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# The influence of balanced and imbalanced resource supply on biodiversity–functioning relationship across ecosystems

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# The influence of balanced and imbalanced resource supply on biodiversity–functioning relationship across ecosystems

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## Abstract

Numerous studies show that increasing species richness leads to higher ecosystem productivity. This effect is often attributed to more efficient portioning of multiple resources in communities with higher numbers of competing species, indicating the role of resource supply and stoichiometry for biodiversity–ecosystem functioning relationships. Here, we merged theory on ecological stoichiometry with a framework of biodiversity–ecosystem functioning to understand how resource use transfers into primary production. We applied a structural equation model to define patterns of diversity–productivity relationships with respect to available resources. Meta-analysis was used to summarize the findings across ecosystem types ranging from aquatic ecosystems to grasslands and forests. As hypothesized, resource supply increased realized productivity and richness, but we found significant differences between ecosystems and study types. Increased richness was associated with increased productivity, although this effect was not seen in experiments. More even communities had lower productivity, indicating that biomass production is often maintained by a few dominant species, and reduced dominance generally reduced ecosystem productivity. This synthesis, which integrates observational and experimental studies in a variety of ecosystems and geographical regions, exposes common patterns and differences in biodiversity–functioning relationships, and increases the mechanistic understanding of changes in ecosystems productivity.

**Keywords:** ecology, biodiversity–ecosystem functioning, stoichiometry, evenness, richness, productivity, nutrient network

## 1. Introduction

The correlation between primary producer diversity and ecosystem productivity is a fundamental and broadly studied relationship in ecology. This relationship has been addressed mainly using bivariate approaches, either envisioning diversity as an emergent property of productivity gradients or proposing a functional influence of diversity on productivity. The latter reasoning has been advanced by numerous empirical studies showing that increasing richness (number of species) drives higher productivity of terrestrial and aquatic ecosystems [1–3]. This effect is attributed to more complete resource use in communities with a higher number of competing species [4,5] or to a greater chance of including a highly productive species in a more diverse community [6]. The influence of productivity on diversity, on the other hand, has a long history of debate in ecology, in particular regarding the general presence or absence of hump-shaped patterns of biodiversity across gradients of productivity [7–12].

Profitable solutions to reconcile both relationships, the effect of diversity on productivity, and vice versa, have been proposed by models [13] and empirical work [5,14,15]. These studies suggest that we can advance our understanding of the relationships between productivity and diversity by (i) recognition that ‘productivity’ refers to different kinds of productivity when invoked for the diversity–productivity or the productivity–diversity relationship; and (ii) advancing to multivariate approaches that account for multiple mechanisms acting simultaneously [9,16].

Concerning (i), producer diversity responds not only to the availability of resources (i.e. the potential productivity); it also influences the realized productivity, because more diverse communities can use the resources more completely. With respect to potential productivity, more species can coexist at higher levels

of resource supply if the resources are provided in balanced ratios [13,15]. Stoichiometric imbalance in resource supply leads to exclusion of poor competitors for the most limiting resource [15,17], restricting the number of species that can coexist [18]. Indeed, more balanced resource supply ratios are expected to enhance the chance for coexistence by allowing trade-offs in resource acquisition to play out [19]. By this theory, changes in absolute and relative availability of resources, not the rate of biomass production itself, alter producer biodiversity. Conversely, the number and identity of coexisting species affects how efficiently the available resources are transferred into biomass production and hence realized productivity. At the same time, an overall increase in resource supply will also affect the realized productivity directly, with or without changes in biodiversity, a mechanism underlying the yield increase from agricultural fertilization or the response of ecosystems to eutrophication.

Concerning (ii), the evidence that biodiversity not only responds to potential productivity but also influences realized productivity [13,14] negates the relevance of simple bivariate analyses, although they are still commonly used in ecology [8,9]. Instead, multivariate frameworks with resource availability (potential productivity), biodiversity and realized productivity as causally connected components promise greater mechanistic insights regarding biodiversity–productivity relationships. Cardinale *et al.* [15] developed a structural equation model (SEM) to illustrate a multivariate approach, in which availability of multiple resources is decomposed into two independent components: overall resource availability and the degree of imbalance among these resources. Their suggested framework was tested with a single freshwater phytoplankton dataset, which—as predicted—found increased species richness and biomass with higher resource availability, reduced richness and productivity with increasing resource imbalance, and greater biomass with increasing richness.

Diversity comprises not just the number of species, but also their relative abundances: greater evenness of species relative abundance contributes to greater diversity. Evenness has been less frequently analyzed in studies on biodiversity–functioning relationships [20], but theory suggests that at the local scale, dominance by a single species (i.e. low evenness) can result in high biomass production when the dominant species has a high resource use efficiency [21]. If dominance by this species is reduced in a more even community, productivity should decrease, because any other species will perform less efficiently. This phenomenon has been confirmed for aquatic [22,23] and terrestrial [24] ecosystems. Furthermore, a meta-analysis by Hillebrand *et al.* [25] showed that increased nutrient supply generally decreases evenness in both terrestrial and aquatic ecosystems, whereas the responses of species richness were more dependent on context and system.

In this study, we present the first general test of the multivariate framework proposed by Cardinale *et al.* [15] across ecosystems (marine, freshwater and terrestrial) and approaches (field observational studies and experiments). We combined SEM with meta-analysis, using the analytical framework proposed by Cardinale *et al.* [15] for each single study and derived the standardized path coefficients as effect sizes for the meta-analysis [26]. In addition to the effects of richness on resource use, we also analyzed effects of evenness within the same framework across systems. Our study, which merges the theory of ecological stoichiometry (ES) with the framework of biodiversity–ecosystem functioning (BEF), aims to increase the mechanistic understanding of how resource use transfers into primary production.

**Table 1.** The number of studies included in the meta-analysis on the role of richness ( $S$ ) and evenness ( $J$ ) in resource use and biomass production of autotrophs. More details on the studies can be found in electronic supplementary material (Table S1).

study type	ecosystem type	habitat	<i>S</i>	<i>J</i>
field observational	terrestrial	grassland	41	40
		forest	1	1
		salt marsh	2	0
	freshwater	lake	10	8
		pond	2	0
		rock pools	1	1
	marine	coastal waters	9	9
		brackish waters	3	3
experimental	freshwater	mesocosm	3	1
		microcosm	1	1
	marine	mesocosm	4	4
		microcosm	1	1
total			78	69

We hypothesized that resource availability would increase realized productivity and species richness ( $H_1$ ), that resource imbalance would decrease realized productivity and diversity (richness and evenness;  $H_2$ ), and that an increased richness would have a positive impact on biomass production ( $H_3$ ). Furthermore, we expected evenness to have a negative impact on realized productivity ( $H_4$ ) if biomass production is maintained by few highly productive, dominant species.

## 2. Methods

### (a) Data sources

We assembled 78 datasets comprising terrestrial, freshwater and marine studies that included information on available resources and producer diversity. This database contains data from published experimental and field observational studies across a broad range of habitats and geographical regions (table 1), amended by the authors' own data. All studies provided the number of species (richness) and 69 studies provided evenness, as Pielou's index [27]. We did not consider experimental studies that manipulated species richness or composition as this could bias our model results, but we included experiments that manipulated resource supply (electronic supplementary material, table S1). To be included in the analysis, studies needed to contain information on total biomass of producers (realized productivity), producer diversity (at least richness) and supply of at least two resources. From 78 datasets, 46 contained information on the supply of three or more resources, mostly nitrogen, phosphorus and potassium (electronic supplementary material, table S1). Depending on the producer community, realized productivity was measured as concentration of chlorophyll *a*, biovolume, above-ground plant biomass or total carbon content of the plant tissue. The measurements of resources included photosynthetically

active radiation and concentrations of total nitrogen, phosphorus, potassium and other elements in water or soil. The total amount of each element was estimated as the sum of organic and inorganic bioavailable fractions. Electronic supplementary material, table S1 contains information on the resources and the biomass measurement for each study.

### (b) Structural equation model

To quantify resource availability and imbalance, we followed the geometrical approach of Cardinale *et al.* [15]. To compare resources, we rescaled resource measurements within each study to have a mean of zero and standard deviation of one. Thus, changes on the multidimensional coordinate system (figure 1) are in units of standard deviation from the mean value of all sampling points within each study. We then defined a reference vector  $y$ , where the change in standard deviation of one resource corresponds to the equal change in all other resources on the multidimensional coordinate system (figure 1). For two resources, vector  $y$  represents the 1 : 1 proportion. No specific stoichiometric requirements (e.g. Redfield ratio of N: P = 16 : 1) are considered. The total amount of resources (resource availability,  $a$ ) was calculated after Cardinale *et al.* [15] as

$$a = \frac{\sum_{i=1}^k r_i y_i}{\|y\|} \quad (2.1)$$

where  $y$  is the reference vector (figure 1), and  $r$  is the resource vector which can be calculated for any  $k$  number of resources ( $R$ )

$$\|r\| = \sqrt{\sum_{i=1}^k (r_i)^2} \quad (2.2)$$

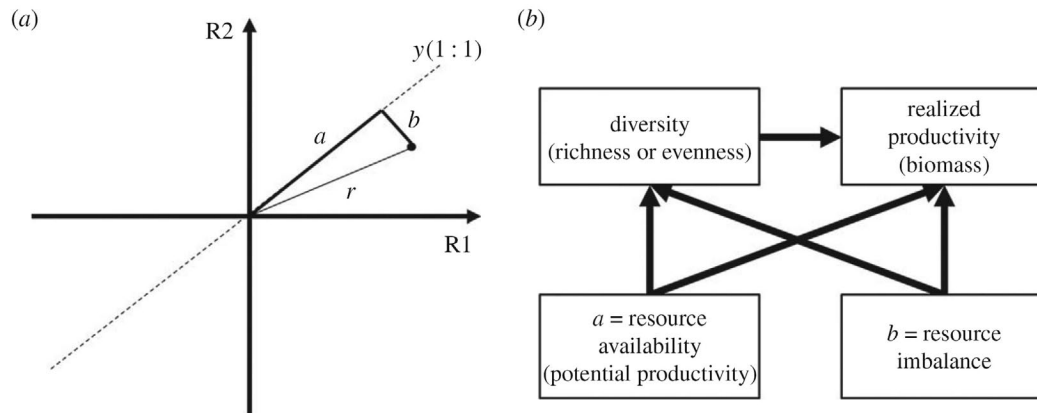
The  $a$  value represents the total amount of available resources. The value is greater than zero when the covariance of two resources is positive, and below zero if the covariance is negative. Positive  $a$  values represent abundant resources, and negative  $a$  values represent scarce resources within each study.

In this study, we defined resource imbalance as a degree of deviation in resource supply from the reference state in a given system. This value was calculated as a perpendicular distance  $b$  from the reference vector  $y$  (figure 1):

$$b = \begin{cases} \arccos\left(\frac{a}{\|r\|}\right) & a \geq 0 \\ 180^\circ - \arccos\left(\frac{a}{\|r\|}\right) & a < 0 \end{cases} \quad (2.3)$$

To quantify the direct and indirect effects of resource availability and imbalance on realized productivity, we followed the set of causal relationships proposed by Cardinale *et al.* [15]. In this model, resource availability and imbalance each have a direct as well as indirect impact (mediated through diversity) on the realized productivity. The model was evaluated separately for each study in our dataset using species number (richness) or Pielou's evenness as diversity variables. Model fitting was performed using maximum-likelihood estimation with robust standard errors in the lavaan package [28] of R statistical software (R version 3.1.1., R core development team, 2015). Prior to fitting the model, we tested bivariate relationships between variables to check for nonlinear relationships. Because we found no significant nonlinearities, no polynomial terms were included in the models. For time series, we first fitted autoregressive models to





**Figure 1.** (a) Geometry used to estimate resource availability  $a$  and imbalance  $b$ . For the sake of simplicity, we present the concept for only two resources (R1 and R2).  $k$  number of resources can be included by adding more dimensions.  $y$  is the 1 : 1 reference vector and  $r$  is the resource vector. (b) Conceptual diagram illustrating causal relationships between resource availability  $a$  and imbalance  $b$ , diversity, and community biomass. For more detail, see description in text.

the data and used lagged values in SEM. The relative importance of paths was compared using Fisher's  $z$ -transformed standardized coefficients ( $\gamma$ ). A chi-square test was used to quantify the overall fit of the model. To enable comparison of all the studies in the meta-analysis, no attempt was made to select a best fitting model. Only the models which were not statistically different from our theoretical model ( $p(\chi^2) > 0.05$ ) were used in the meta-analysis and are illustrated in this manuscript.

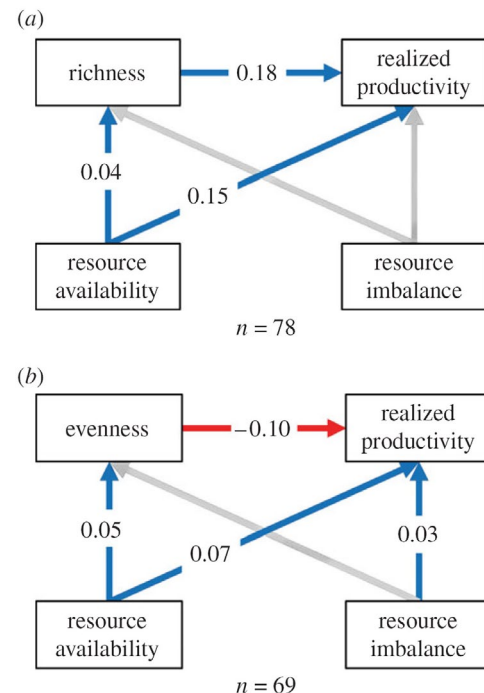
### (c) Meta-analysis

Standardized path coefficients from the SEMs were used as effect size estimates in the meta-analysis with the sample variance adjusted by the sample size. To calculate the overall effect size for each path, we fitted multivariate mixed effects models accounting for differences between study types (field study or experiment) and ecosystem types (terrestrial, freshwater, marine) using the metafor package [29] in R (R v. 3.1.1., R core development team, 2015). While calculating the summary effect, the effect sizes from each study were weighted by the inverse of the study variance. Models were fitted using restricted maximum-likelihood estimation, and the  $Q$  test was used to test for residual heterogeneity. As the effects significantly differed between study and ecosystem types, we reanalyzed the data separately for each group, which reduced heterogeneity considerably.

## 3. Results

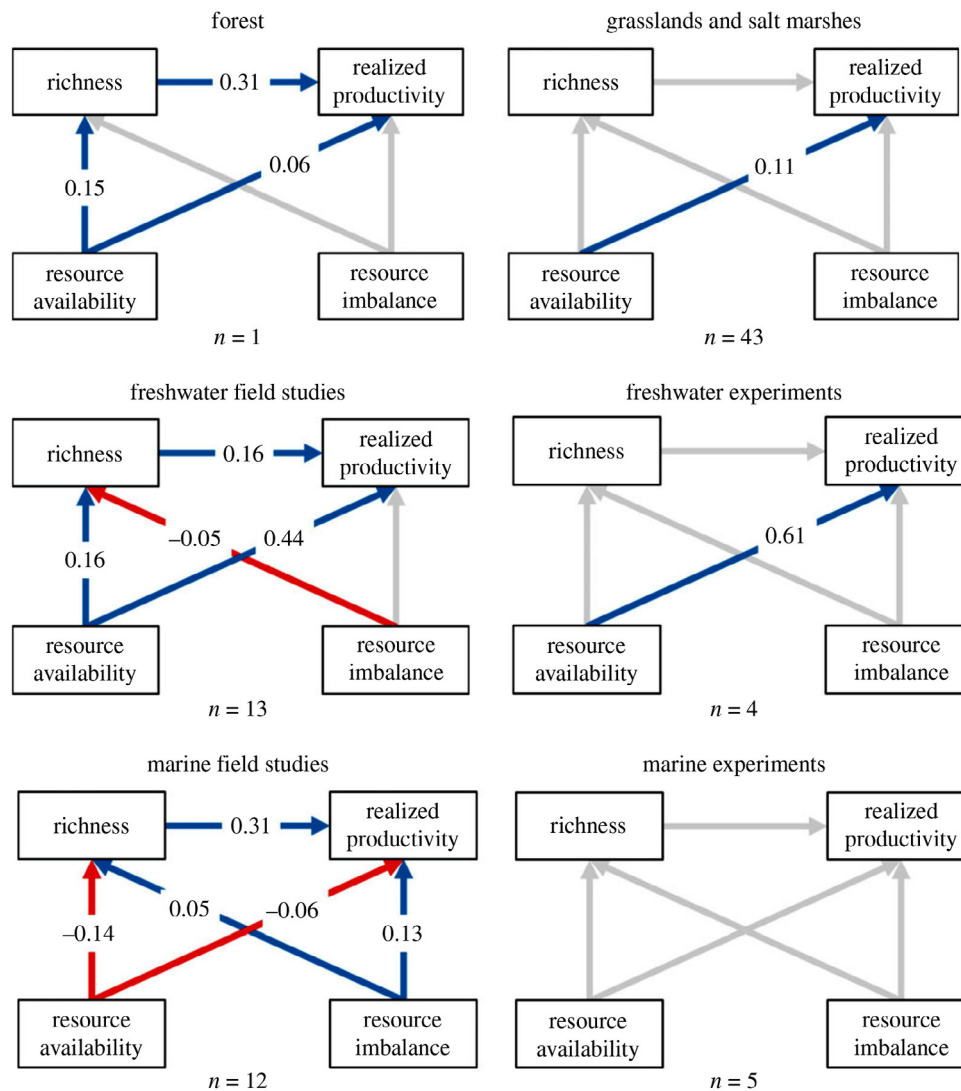
### (a) Impact of resource availability on diversity and productivity

Overall resource availability directly increased realized productivity (standardized coefficient ( $\gamma$ ) = 0.15) and diversity (richness,  $\gamma$  = 0.04; evenness  $\gamma$  = 0.05; figure 2). However, these effects were highly variable between the studies. In field observational studies, effects of resource availability on producer biomass (realized productivity) and diversity varied depending on the ecosystem type (figures 3 and 4). In forests, resource availability increased both species richness ( $\gamma$  = 0.15) and evenness ( $\gamma$  = 0.12), but it should be stressed that this result is due to a single study (GAM01). In grasslands and salt marshes, resource availability increased realized productivity ( $\gamma$  = 0.11), but had no effect on richness or evenness. In freshwater ecosystems, higher resource availability led to higher realized productivity ( $\gamma$  = 0.44) and higher species richness ( $\gamma$  = 0.16). Surprisingly,



**Figure 2.** Summary of meta-analysis results for the SEM with richness (a) and evenness (b) over all studies. Effect sizes are shown as standardized path coefficients.  $n$  is the number of studies. Blue and red paths are positive and negative relationships, respectively, and grey paths are non-significant relationships.

negative effects of resource availability on biomass production ( $\gamma$  = -0.06) and richness ( $\gamma$  = -0.14) were observed for marine ecosystems. In experiments, resource availability affected neither richness nor evenness, but had a strong positive impact on realized productivity in freshwater experiments ( $\gamma$  = 0.61). Evenness was not affected by changing resource supply in freshwater or in marine systems, and this pattern was consistent among studies (see electronic supplementary material). We found significantly positive effects of resource availability on evenness in four of 69 studies included in the meta-analysis. The only significantly negative effect of resource availability on evenness was found in a long-term study on phytoplankton in the western English Channel (Western Channel Observatory, station L4;  $\gamma$  = -0.19,  $p$  = 0.012).



**Figure 3.** Summary of meta-analysis results for the SEM with richness over all studies. Shown are effect sizes as standardized path coefficients.  $n$  is the number of studies. Blue and red paths are positive and negative relationships, respectively and grey paths are non-significant relationships.

### (b) Impact of resource imbalance on diversity and productivity

In general, resource imbalance had no effect on diversity and had a marginal positive effect on the realized productivity (figure 2). The positive effects on realized productivity and species richness were primarily found in marine ecosystems (figure 3), driven by five long-term (11 years) studies on coastal phytoplankton off the coast of the Netherlands. In freshwater ecosystems, resource imbalance had a weak negative effect on species richness ( $\gamma = -0.05$ ), but in some studies (e.g. eutrophic lakes in the United States, HILL04), resource imbalance increased richness (electronic supplementary material, figure S3). Resource imbalance did not affect productivity in marine or freshwater experiments or in terrestrial ecosystems.

### (c) Interactions between richness and productivity

Overall, richness and realized productivity positively covaried ( $\gamma = 0.18$ ) (figure 2a). However, separating study types (field observational study or experiment) highlighted that the significant effects were found only in field studies. The strongest relationship

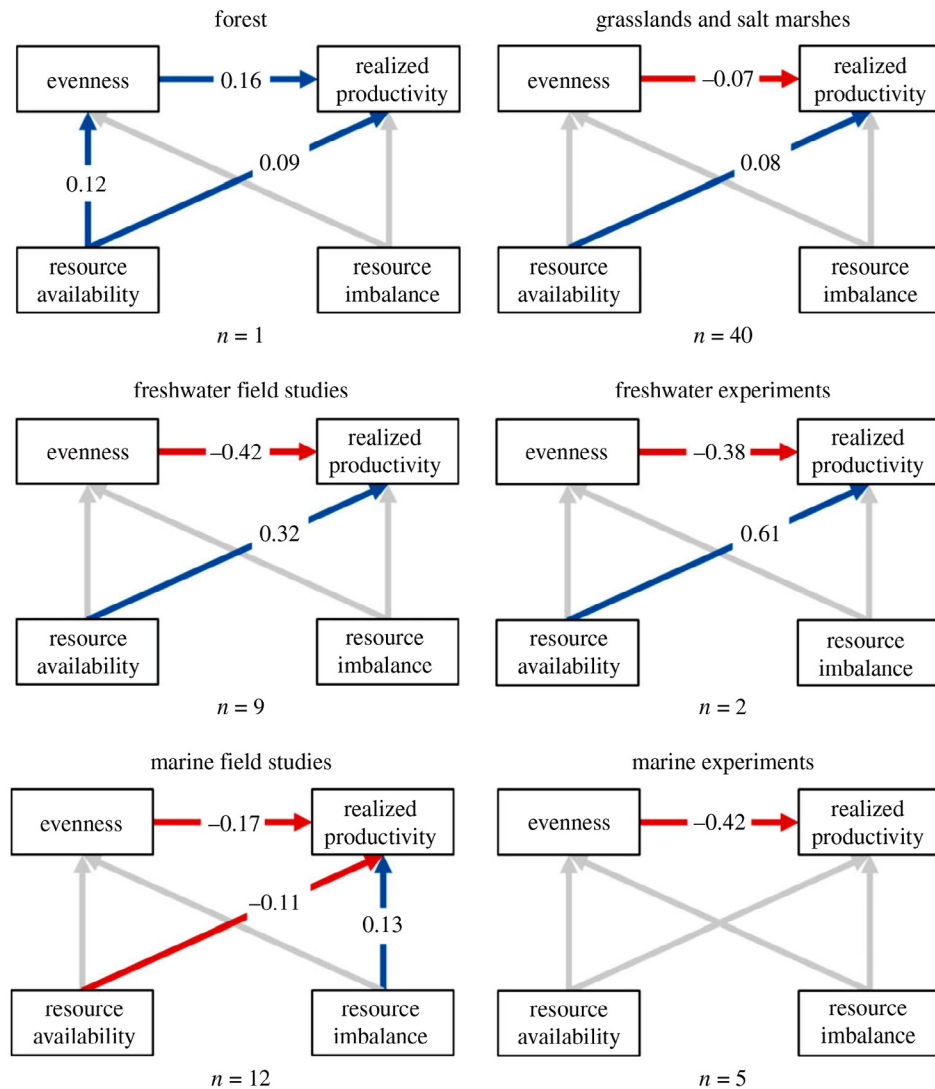
between richness and biomass production was observed in marine ecosystems (figure 3). The only field study showing a significantly negative effect of richness on productivity ( $\gamma = -0.18$ ,  $p = 0.038$ ) was a study on plants in salt marshes (TREIBSEL, electronic supplementary material, figure S5). In general, no relationship between richness and realized productivity was found in grasslands and salt marshes.

### (d) Interactions between evenness and productivity

As predicted, we found an overall negative relationship between evenness and realized productivity ( $\gamma = -0.10$ ) in aquatic and terrestrial studies (figure 2b). The strongest relationship was observed in freshwater (field studies:  $\gamma = -0.42$ ; experiments:  $\gamma = -0.38$ ) and in marine experiments ( $\gamma = -0.42$ ). In contrast, productivity increased with evenness in forests ( $\gamma = 0.16$ ,  $p < 0.001$ ).

## 4. Discussion

Across ecosystems and study types, the realized productivity of autotrophs was largely influenced by the availability of resources. In observational studies, these effects were either direct



**Figure 4.** Summary of meta-analysis results for the SEM with evenness (for more detail, see electronic supplementary material, table S2). Shown are effect sizes as standardized path coefficients.  $n$  is the number of studies. Blue and red paths are positive and negative relationships, respectively and grey paths are non-significant relationships.

or mediated by changes in the number of species, confirming previous findings that higher species richness leads to higher efficiency in resource use and, in consequence, to higher biomass production [4, 14, 15, 25]. However, neither resource availability nor imbalance significantly affected evenness, which suggests that the dominance structure of autotrophs is primarily driven by factors other than resources, such as trophic interactions or external forces such as warming, drought, salinity or changes in pH. Such effects on evenness have been previously reported in the literature. For example, a meta-analysis across ecosystems showed that herbivory enhances producer evenness [25]. Comparably, greater evenness with lower soil moisture was observed in experimental plant communities [30].

Surprisingly, in marine ecosystems, biomass and the number of phytoplankton species decreased with higher resource supply, but increased in response to resource imbalance. These results were largely driven by studies on pelagic ecosystems off the coast of the Netherlands. These coastal waters are generally turbid systems with high proportion of dissolved organic nutrients [31]. Consequently, available nitrogen and phosphorus might be primarily incorporated by heterotrophic microbes and not by

phytoplankton. Including availability of light as one of the limiting resources for phytoplankton growth in turbid waters could change the shape of examined relationships. Contrasting results for phytoplankton at the station L4 in the western English Channel (resource availability → richness,  $\gamma = 0.31$ ,  $p < 0.001$ ; resource availability → realized productivity,  $\gamma = 0.28$ ,  $p < 0.001$ ; non-significant relationships with resource imbalance), which contained information on light availability (electronic supplementary material, table S1), support this interpretation. Station L4 is seasonally stratified and also characterized by lower turbidity than stations along the coast of the Netherlands [32]. These results highlight the importance of light availability for autotrophic growth in ecosystems where nutrients are replete, and suggest that interpretation of the resource supply–productivity relationships in plants, particularly in aquatic systems, might be misleading if the influence of light is not considered [33].

In aquatic experimental studies and unmanipulated grasslands, we found significant relationships between resource availability and realized productivity, but no significant effect of resource availability or imbalances on diversity. These results are broadly consistent with previous meta-analyses; for example,



Elser *et al.* [34] demonstrated that across ecosystems, productivity generally increases with nutrient supply. Although experimental nutrient supply in many ecosystems tends to lead to loss of plant evenness or richness [25], the diversity of unmanipulated grasslands probably arises from many interacting processes (e.g. resource supply, trophic interactions, invasion, etc.) across a broad range of observed soil resources. Thus, in the absence of significantly elevated nutrients, our results demonstrate that grassland diversity is not tightly coupled to soil nutrients. Further, the richness gradients in the aquatic experimental studies might not represent biodiversity of natural communities, thus constraining the responsiveness of diversity to the experimental manipulations [35]. Aquatic communities in experimental studies may suffer from bottle (enclosure) effects, thereby preventing the growth of some species while favoring others, particularly with nutrient amendments. In addition, strong nutrient recycling in closed experimental systems might lead to overestimation of the effects related to enhanced resource supply. In some experiments included in our analysis (electronic supplementary material, table S1), nutrients were added to the system, often in higher proportions and at different ratios than in the natural environment. Other environmental drivers such as turbidity and grazing effects are altered in experiments compared with natural systems [35].

As expected, we found an overall positive effect of species richness on realized productivity of autotrophs in the field. The only field study showing a negative response of biomass production to increasing species richness was a study on plants in salt marshes (TREIBSEL, electronic supplementary material), where salinity and water regime, rather than nutrients, were the main drivers of diversity and biomass [36–39]. The limited ability of our model to explain variation in richness and realized productivity in salt marshes (only 8% for richness and 4% for realized productivity) seems to confirm that we did not quantify the key factors influencing this system. Our simplistic model typically explained a large proportion of variation in biomass production, but only small amounts of variation in diversity (electronic supplementary material, table S1), emphasizing the importance of other factors such as disturbance [40] and trophic interactions for shaping community structure.

The overall negative relationship between evenness and biomass production confirms our hypothesis that most communities are dominated by a few highly productive species; reducing the dominance by these species decreases the realized productivity. Biomass production increased with evenness only in forests, which is consistent with results from a global meta-analysis exploring drivers of diversity–productivity relationships in forests [41]. Higher heterogeneity of functional traits (e.g. shade tolerance, root traits) in more even forest communities might significantly increase complementarity in resource use and consequently productivity [41]. However, our model explained only 10% of the variance in total tree biomass, which again suggests that the measured resources were not the main drivers of the system in this study. Environmental changes such as management for preferred species [42], stand age [43] or differences in soil moisture [44] could be potentially more important factors for shaping tree distribution and biomass.

In general, our analysis emphasizes the importance of diversity for primary productivity of natural ecosystems. The role of diversity remains largely unappreciated in experimental aquatic studies, probably because the levels of diversity are limited in these experiments and the effects of manipulations are often stronger than in the natural environment. Moreover, based on

the field observational studies, we can partly support  $H_1$ , i.e. that resource availability increases producer biomass and diversity. Resource availability had a positive effect on biomass and richness, but did not affect evenness except in forests. Interestingly, the direct effect of resource supply on productivity ( $\gamma = 0.15$  in the SEM with richness;  $\gamma = 0.07$  in the SEM with evenness) was stronger overall than the indirect effect mediated by diversity (for richness:  $\gamma = 0.04 \cdot 0.18 = 0.01$ ; for evenness:  $\gamma = -0.10 \cdot 0.05 = -0.01$ ), suggesting that the role of diversity for biomass production across ecosystems is rather weak when compared with the direct effect of resources on realized productivity, consistent with other such studies [15,16].

Resource imbalance only reduced diversity in the freshwater field studies (figure 2). As this effect was marginal ( $\gamma = -0.05$ ) and did not appear in other types of ecosystems, we reject  $H_2$ . The surprisingly weak effects of resource imbalance on diversity and realized productivity can appear as a result of a narrow range of  $b$  caused by the limited number of resources included in our analysis (mostly N and P). This should be further explored using data from studies with contrasting resource ratios and naturally occurring diversity gradients. In long-term studies, seasonality in resource supply can also play a role in limiting the absolute range of resource imbalance. Comparing the results among seasons could bring a new insight into the framework proposed by Cardinale *et al.* [15] and explored in this article.

As hypothesized, biomass production generally increased with the number of species ( $H_3$ ) but was reduced in more even communities ( $H_4$ ). However, a positive impact of evenness on biomass was found in forests, suggesting overyielding in this type of ecosystem.

In spite of the power of SEM and meta-analytical approaches, our interface has some limitations. First, our measures of resource availability and imbalance are based on equal supply of resources, ignoring physiological requirements of the organisms and their stoichiometric plasticity. However, a major advantage of this measure is that it combines multiple resources despite of their type, units and ranges. Second, the number of resources included in our analysis is rather low and conclusions might be misleading if the most limiting resource (e.g. light for aquatic communities) is omitted, as discussed above. Finally, we incorporated only the effects of resources, because the lack of consistent data for other potentially important environmental factors would not allow for comparison of effects across ecosystems. However, the multivariate approach which we used [15] integrates the effects of potential productivity (total resource supply) on diversity, and the effects of diversity on realized productivity, advancing mechanistic understanding of these relationships. For the first time, to the best of our knowledge, this approach has been applied to datasets spanning a wide variety of ecosystems, elucidating similarities and differences in the response among ecosystem types.

Although our simple model did not account for all potentially influential drivers of diversity–productivity relationships (e.g. consumers, disturbance), our meta-analysis demonstrates that in the natural environment richness significantly affects realized productivity independent of the ecosystem type, although the absolute effect on biomass was weak. However, we found no evidence that evenness is directly related to changes in resource supply, suggesting that trophic interactions (e.g. herbivory) probably play a key role in shaping the dominance structure of the producer community. We expect that this meta-analysis will stimulate further studies evaluating the importance of evenness for ecosystem functioning.

**Data accessibility** — The datasets used for the meta-analysis have been deposited in the Dryad Digital Repository doi 10.5061/dryad.h50d9. The raw data can be accessed by contacting the corresponding author.

**Authors' contributions** — H.H., A.L., S.A.J.D., E.D., W.S.H., C.A.K., H.O.V., E.S., M.S., J.U. and D.B.W. contributed to the design of the study. All authors contributed to data interpretation and manuscript editing. A.L. performed data analyses and wrote the first draft of the manuscript.

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## The influence of balanced and imbalanced resource supply on biodiversity-functioning relationship across ecosystems

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### Supplementary material

Table S1. Studies included in the meta-analysis. Coefficient of determination ( $r^2$ ) indicates how well our SEM explains the variability of richness, evenness and realized productivity. Studies being a part of the Nutrient Network (see Borer et al. 2014 for details) are marked with the asterisk. N, P, K etc. are total availabilities of the elements in water or soil; PAR is photosynthetic active radiation.

Study ID	Study type	Ecosystem type	Habitat	Resources	Biomass measure	Sampling size	$r^2$ (richness)	$r^2$ (evenness)	$r^2$ (productivity)
HILL01	field study	freshwater	lake	N, P	chlorophyll a (mg l <sup>-1</sup> )	100	0.25	0.04	0.52
HILL02	field study	freshwater	lake	N, P	NPP (g C m <sup>-2</sup> yr <sup>-1</sup> )	23	0.08	NA	0.39
DECL01	experiment	freshwater	mesocosm	N, P (manipulated)	chlorophyll a (mg l <sup>-1</sup> )	77	0.09	0.02	0.42
STRIE01	experiment	freshwater	mesocosm	N, P (manipulated)	chlorophyll a (mg l <sup>-1</sup> )	41	0.12	NA	0.60
URABE01	field study	freshwater	lake	N, P	chlorophyll a (mg l <sup>-1</sup> )	77	0.25	0.01	0.55
EPA01	field study	freshwater	lake	N, P	chlorophyll a (mg l <sup>-1</sup> )	540	0.14	NA	0.34
LEWA01	experiment	marine	mesocosm	N, P (manipulated)	biomass (mg C l <sup>-1</sup> )	12	0.49	0.34	0.70
VENTE01	field study	terrestrial	grassland	K, N, P, Ca, Mg, Fe	biomass (g m <sup>-2</sup> )	53	0.28	NA	0.52
HILL03	experiment	freshwater	microcosm	N, P (manipulated)	biovolume (mm <sup>3</sup> l <sup>-1</sup> )	90	0.20	0.02	0.40
HILL04	field study	freshwater	lake	N, P	biovolume (mm <sup>3</sup> l <sup>-1</sup> )	226	0.03	0.02	0.52
STRIE02	experiment	freshwater	mesocosm	N, P (manipulated)	biovolume (mm <sup>3</sup> l <sup>-1</sup> )	60	0.49	NA	0.78
LEWA02	experiment	marine	mesocosm	N, P	biovolume (mm <sup>3</sup> l <sup>-1</sup> )	24	0.02	0.01	0.08
LEWA03	experiment	marine	mesocosm	N, P	biomass (mg C l <sup>-1</sup> )	12	0.67	0.06	0.11
LEWA04	experiment	marine	mesocosm	N, P	biomass (mg C l <sup>-1</sup> )	12	0.05	0.07	0.84
HILL05	experiment	marine	microcosm	N, P (manipulated)	biovolume (mm <sup>3</sup> l <sup>-1</sup> )	59	0.02	0.03	0.31
LEMMENS	field study	freshwater	pond	N, P	biovolume (mm <sup>3</sup> l <sup>-1</sup> )	35	0.06	NA	0.10
PONDSCAPE	field study	freshwater	pond	N, P	biovolume (mm <sup>3</sup> l <sup>-1</sup> )	117	0.03	NA	0.26
HILL06	field study	freshwater	lake	N, P, PAR	biomass (mg C l <sup>-1</sup> )	131	0.12	0.04	0.47
AMCAMP*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>-2</sup> )	30	0.05	0.15	0.23
AZI*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>-2</sup> )	29	0.02	0.06	0.18
BARTA*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>-2</sup> )	30	0.09	0.09	0.06

BLDR*	field study	terrestrial	grassland	K, N, P	biomass (g m2-1)	20	0.23	0.16	0.08
BNCH*	field study	terrestrial	grassland	K, N, P	biomass (g m2-1)	30	0.25	0.30	0.13
BOGONG*	field study	terrestrial	grassland	K, N, P	biomass (g m2-1)	30	0.17	0.22	0.03
BTTR*	field study	terrestrial	grassland	K, N, P	biomass (g m2-1)	30	0.11	0.01	0.09
BURRAWAN*	field study	terrestrial	grassland	K, N, P	biomass (g m2-1)	30	0.10	0.17	0.18
CDPT*	field study	terrestrial	grassland	K, N, P	biomass (g m2-1)	60	0.25	0.11	0.29
CDCR*	field study	terrestrial	grassland	K, N, P	biomass (g m2-1)	47	0.30	0.01	0.28
COWI*	field study	terrestrial	grassland	K, N, P	biomass (g m2-1)	30	0.13	0.01	0.38
FNLY*	field study	terrestrial	grassland	K, N, P	biomass (g m2-1)	17	0.67	0.11	0.35
FRUE*	field study	terrestrial	grassland	K, N, P	biomass (g m2-1)	30	0.05	0.05	0.01
GILB*	field study	terrestrial	grassland	K, N, P	biomass (g m2-1)	30	0.04	0.18	0.13
CBGB*	field study	terrestrial	grassland	K, N, P	biomass (g m2-1)	54	0.01	0.01	0.01
HILL07	field study	freshwater	lake	N, P	biovolume (mm3 l-1)	80	0.05	0.02	0.31
HILL08	field study	freshwater	lake	N, P	biovolume (mm3 l-1)	78	0.08	0.01	0.55
COMTESS	field study	terrestrial	grassland, saltmarsh	K, P	biomass (g m2-1)	177	0.08	NA	0.04
TREIBSEL	field study	terrestrial	saltmarsh	K, P	biomass (g m2-1)	111	0.07	NA	0.28
HANS	field study	marine	brackish	N, P	chlorophyll a (mg l-1)	260	0.13	0.01	0.33
NOORD	field study	marine	coastal	N, P	chlorophyll a (mg l-1)	154	0.08	0.05	0.22
ROTT	field study	marine	coastal	N, P	chlorophyll a (mg l-1)	88	0.03	0.01	0.12
TER	field study	marine	coastal	N, P	chlorophyll a (mg l-1)	35	0.11	0.08	0.35
VLISS	field study	marine	brackish	N, P	chlorophyll a (mg l-1)	256	0.25	0.01	0.22
WAL01	field study	marine	coastal	N, P	chlorophyll a (mg l-1)	157	0.06	0.03	0.27
WAL02	field study	marine	coastal	N, P	chlorophyll a (mg l-1)	159	0.01	0.07	0.07
LOD	field study	marine	brackish	N, P	chlorophyll a (mg l-1)	272	0.13	0.01	0.25
HOD01	field study	marine	coastal	N, P, PAR	biovolume (mm3 l-1)	17	0.21	0.01	0.69
HOD02	field study	marine	coastal	N, P, PAR	biovolume (mm3 l-1)	10	0.31	0.18	0.91
HOD03	field study	marine	coastal	N, P, PAR	biovolume (mm3 l-1)	14	0.03	0.22	0.61
GAM01	field study	terrestrial	forest	N, C	biomass (kg m2-1)	1627	0.02	0.01	0.10
L4	field study	marine	coastal	N, PAR	biomass (mg C l-1)	174	0.09	0.05	0.45
DONK01	field study	freshwater	lake	N, P	biovolume (mm3 l-1)	36	0.04	0.01	0.58



DONK02	field study	freshwater	lake	N, P	chlorophyll a (mg l <sup>-1</sup> )	55	0.05	0.05	0.08
GLAC*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	29	0.18	0.15	0.01
HALL*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.10	0.12	0.08
HART*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.30	0.03	0.08
HNVR*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.09	0.16	0.26
KINY*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.12	0.10	0.06
LANCASTER*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	26	0.06	0.09	0.24
LEAD*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.04	0.13	0.23
LOOK*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.08	0.01	0.31
MTCA*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	8	0.50	0.03	0.70
PAPE*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	10	0.03	0.07	0.33
SAGE*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.29	0.04	0.41
SAVA*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	20	0.07	0.01	0.50
SEDG*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	29	0.07	0.09	0.16
SERENG*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	29	0.22	0.11	0.17
SEVI*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	40	0.05	0.01	0.07
SHPS*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	38	0.02	0.05	0.25
SIER*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.26	0.04	0.15
SMITH*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.06	0.07	0.27
SPIN*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.04	0.02	0.11
SUMM*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.03	0.01	0.10
TEMPLE*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	25	0.05	0.04	0.17
TYSO*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	40	0.04	0.01	0.24
UKUL*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.06	0.05	0.14
UNC*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.15	0.08	0.22
VALM*	field study	terrestrial	grassland	K, N, P	biomass (g m <sup>2</sup> -1)	30	0.07	0.01	0.11
MEIER00	field study	freshwater	rock pools	N, P	biovolume (mm <sup>3</sup> l <sup>-1</sup> )	30	0.26	0.07	0.56

† Borer et al. 2014 Finding generality in ecology: a model for globally distributed experiments. *Methods Ecol. Evol.* **5**: 65-73.

Table S2. Summary of results from meta-analysis of model paths with richness, including overall effect size (estimate), its significance ( $p$ ) and 95% confidence intervals (CI).

	estimate	$p$	95% CI
<b>Grasslands and saltmarshes (n=43)</b>			
resource availability -> richness	-0.03	0.24	-0.08, 0.02
resource availability -> realized productivity	0.11	< 0.001	0.06, 0.16
resource imbalance -> richness	0.03	0.21	-0.02, 0.08
resource imbalance -> realized productivity	-0.02	0.38	-0.08, 0.03
richness -> realized productivity	-0.04	0.14	-0.09, 0.01
<b>Freshwater field studies (n=13)</b>			
resource availability -> richness	0.16	< 0.001	0.11, 0.21
resource availability -> realized productivity	0.44	< 0.001	0.39, 0.49
resource imbalance -> richness	-0.05	0.047	-0.10, -0.001
resource imbalance -> realized productivity	-0.03	0.35	-0.07, 0.03
richness -> realized productivity	0.16	< 0.001	0.11, 0.21
<b>Freshwater experimental studies (n=4)</b>			
resource availability -> richness	-0.03	0.66	-0.15, 0.09
resource availability -> realized productivity	0.61	< 0.001	0.49, 0.74
resource imbalance -> richness	-0.01	0.84	-0.13, 0.11
resource imbalance -> realized productivity	-0.09	0.17	-0.21, 0.04
richness -> realized productivity	-0.03	0.63	-0.15, 0.09
<b>Marine field studies (n=12)</b>			
resource availability -> richness	-0.14	< 0.001	-0.19, -0.09
resource availability -> realized productivity	-0.06	< 0.001	-0.11, -0.01
resource imbalance -> richness	0.05	0.04	0.00, 0.10
resource imbalance -> realized productivity	0.13	< 0.001	0.08, 0.18
richness -> realized productivity	0.31	< 0.001	0.26, 0.36
<b>Marine experimental studies (n=5)</b>			
resource availability -> richness	0.04	0.69	-0.15, 0.23
resource availability -> realized productivity	0.05	0.63	-0.14, 0.24
resource imbalance -> richness	0.09	0.34	-0.10, 0.29
resource imbalance -> realized productivity	-0.13	0.19	-0.32, 0.06
richness -> realized productivity	0.01	0.88	-0.18, 0.21

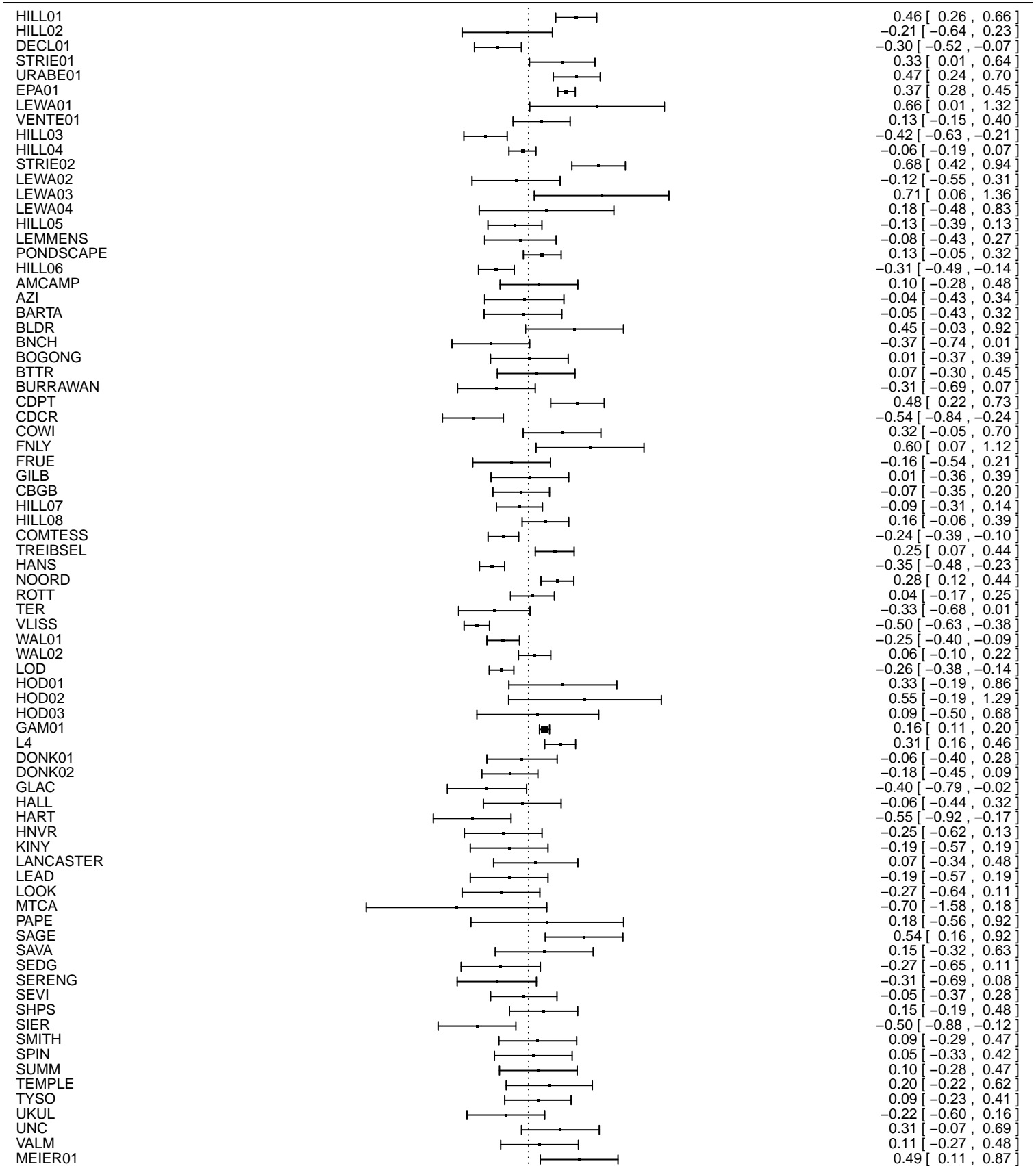
Table S3. Summary of results from meta-analysis of model paths with evenness, including overall effect size (estimate), its significance ( $p$ ) and 95% confidence intervals (CI).

	estimate	$p$	95% CI
<b>Grasslands and saltmarshes (n=40)</b>			
resource availability -> evenness	0.01	0.74	-0.05, 0.07
resource availability -> realized productivity	0.08	0.01	0.02, 0.14
resource imbalance -> evenness	-0.02	0.44	-0.08, 0.04
resource imbalance -> realized productivity	-0.03	0.32	-0.09, 0.03
evenness -> realized productivity	-0.07	0.02	-0.13, -0.01
<b>Freshwater field studies (n=9)</b>			
resource availability -> evenness	-0.001	0.98	-0.07, 0.07
resource availability -> realized productivity	0.32	< 0.001	0.25, 0.39
resource imbalance -> evenness	-0.001	0.83	-0.08, 0.06
resource imbalance -> realized productivity	0.02	0.66	-0.05, 0.09
evenness -> realized productivity	-0.42	< 0.001	-0.49, -0.35
<b>Freshwater experimental studies (n=2)</b>			
resource availability -> evenness	-0.09	0.24	-0.25, 0.06
resource availability -> realized productivity	0.39	< 0.001	0.23, 0.54
resource imbalance -> evenness	0.10	0.21	-0.06, 0.25
resource imbalance -> realized productivity	-0.01	0.91	-0.16, 0.15
evenness -> realized productivity	-0.38	< 0.001	-0.53, -0.22
<b>Marine field studies (n=12)</b>			
resource availability -> evenness	0.05	0.07	-0.00, 0.10
resource availability -> realized productivity	-0.11	< 0.001	-0.16, -0.06
resource imbalance -> evenness	-0.05	0.06	-0.10, 0.00
resource imbalance -> realized productivity	0.13	< 0.001	0.08, 0.18
evenness -> realized productivity	-0.17	< 0.001	-0.22, -0.12
<b>Marine experimental studies (n=5)</b>			
resource availability -> evenness	0.13	0.18	-0.06, 0.32
resource availability -> realized productivity	0.07	0.48	-0.12, 0.26
resource imbalance -> evenness	0.03	0.78	-0.17, 0.22
resource imbalance -> realized productivity	-0.11	0.25	-0.30, 0.08
evenness -> realized productivity	-0.42	< 0.001	-0.61, -0.23

Table S4. Researchers not included as the coauthors, who significantly contributed to the data collection. The Nutrient Network site PIs are marked with asterisks.

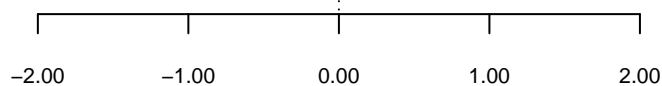
Name	Affiliation
Lena Eggers	WasserCluster Lunz, Austria
Thomas Hansen	GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany
Carolyn Harris	Plymouth Marine Laboratory, UK
Dorothee Hodapp	ICBM, University of Oldenburg, Germany
Birte Matthiessen	GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany
Timothy Smyth	Plymouth Marine Laboratory, UK
Jane Soininen	University of Helsinki, Finland
Martin Wassen	Utrecht University, The Netherlands
E. Malcolm S. Woodward	Plymouth Marine Laboratory, UK
Jeroen Van Wichelen	Ghent University, Belgium
María José Villena Alvarez	Laboratorios Tecnológicos de Levante, Spain
Andrew MacDougall*	Univeristy of Guelph, Canada
Anita C. Risch*	Swiss Federal Institute for Forest, Snow and Landscape Research, Switzerland
Brett Melbourne*	University of Colorado, USA
Carla M D'Antonio*	University of California, Santa Barbara, USA
Carly Stevens*	Lancaster University, UK
Chengjin Chu*	Lanzhou University, China
David Pyke*	USGS Forest and Rangeland Ecosystem Science Center, USA
David Wedin*	University of Nebraska, Lincoln, USA
Ellen I. Damschen*	University of Wisconsin, USA
Janneke Hille Ris Lambers*	University of Washington, USA
Jennifer Firn*	Queensland University of Technology, Australia
John G. Lambrinos*	Oregon State University, USA
John L. Orrock*	University of Wisconsin, USA
John Morgan*	La Trobe University, Australia
Jonathan D. Bakker*	University of Washington, USA
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Kathryn L. Cottingham*	Dartmouth College, USA
Kendi Davies*	University of Colorado, USA
Kirsten S. Hofmockel*	Iowa State University, USA
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Peter Adler*	Utah State University, USA
Peter D. Wragg*	University of Minnesota, USA
Philip A Fay*	USDA-ARS Grassland Soil and Water Research Lab, USA
Rebecca L. McCulley*	University of Kentucky, USA
Scott Collins*	University of New Mexico, USA
Suzanne M Prober*	CSIRO, Australia
T. Michael Anderson*	Wake Forest University, USA
Yann Hautier*	University of Oxford, UK
Yvonne Buckley*	The University of Queensland, Australia
Lars Brudvig*	Michigan State University, USA

Figure S1-10. Effect sizes as standardized path coefficients ( $\pm$  95% CI) for each model path and each study. Different size of the points corresponds to the sample size.



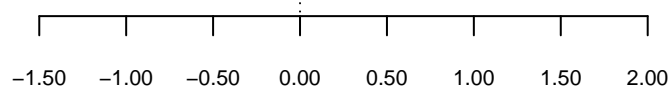
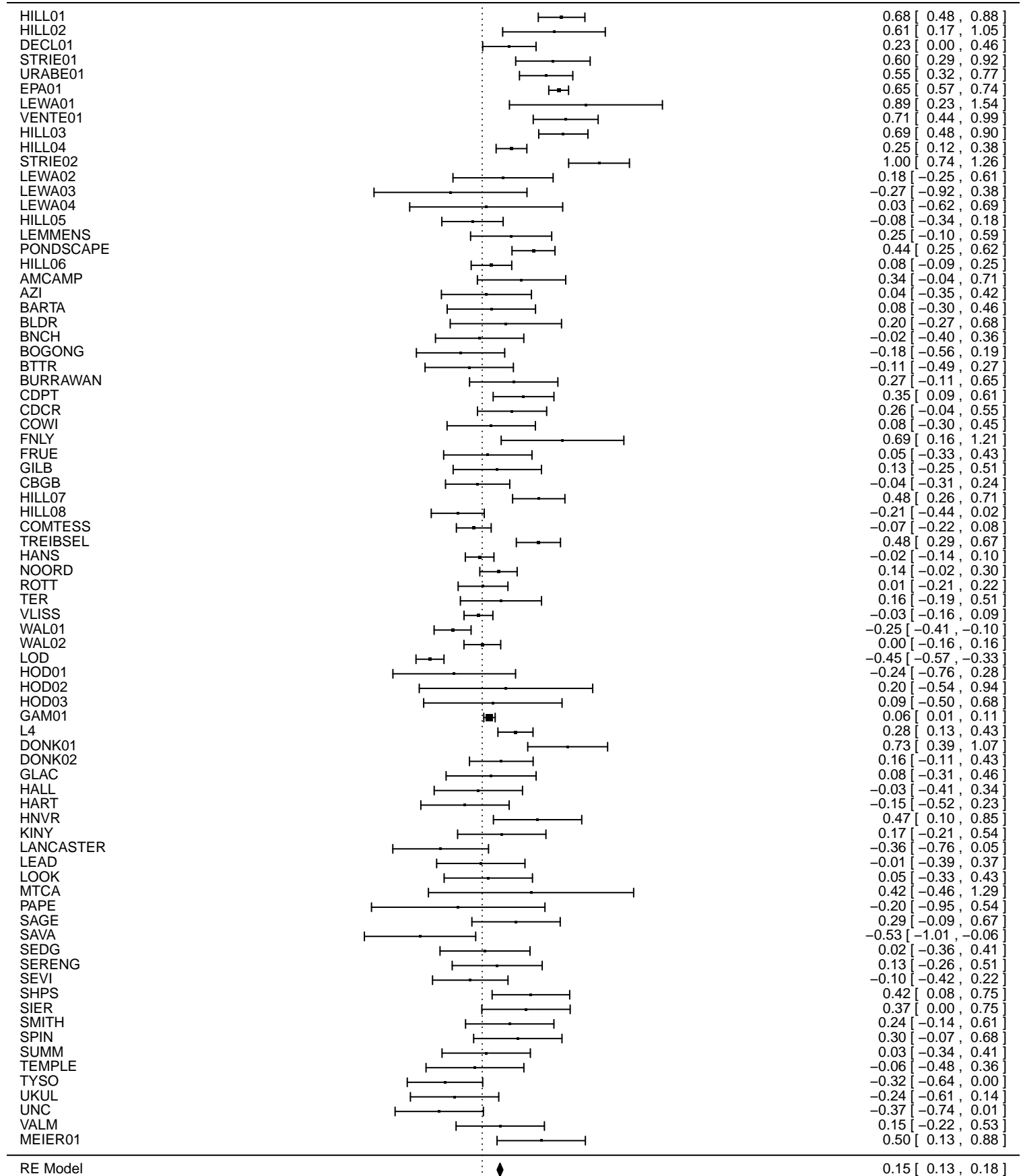
RE Model

0.03 [ 0.01, 0.06 ]

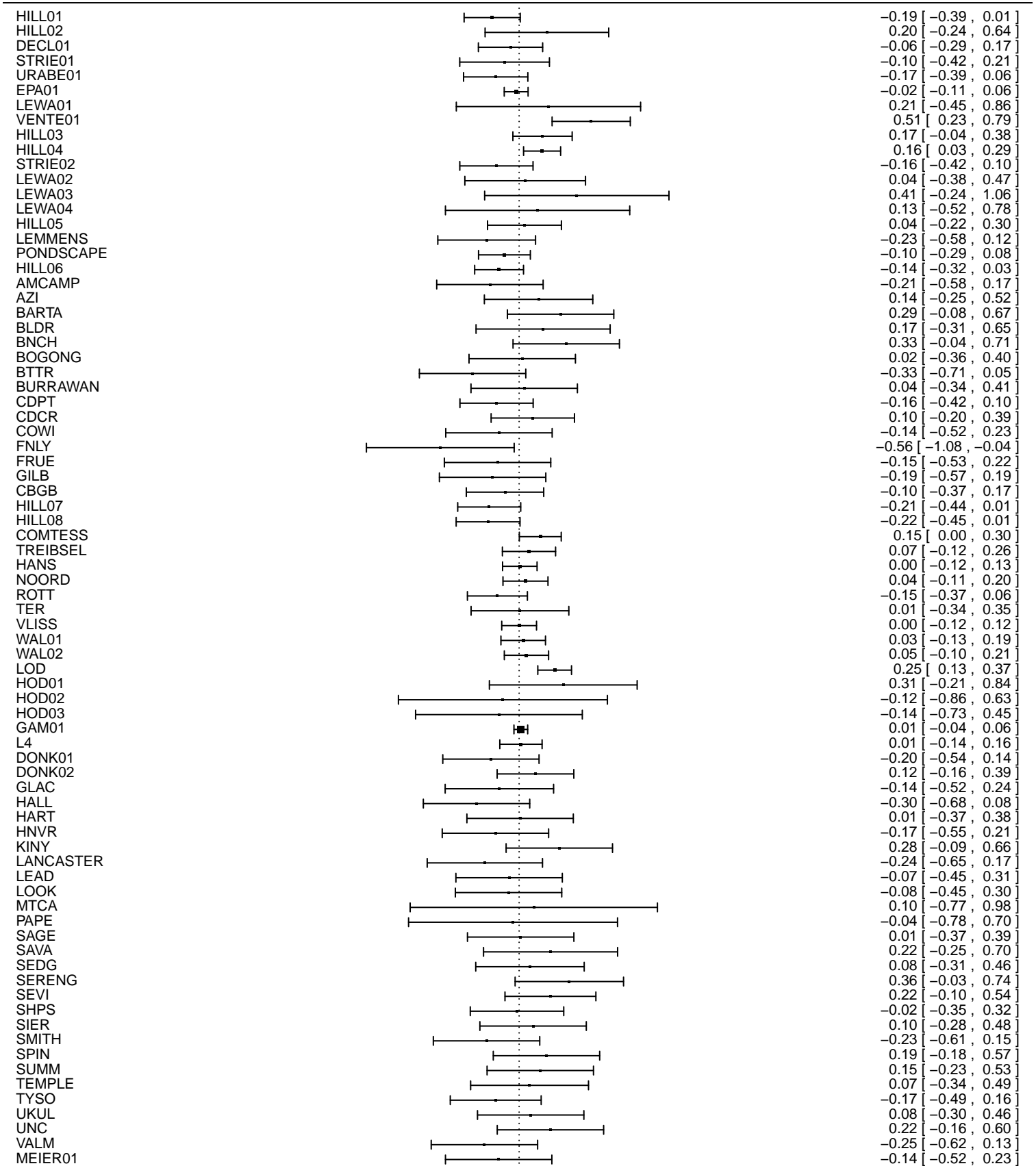


Resource availability -> richness

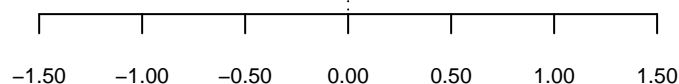




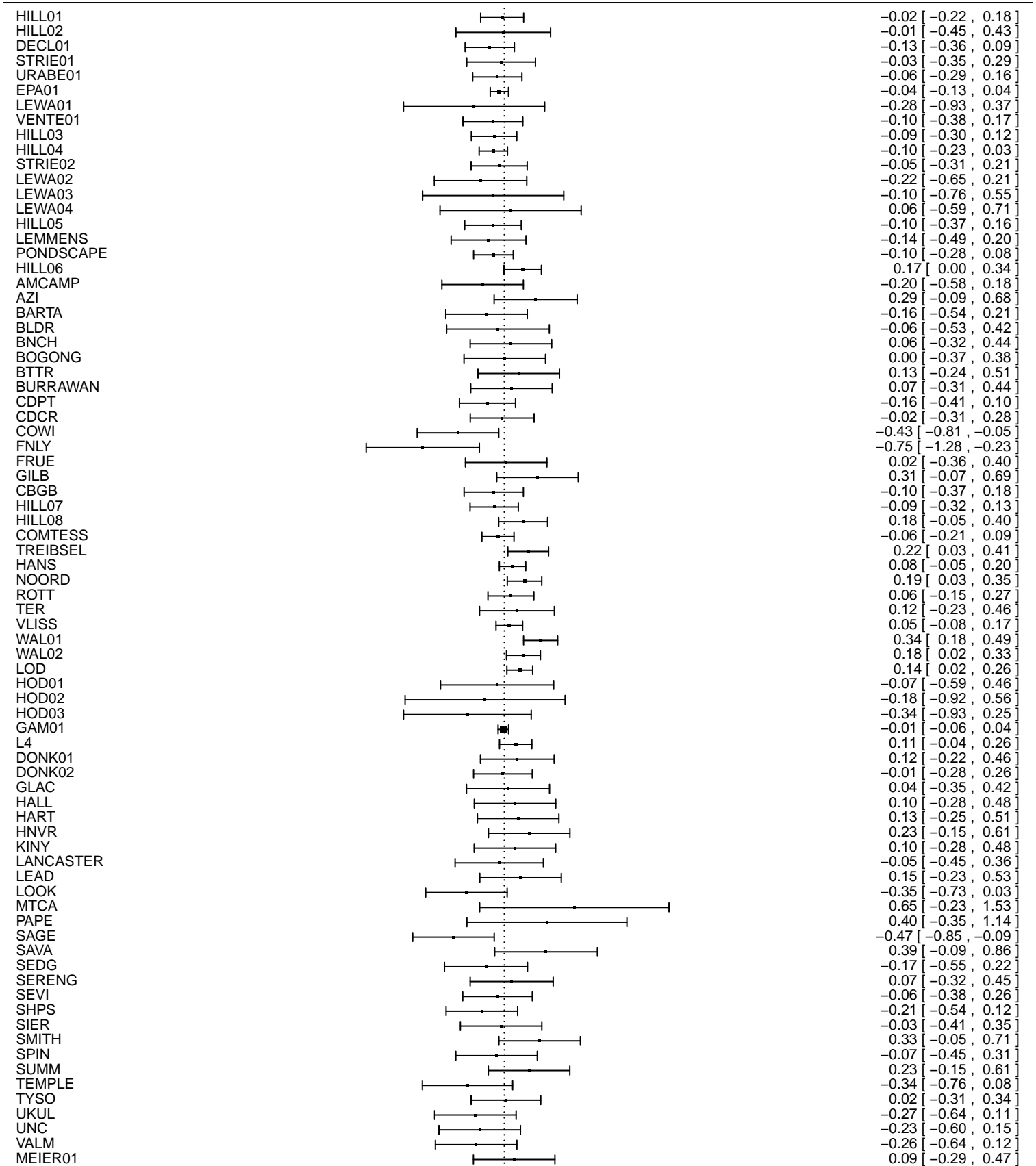
Resource availability → realized productivity



RE Model 0.01 [-0.01, 0.04]

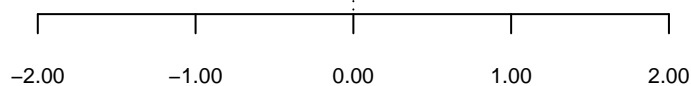


Resource imbalance -> richness

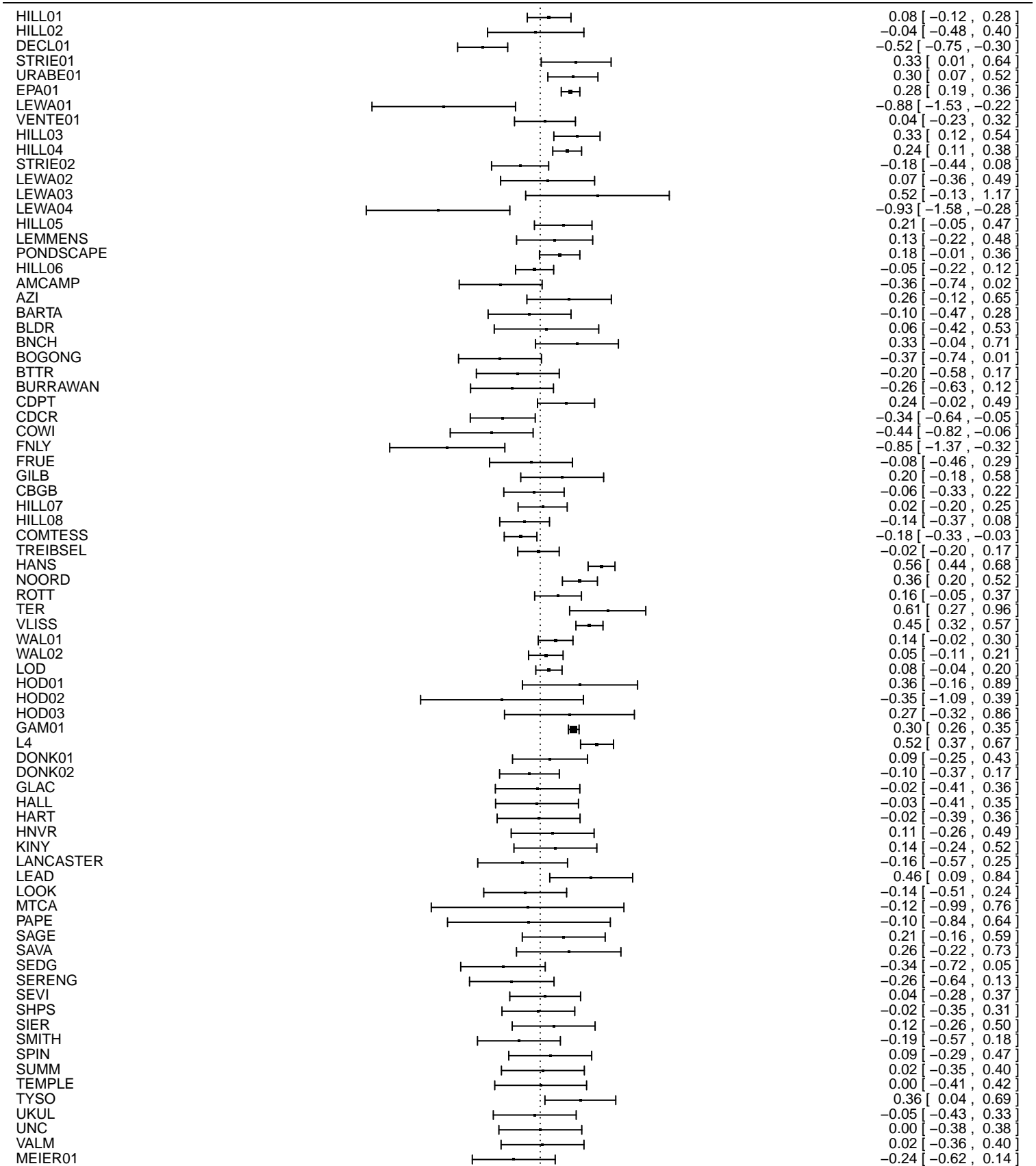


RE Model

0.01 [-0.01, 0.04]

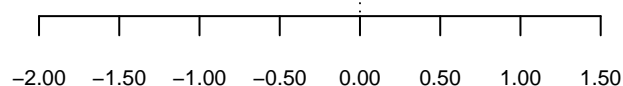


Resource imbalance -> realized productivity

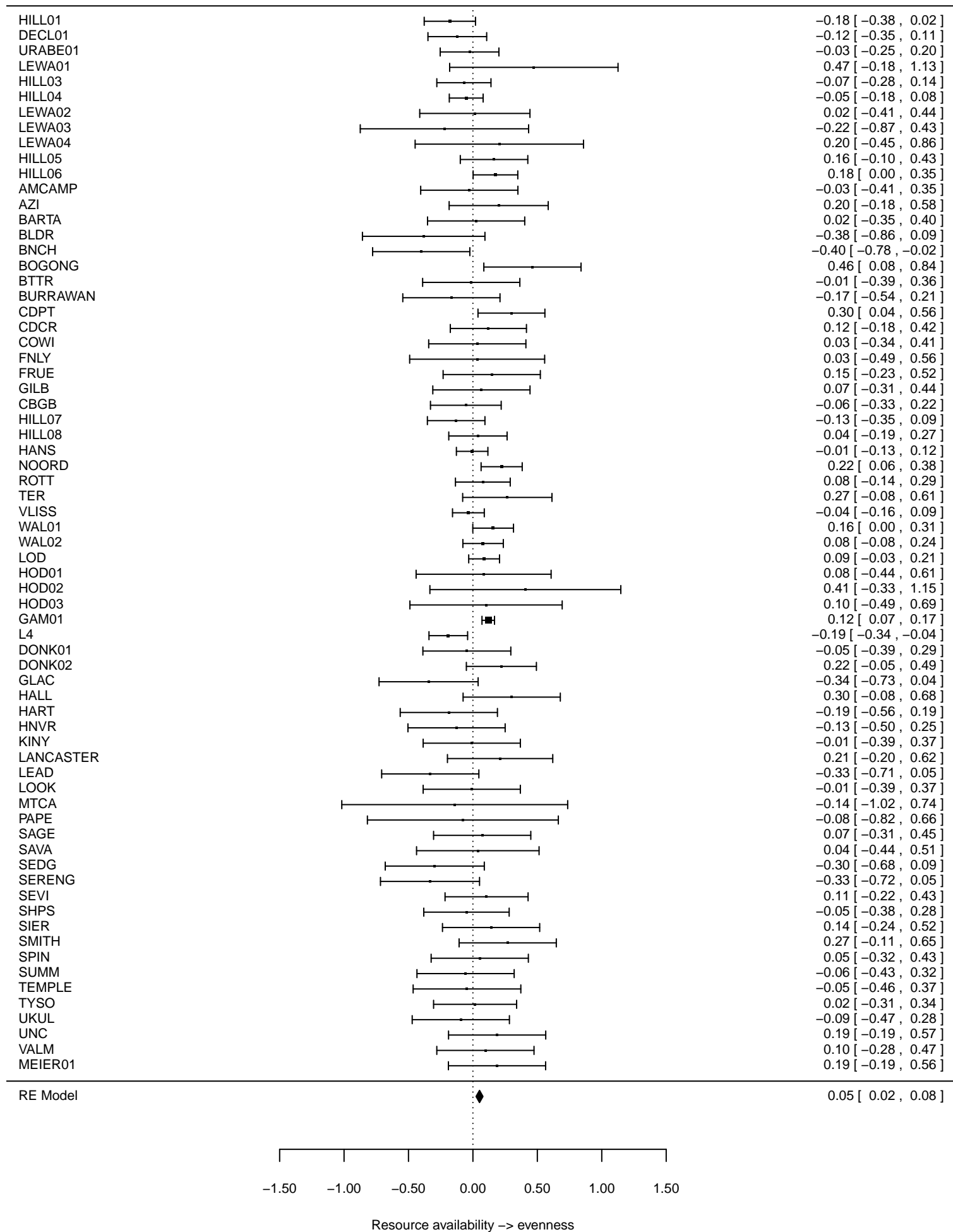


RE Model

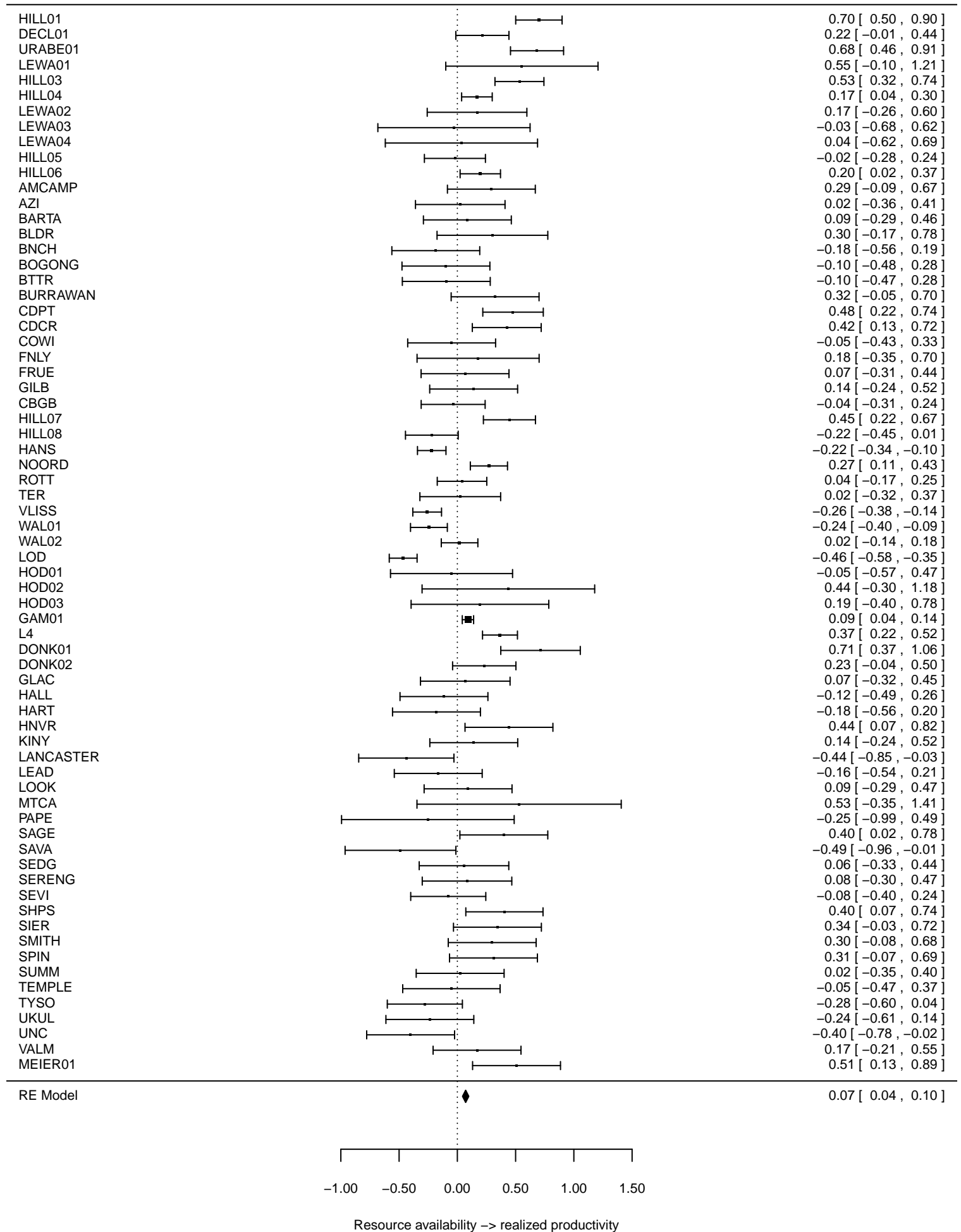
0.18 [ 0.15, 0.20 ]

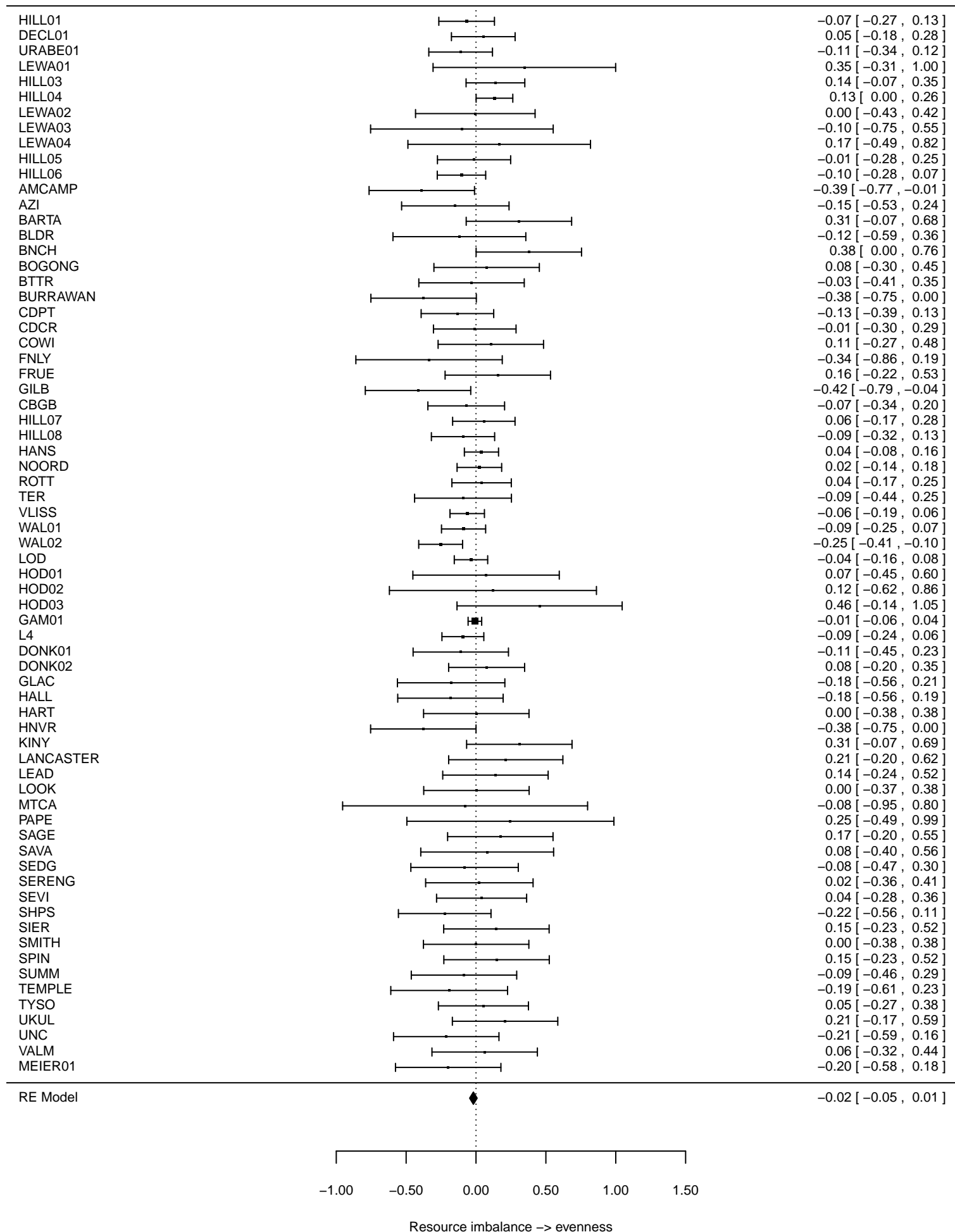


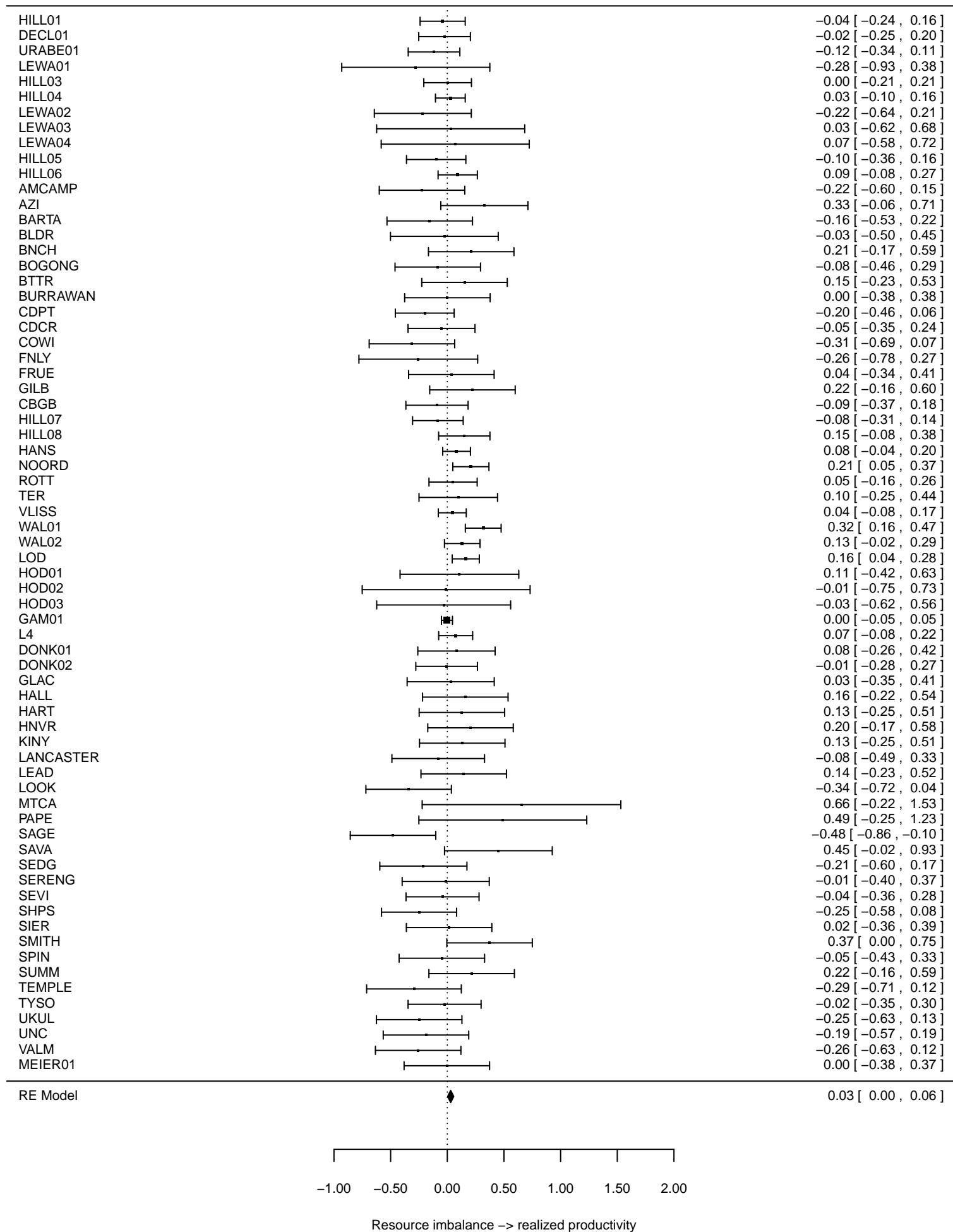
Richness -> realized productivity











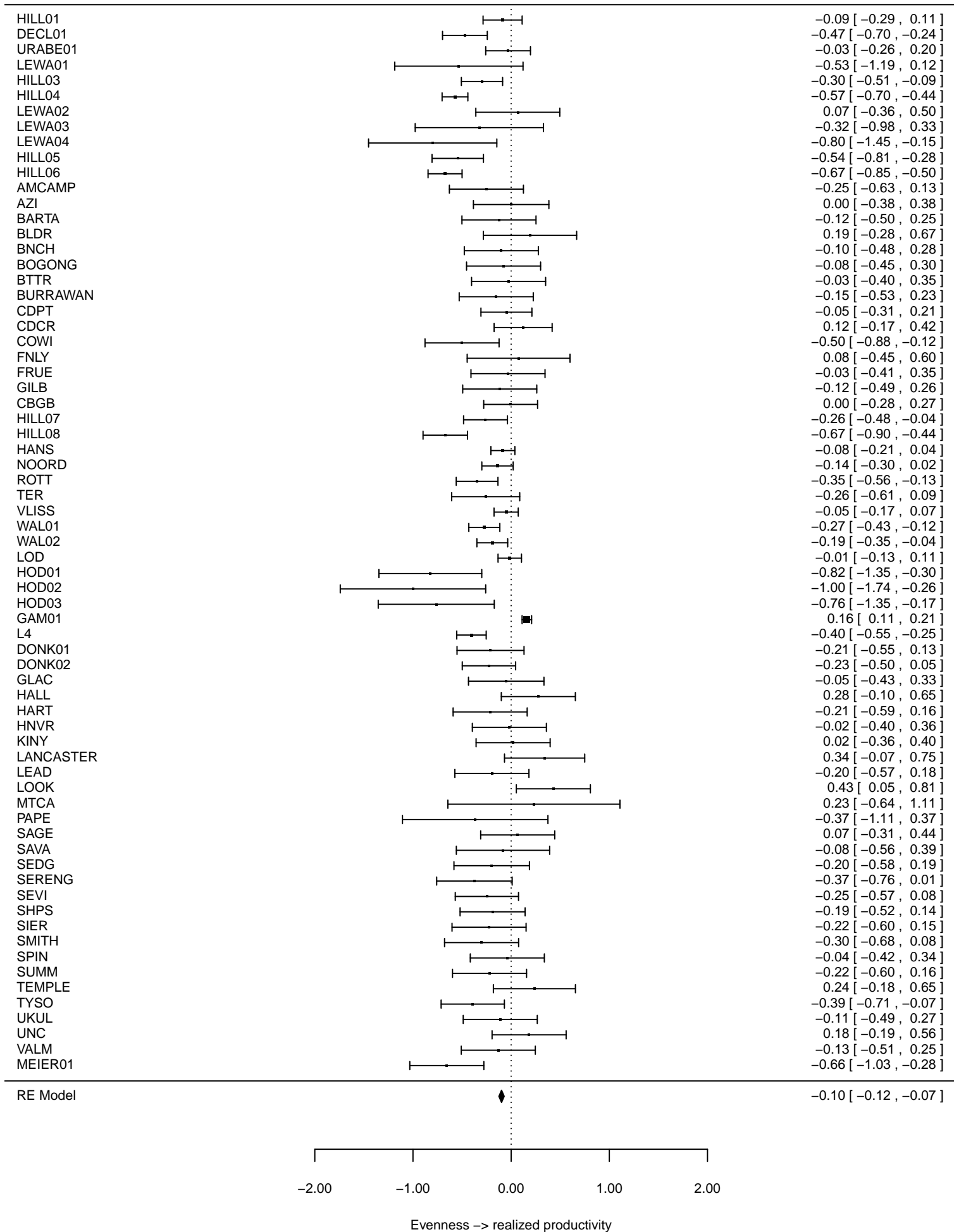


Figure S11. Correlations between effect sizes and diversity range for 78 studies included in the meta-analysis. Srange is richness range; bSstand is effect size of resource imbalance (b) on species richness (S); aSstand is effect size of resource availability (a) on S; SBstand is effect size of S on producer biomass (B).

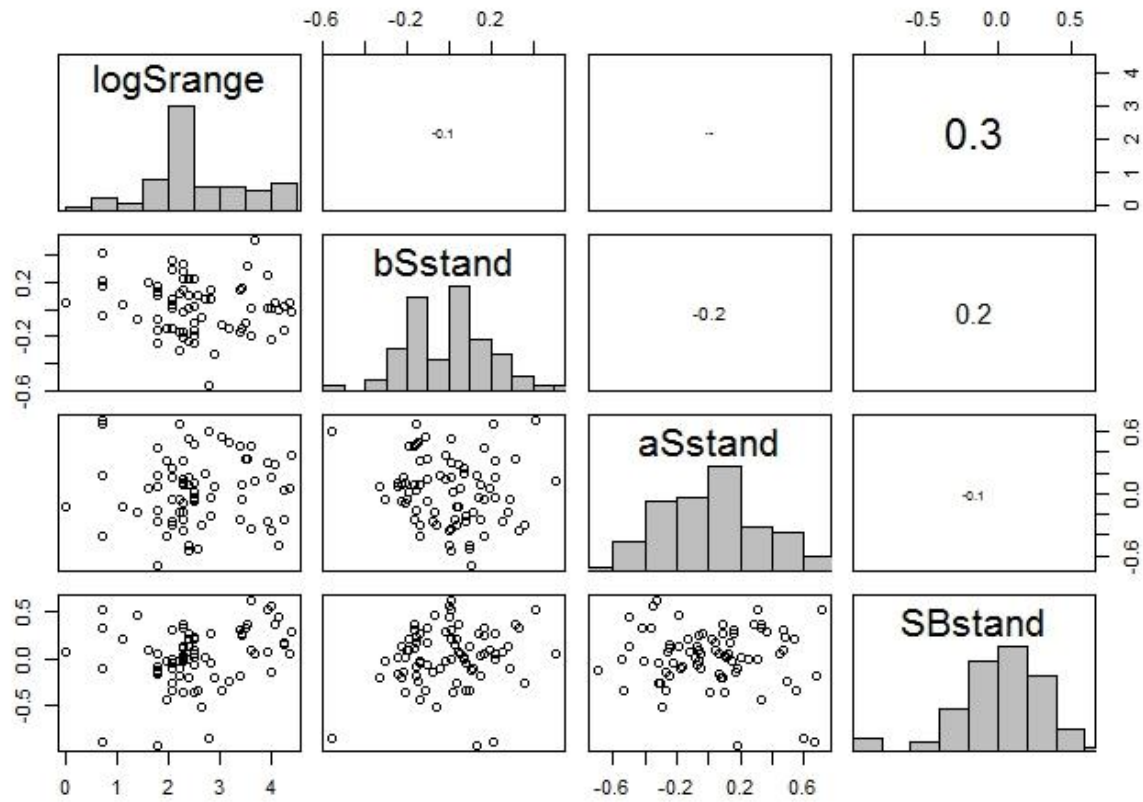


Figure S12. Correlations between effect sizes and resource range for 78 studies included in the meta-analysis. bSstand is effect size of resource imbalance (b) on species richness (S); aSstand is effect size of resource availability (a) on S; SBstand is effect size of S on producer biomass (B); brange is a range of b.

