represent means and two-times standard errors of observed stand volume, respectively. Lines are fitted relationships between stand volume (y axis) and species richness in the plot (x axis, note reverse order from high to low values) from Bayesian models. Solid lines represent significant declines of stand volume with species loss. Each richness level from each extinction scenario contained at least 12 plots.

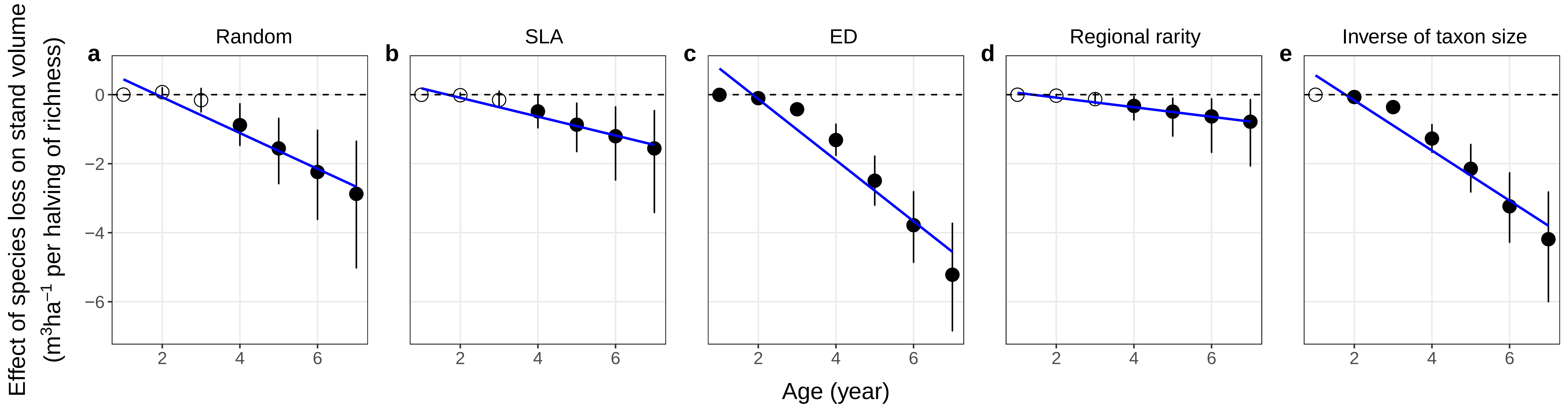
Figure 3 | Effects of species loss on stand volume strengthen with forest age along five types of extinction scenarios. Species loss is random (a) or directed by specific leaf area (SLA; b), evolutionary distinctiveness (ED; c), regional rarity (d) or inverse of taxon size (from small family, e). Points and vertical lines represent medians and 95% credible intervals (CI) of estimated net effect of species loss across richness levels, respectively. Filled points represent significant effects of species loss on stand volume. Blue lines are the fitted relationships between age and net effect of species loss. Results are considered as significant if their 95% CI excludes zero.

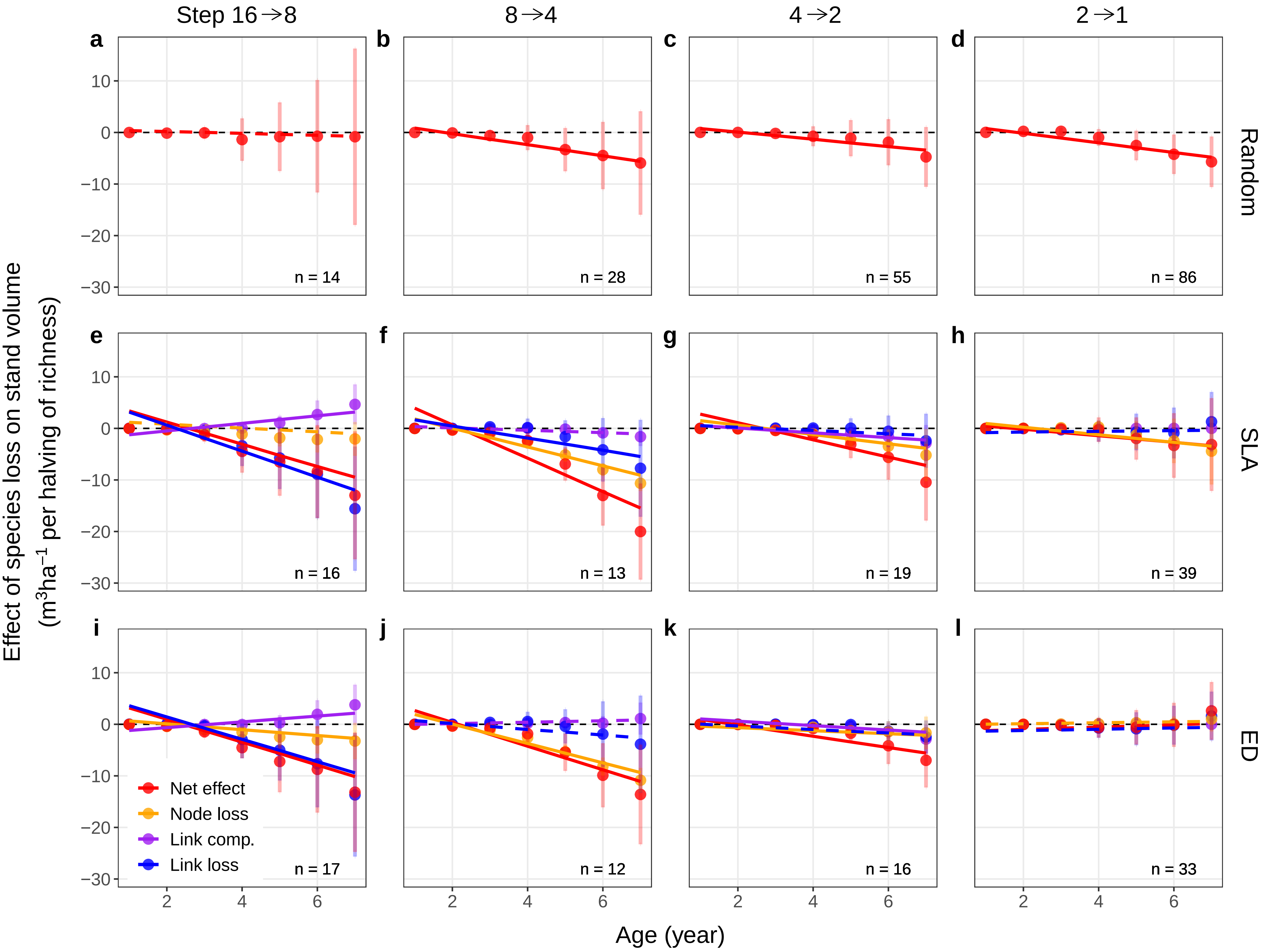
Figure 4 | Net effects of species loss and their additive components (node-loss, link-loss and link-compensation effects) on stand volume in different extinction steps across forest ages for random and effectively non-random (directed by SLA and ED; abbreviations defined in Fig. 2) extinction scenarios. Points and vertical lines represent the means and two-times standard errors of observed effects of species loss. Lines are fitted relationships between forest age and species loss effect from Bayesian models. Solid lines represent significant changes of species loss effect with forest age. n represents the average number of 1-mu plots across ages used in each panel.

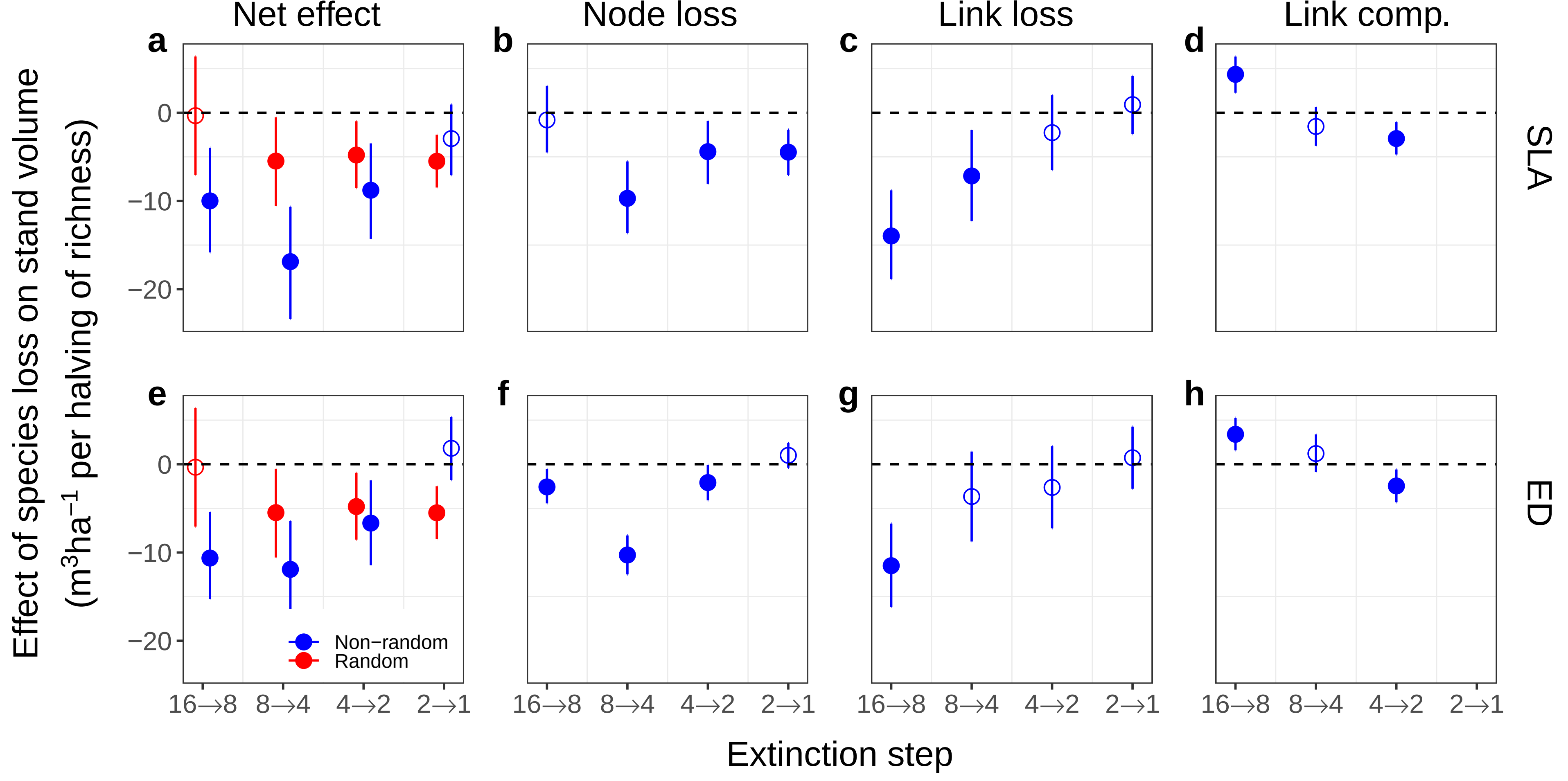
Figure 5 | Net effects of species loss and their additive components (node-loss, link-loss and link-compensation effects) on stand volume in different extinction steps at the latest age for random (red) and effectively non-random (blue; directed by SLA and ED, abbreviations defined in Fig. 2) extinction scenarios. Points and vertical lines represent the medians and 95% CI of estimated effects of species loss from Bayesian models. Filled points represent significant effects of species loss on stand volume. Results are considered significant if their 95% CI exclude zero.


a
Pre-extinction community
Post-extinction community
A
B
C
D
$\delta_{AB} = 0$
$\delta_{AC} > 0$
$\delta_{BC} > 0$
$\delta_{AD} > 0$
$\delta_{BD} > 0$
$\delta_{CD} < 0$
Extinction
D
C
C
D
$\delta_{CD} < 0$
$\delta_{CD} < 0$
$\delta_{CD} > 0$
$\delta_{CD} < 0$
Monoculture productivity: A > B > C > D
b
Pre-extinction community
Post-extinction community
A
B
C
D
Node loss
>
D
C
C
D
Negative node-loss effect
Lost species have higher monoculture productivity than remaining species
After removal of the node difference
A
B
C
D
Link loss
>
D
C
C
D
Negative link-loss effect
Lost links are dominated by niche partitioning or facilitation
A
B
C
D
Link compensation
>
D
C
C
D
Negative link-compensation effect
Strong competition between remaining species


a
Random
b
SLA
c
ED
d
Regional rarity
e
Inverse of taxon size
Stand volume (m^3ha^{-1})
40
30
20
10
0
16
8
4
2
1
Species richness
Age
1
2
3
4
5
6
7


Effect of species loss on stand volume
(m^3ha^{-1} per halving of richness)
a
Random
b
SLA
c
ED
d
Regional rarity
e
Inverse of taxon size
0
−2
−4
−6
2
4
6
Age (year)


Step 16→8
8→4
4→2
2→1
a
b
c
d
e
f
g
h
i
j
k
l
Random
SLA
ED
10
0
−10
−20
−30
n = 14
n = 28
n = 55
n = 86
n = 16
n = 13
n = 19
n = 39
n = 17
n = 12
n = 16
n = 33
2
4
6
Net effect
Node loss
Link comp.
Link loss
Effect of species loss on stand volume
(m³ha⁻¹ per halving of richness)
Age (year)


Net effect
Node loss
Link loss
Link comp.
a
b
c
d
e
f
g
h
SLA
ED
0
−10
−20
Effect of species loss on stand volume
(m^3ha^{-1} per halving of richness)
Non−random
Random
16→8
8→4
4→2
2→1
Extinction step