Multi-trophic guilds respond differently to changing elevation in a subtropical forest

Julia Binkenstein¹,¹⁰, Alexandra-Maria Klein¹, Thorsten Assmann², François Buscot³,⁴, Alexandra Erfmeier⁴,⁵, Keping Ma⁶, Katherina A. Pietsch⁷, Karsten Schmidt⁸, Thomas Scholten⁸, Tesfaye Wubet³,⁴, Helge Brueelheide⁹,⁴, Andreas Schuldt²,⁴,⁹, Michael Staab¹,¹⁰

¹Department of Nature Conservation and Landscape Ecology, Faculty of Environment and Natural Resources, University of Freiburg, Tennenbacher Straße 4, 79106 Freiburg, Germany.

²Leuphana University Lüneburg, Institute of Ecology, Scharnhorststr. 1, 21335 Lüneburg, Germany.

³UFZ-Helmholtz Centre for Environmental Research, Department of Soil Ecology, Theodor-Lieser-Straße 4, 06120 Halle (Saale), Germany.

⁴German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany.

⁵University of Kiel, Institute for Ecosystem Research, Olshausenstrasse 75, 24118 Kiel, Germany.

⁶Chinese Academy of Sciences, Institute of Botany, Beijing 100093, China.

⁷University of Leipzig, Department of Special Botany and Functional Biodiversity, Johannissallee 21-23, 04103 Leipzig, Germany.

⁸University of Tübingen, Department of Geosciences, Chair of Soil Science and Geomorphology, Rümelinstraße 19-23, 72070 Tübingen, Germany.
Martin Luther University Halle-Wittenberg, Institute of Biology/Geobotany and Botanical Garden, Am Kirchtor 1, 06108 Halle, Germany.

Julia Binkenstein and Michael Staab contributed equally to this manuscript.

Corresponding author: Julia Binkenstein, Department of Nature Conservation and Landscape Ecology, Faculty of Environment and Natural Resources, University of Freiburg, Tennenbacher Straße 4, 79106 Freiburg, Germany. E-mail: julia.binkenstein@gmx.de

Decision date: 25-Aug-2017

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: [10.1111/ecog.03086].

'This article is protected by copyright. All rights reserved.'
ABSTRACT

Negative relationships between species richness and elevation are common and attributed to changes in single environmental properties associated to elevation, such as temperature and habitat area. However, research has lacked taxonomic breadth and comprehensive elevation studies that consider multiple groups from different trophic levels are rare. We thus analysed 24 groups of plants, arthropods, and microorganisms grouped into six trophic guilds (predators, detritivores, herbivores, plants, bacteria and fungi) along a relatively short elevational gradient (~600 m) in a subtropical forest in south-east China. The total species richness of all organisms was not related to elevation, nor was the richness of plants, herbivores or microorganisms. However, species richness and abundance in two major trophic guilds of arthropods changed with elevation, which was mediated by changes in elevation-associated habitat properties. Specifically, deadwood mass increased with elevation, which increased detritivore richness indirectly via detritivore abundance, thus supporting the ‘more individuals hypothesis’. In contrast, lower predator richness at higher elevations was directly related to lower mean temperatures, which had no effect on abundance. Our study demonstrates that even along relatively short gradients, elevation can have strong direct and abundance-mediated effects on species richness, but with effects varying from positive to negative signs depending on local resource availability and the characteristics of groups or trophic guilds. If elevation positively influences local environmental properties that benefit a given group, richness can increase towards higher elevations. Thus, the effect of global change in mountainous regions should be evaluated within the local environmental context using multi-taxon approaches.

‘This article is protected by copyright. All rights reserved.’
Keywords: Arthropods, BEF-China, biodiversity, elevational gradient, Gutianshan National Nature Reserve, more individuals hypothesis, multi-trophic diversity
Introduction

Elevational changes in species assemblages and richness caught the attention of naturalists more than a century ago (von Humbold 1849, Wallace 1876). They noted a decrease of biodiversity with increasing elevation, which has since then been confirmed and generalised for many taxonomic groups (Rahbek 1995, McCain and Grytnes 2010). Further studies also reported different diversity patterns along elevational gradients: mid-elevational peaks, low-elevational plateaus or a combination of both, which were closely related to the specific ecology of the studied taxon (e.g. McCain 2007, McCain and Grytnes 2010, Lee and Chun 2015). More recently, elevation gradients and montane biota have received increased attention, as the narrow elevational distribution ranges of many species make them particularly sensitive to global climate change (La Sorte and Jetz 2010, McCain and Colwell 2011).

Conceptually, the four main drivers of variation in species richness along elevational gradients are climate, space, evolutionary history and biotic processes (McCain and Grytnes 2010). Elevation above sea level (a.s.l.) directly affects climatic properties, such as temperature, air pressure and solar radiation, as well as available land area (Körner 2007, Classen et al. 2015, Colwell et al. 2016). Furthermore, elevation can locally (on small scales) be correlated to environmental properties, such as biogeochemical soil properties (e.g. Behrens et al. 2014), which are on larger scales not strongly related to elevation (Körner 2007, Barry 2008). Thus, elevation shapes habitats in manifold ways, e.g. by elevational zonation of vegetation types, and strongly influences species diversity and composition. However, relationships between diversity and elevation may also be influenced by past or present land use and by gradients in
local resource availability e.g. when rare but major weather events dramatically affect local habitats (Parmesan et al. 2000).

Many hypotheses have been postulated to explain changes in species richness along geographical gradients (Rhode 1992). Among them, the ‘more individuals hypothesis’ (Srivastava and Lawton 1998) has received considerable attention (e.g. Hurlbert 2004, Yee and Juliano 2007, McGlynn et al. 2010). This hypothesis is based on species-energy theory (Wright 1983) and assumes a higher probability to have more species in a local community when there are more individuals, a pattern that has empirical support (reviewed by Stirling and Wilsey 2001). Thus, this hypothesis is conceptually linked to resource availability, predicting that more (e.g. food) resources increase species abundances within a community, which allows more species to coexist by facilitating larger population sizes and, consequently, lower local extinction probabilities for each species (Srivastava and Lawton 1998, see also Evans et al. 2005). As along elevation gradients the availability of manifold resources changes, including temperature which is directly related to primary productivity (Körner 2007), ‘more individuals’ mechanisms could contribute to explaining the observed changes in species richness. This makes it interesting to test if changes in species richness are mediated indirectly via species abundance, or if they are directly associated to the environment.

To date, studies examining elevation gradients have predominantly focused on single organism groups (e.g. Rahbek 1997, Sanders et al. 2007, Baur et al. 2014, Classen et al. 2015). Congruence in elevational patterns of species richness from multiple organism groups was only rarely investigated (Kessler et al. 2001, Kitching et al. 2011, Peters et al. 2016). Likewise, most previous studies focused on taxonomic entities (but see Staunton et al. 2011, Röder et al. 2017) instead of addressing groups of
organisms linked by their trophic ecology (i.e. trophic guilds, see Simberloff and Dayan 1991). This is surprising. Given that cross-taxon congruence of species richness is variable (e.g. Westgate et al. 2014), single taxonomic groups are unlikely to be suitable proxies for overall biodiversity patterns. Recently, Schuldt et al. (2015) confirmed the high nonlinearity of diversity relationships among different organism groups for a well-studied subtropical Chinese forest (Bruehleide et al. 2011), and the authors suggested elevation as one of the drivers potentially contributing to spatial changes in diversity in their study system.

Here we provide an in-depth analysis of this unique dataset containing 24 groups of plants, arthropods, and microorganisms (Schuldt et al. 2015) to disentangle the relative impact of elevation-associated effects across trophic levels. In particular, we test if and how the species richness and abundance of trophic guilds covary with elevation-associated environmental variables. Finally, we assess the extent to which the relationship between species richness and the environment is direct (e.g. due to space availability), or rather mediated indirectly via abundance (following the ‘more individuals hypothesis’).

Materials and Methods

Study site

The study was conducted in the Gutianshan National Nature Reserve (GNNR, 29°08’-29°17’ N, 118°02’-118°11’ E), Zhejiang Province, in subtropical south-east China. The region is characterized by mountain ranges (online supplementary material, Fig. A1) and has a monsoon climate. Typical for this region are rare but severe ice storms (Zhou et al. 2011), which open the canopy and are important drivers of natural succession, as

‘This article is protected by copyright. All rights reserved.’
last observed in 2008. The GNNR covers ~8000 ha of evergreen mixed broadleaved forest between 250-1260 m elevation a.s.l. Two dominant canopy tree species are *Castanopsis eyrei* (Champ. ex Benth.) Tutch. (Fagaceae) and *Schima superba* Gardn. et Champ. (Thecaceae). Within the scope of the 'Biodiversity-Ecosystem Functioning (BEF) China' project 27 study plots (30 m × 30 m) were established in 2008 (Bruelheide et al. 2011). The plots were randomly distributed across the accessible parts of the GNNR, covering a wide range of woody (tree and shrub) species richness (25-69 per plot) and tree age (<20 to >80 years). For more details on the study region and plot selection see Bruelheide et al. (2011). A map of the GNNR can be found in Staab et al. (2014).

**Species sampling and trophic guilds**

We used data on 24 organism groups originally compiled by Schuldt et al. (2015) (see also Schuldt et al. 2017). The data include producers (plants), consumers (arthropods) and microorganisms (Table 1), and were classified according to their ecology into six trophic guilds (see online supplementary material). We sampled the trophic guild ‘plants’ by a full-plot tree and shrub inventory and a herb layer inventory in the central 10 m × 10 m of each plot in 2008. Arthropod consumers were sampled quantitatively with a multitude of methods (pitfall traps, beating low vegetation, flight interception traps, reed-filled trap nests for cavity-nesting Hymenoptera, baiting of ants) in various campaigns between 2008-2012. Based on trophic ecology, arthropods were assigned to ‘predators’ (Araneae, Chilopoda, Formicidae, cavity-nesting wasps and their parasitoids), ‘detritivores’ (Cerambycidae, Diplopoda, Scolytidae) and ‘herbivores’ (Lepidoptera, Curculionidae). ‘Bacteria’ (many phyla) and ‘fungi’ (arbuscular and

‘This article is protected by copyright. All rights reserved.’
ectomycorrhiza, saprophytic and pathogenic fungi) were sampled based on DNA sequences (as molecular operational taxonomic units: OTUs) extracted from the upper 0–10 cm of soil cores collected in September 2012. In summary, our exhaustive sampling yielded species richness and abundance data for plants, predators and herbivores, and OTUs (equivalent to species richness, abundance could not be scored for microorganisms, see online supplementary material) for bacteria and fungi. For detailed descriptions of all sampling procedures and DNA barcoding see the online supplementary material.

Environmental variables
The centres of the 27 plots were located between 247 and 869 m a.s.l., which was determined using a digital elevation model based on Shuttle Radar Topography Mission data (SRTM v4, Jarvis et al. 2008) with a resolution of 90 m. Compared to related studies (Kessler et al. 2001, Peters et al. 2016) investigating elevation gradients of several km, this gradient is short. Nevertheless, our elevation gradient is representative for the wider landscape in subtropical south-east China, e.g. for the mountainous areas of the provinces Anhui, Jiangxi, and Zhejiang. Even though the highest peaks in the region exceed 2000 m a.s.l., the great majority of the land surface is lower, completely forested (Fig. A1) and in the range covered by our study. The short gradient has the advantage of a homogenous vegetation along the elevation range covered, resulting in a permeable habitat without elevational zonation, which we see as a particular strength of our study. This allows dividing elevation, which is itself a proxy for changes in environmental conditions, into its properties without biases of habitat zonation that may restrict species ranges and diversity.
Data on two important variables directly related to elevation, mean annual temperature (MAT) and mean available land area (MAA) (Körner 2007; McCain & Grytnes 2010), were collected to test their influence on species richness and abundance. Temperature per plot was aggregated from standard data loggers (online supplementary material). The digital elevation model was used to calculate land area of different elevation bands in 50 m steps ranging from 200 to 900 m a.s.l. within a 20 km radius from the geographic centre of the GNNR. Plots were assigned to the area values of the band they were located in.

Several other variables known to affect species diversity, e.g. of plants and soil microorganisms, may in our study site be related to elevation, including soil properties such as pH and C:N-ratio (Fierer et al. 2011). Thus, we determined soil pH, soil carbon (C) and nitrogen (N) content for each plot.

The successional age of a forest relates to many structural habitat properties affecting species diversity. In anthropogenically influenced forests, successional age can increase with elevation, since low-elevation habitats tend to be more prone to past and present land-use (Kumar and O’Donnell 2009, Vadeboncoeur et al. 2012). To account for this, we quantified the tree age of our study plots (Brueiheide et al. 2011).

One variable frequently related to the successional age of forests is deadwood (e.g. Lasky et al. 2014). The biomass of deadwood can be larger at higher elevations where forests are relatively older if they have been used less by humans, such as in our study area. Deadwood is an important food resource for macro- and microscopic detritivores and known to exert bottom-up effects on their diversity (Floren et al. 2015). Thus, we estimated deadwood mass with an inventory of woody debris conducted in winter 2008/2009.
The aspect (i.e. the orientation of a slope) is related to local microclimate and may be correlated to the impact of meteorological events. Thus, aspect may influence elevational diversity patterns, e.g. if the specific orientation results in (micro-) climates that would be typical for lower or higher elevations. We therefore quantified aspect eastness and northness (Beers et al. 1966) for all plots. More details on environmental variables are described in the online supplementary material.

Statistics
All statistical analyses were conducted in R 2.15.3 (R Development Core Team 2013). To evaluate a priori if linear models are appropriate for the data, we performed Goldfeld-Quandt tests for variance homogeneity and Shapiro-Wilk tests for normal distribution of residuals. Both assumptions were met for all cases after deadwood mass and the abundances of trophic guilds were log-transformed.

To determine the sign of the correlation between elevation and total species richness (all organism groups combined), the richness and abundance of trophic guilds, and the environmental variables, we first calculated simple univariate linear regressions (Table 1). An exception was the relationship between elevation and deadwood mass that was asymptotic and fitted by a Michaelis-Menten-type model using the R-function ‘nls’. We also calculated univariate linear regressions for the relationship between species richness and abundance of the single trophic guilds.

As specified above, elevation is a proxy for environmental changes known to correlate with species richness and abundance. We used multiple linear models with the fixed effects MAT, MAA, deadwood mass, tree age, soil pH, soil C:N ratio, eastness and northness to identify which elevation-associated environmental variables are related
to the species richness and abundance of the six trophic guilds. Those models were calculated with scaled (between 0 and 1) responses to allow comparison of correlations. Similarly, environmental variables were standardized (mean=0, SD=±1). For the analyses of detritivores and fungi, we excluded three young (22-36 years) mid-elevation plots with very little deadwood (i.e. outliers).

The full models contained slightly different sets of predictor variables, because the model structure for each trophic guild was based on general ecological relationships and a priori considerations of correlations between elevation, species richness/abundance and environmental variables (details in online supplementary material and Table A1). For example, detritivore but not predator models contained deadwood mass, as we had early indications that elevation patterns of detritivores are primarily driven by deadwood. Before fitting full models, collinearity among all environmental variables was assessed. In case two environmental variables were correlated with Spearman's ρ>0.7 (Dormann et al. 2013) we retained the variable that is in our opinion ecologically more directly interpretable. We used the function ‘dredge’ (R-package 'MuMIn', Barton 2013) to find minimal most-parsimonious models with lowest AICc for each trophic guild (Burnham et al. 2011).

Informed by the a priori information obtained from the minimal richness models we performed path analyses (PA) in the R-package ‘lavaan’ (Rosseel 2012) to disentangle direct and indirect effects of the directly elevation-associated environmental variables MAT and MAA and of guild-specific environmental variables. For PA, all richness/abundance values and environmental variables were standardized (mean=0, SD=±1). Environmental variables included in the guild-specific PAs were based on the minimal (i.e. most parsimonious) richness models and thus differed among guilds.
Except for bacteria and fungi, species richness and abundance were included in the same guild-specific PAs, to test for the predictions of the ‘more individuals hypothesis’. Doing so allows disentangling if changes in species richness are directly related to the environment, or if they are indirect and caused by changes in species abundance.

More details on statistical analyses, including information on variable selection and model selection, are provided in the online supplementary material.

**Results**

The species richness and abundance of two trophic guilds, predators and detritivores, correlated with elevation (Table 1). Predator richness decreased with increasing elevation ($p=0.002$; Fig. 1a), while detritivore richness showed the opposite pattern and increased ($p<0.001$; Fig. 1b). The richness of plants, herbivores, bacteria and fungi did not change with elevation, as did total species richness, neither when including bacteria and fungi, nor when excluding microorganisms (see Table 1 for summary statistics of all linear regressions). Individual regressions of all 24 organism groups were mostly unrelated to elevation (see online supplementary material, Table A2). Similar to species richness, predator abundance decreased towards higher elevations ($p=0.028$; Fig. 1c), whereas detritivore abundance increased ($p=0.012$, Fig. 1d). For those two trophic guilds, there was a strong positive relationship between species richness and abundance (predators: $p=0.006$, Fig. 3a; detritivores: $p<0.001$, Fig. 3b; see online supplementary material Table A3). Abundances of the other trophic guilds were not related to species richness or elevation (Fig. A2).

Several of the environmental variables were also related to elevation. MAT, MAA ($p<0.001$; Fig. 2a) and soil pH ($p=0.017$) decreased with increasing elevation.
(Table 1). In contrast, deadwood mass increased (Michaelis-Menten model: $p<0.001$; Table 1; Fig. 2b). The aspect components and tree age were not related to elevation.

Dividing elevation into its influences on the environment, we found effects of elevation-related environmental variables on the species richness and abundance of predators and detritivores. Predator richness increased with MAT ($p=0.002$; Fig. 3c; see Table 2 for summary results of the minimal models for each trophic guild) and was best explained by a minimal model containing only this variable. Accordingly, the best model for predator abundance contained MAT as the only parameter, albeit as non-significant trend ($p=0.097$; Fig. 3e). Detritivore richness was negatively affected by eastness ($p=0.053$) but increased with tree age ($p=0.017$) and deadwood mass ($p=0.061$; Fig. 3d), which was the only variable retained in the detritivore abundance model (positive relationship, $p<0.001$; Fig. 3f).

Species richness of the other trophic guilds was not significantly related to elevation-associated variables but to other environmental variables in plants and fungi (Table 2). Plant richness was positively associated to northness ($p=0.046$), while the minimal plant abundance model contained a positive influence of eastness ($p=0.028$) and a negative influence of tree age ($p<0.001$). Herbivore richness and abundance could not be explained by any environmental variable, which was likewise the case for bacterial OTU richness. In contrast, fungi OTU richness increased with tree age ($p<0.001$) and northness ($p=0.042$) and decreased with eastness ($p=0.024$). Soil pH and C:N ratio were never retained in a minimal model (Table 2; Table A1).

The PAs indicated how elevation indirectly affected trophic guilds and strengthened the results obtained by the linear models (Fig. 4). Predator richness decreased with elevation via MAT ($p=0.023$) but not via MAA (Fig. 4a). Predator
abundance, in contrast, was not affected by elevation via both variables but had a positive effect on predator species richness ($p=0.007$; Fig. 4a). Detritivore richness was indirectly affected by elevation via tree age ($p=0.012$; Fig. 4b). This variable also had a positive effect on deadwood mass ($p=0.004$), which was not significantly related to elevation in the PA ($p=0.059$; note that the detritivore analyses are based on a reduced dataset) and had no direct effect on detritivore richness. However, deadwood had an indirect positive effect on species richness that was mediated by abundance ($p=0.019$), which was, in turn, strongly and positively affecting species richness ($p<0.001$). Additionally, eastness had a negative effect on detritivore abundance ($p=0.015$; Fig 4b) but not on species richness. Fungal species richness was positively related to tree age ($p=0.004$; Fig. A3) via elevation ($p=0.042$) and was associated with both aspect components, i.e. positively with northness ($p=0.022$) and negatively with eastness ($p=0.026$). Neither MAT nor MAA were directly or indirectly (via abundance) associated with herbivore, plant, bacteria or fungi richness ($p>0.05$ in all cases; Fig. A3), but plant abundance decreased with elevation via MAA ($p=0.039$) without affecting plant species richness.

Discussion

Our study shows that even along short elevation gradients, species richness and abundance can strongly change with elevation. While the total species community was not related to elevation, two functionally important trophic guilds, predators and detritivores, showed contrasting patterns. These could be attributed to elevation-induced changes in MAT, tree age and deadwood mass, which affected species richness either directly or, agreeing with a ‘more individuals’ mechanism, indirectly via abundance.
Globally, temperature and space availability are prominent environmental properties affecting species along elevational gradients across organism groups and localities (McCain & Grytnes 2010). Although temperature and available area are, as expected, closely tied to elevation in the GNNR, our PA indicated that statistically the ca. 3°C difference in MAT among plots, but not area, explains predator species richness. Being mobile ectothermic organisms in a high trophic level, the activity and foraging of those arthropods depends, among other factors, on ambient temperature. At the community level, higher foraging activity and efficiency in warmer low-elevation environments, potentially also affecting food web structure, is likely (Roslin et al. 2017), as it has recently been demonstrated for host-parasitoid systems in the GNNR (Staab et al. 2016) and subtropical Australia (Maunsell et al. 2015). Lower temperatures at higher elevations can limit resource accessibility, resulting in lower numbers of individuals and lower overall diversity of ectothermic species in relatively cooler regions (e.g. Sanders et al. 2007). Therefore, we expected an abundance-driven relationship, following a 'more-individuals hypothesis' mechanism (Srivastava and Lawton 1998). While predator richness increased with predator abundance, statistical support for relationships between abundance and the environment was weak. This might be related to the high share of ants (72.8% of predator individuals), as aggregated ant abundances could be biased by the variable individual numbers among colonies (Gotelli et al. 2011). However, in congruence with the positive relationship between predator richness and MAT, it is more likely that temperature may directly affect predator species richness, for example if species-specific physiological limits preclude certain species of the local species pool from the relatively cooler sites at higher elevations (Hawkins et al. 2003). Furthermore, if general prey availability would be reduced at

'This article is protected by copyright. All rights reserved.'
higher elevations this could likewise contribute to lower predator richness (e.g. Siemann et al. 1998).

It might seem surprising that detritivore species richness and abundance increased with elevation, a pattern that has only rarely been recorded, for example in few studies on frogs and plants (reviewed in McCain & Grytnes 2010). The observed increase was neither determined by temperature nor by area. We thus re-evaluated the large body of data available for the GNNR (Bruelheide et al. 2011), because the sign of the resulting correlations strongly contradicted accepted ecological knowledge. We found that successional age, in addition to having a direct positive effect on detritivore richness, also mediated the general relationship between elevation and detritivores. In our study region, high-elevation forests tend to be more remote from settlements and have, compared to lower-elevation plots, historically been less influenced by anthropogenic activities. Successional age influences manifold properties within a forest stand, including organic biomass and microhabitat diversity (Fenton and Bergeron 2008, Klimes et al. 2012). A microhabitat that accumulates with succession but can itself also be related to elevation is deadwood. For many detritivores, deadwood provides shelter and the larvae or imagines (or both) feed on deadwood (saproxylics). The larger deadwood amount at higher elevations caused a bottom-up effect on detritivore richness (see meta-analysis by Lassauce et al. 2011) by increasing detritivore abundance, which is supported by the indirect effect of deadwood on species richness via abundance. This points to a 'more-individuals hypothesis' mechanism: more deadwood increases resource availability for saproxylic arthropods, which translates into larger individual numbers and more coexisting species (Srivastava and Lawton 1998, see also Hurlbert 2004, Yee and Juliano 2007). Nevertheless, high deadwood

‘This article is protected by copyright. All rights reserved.’
mass could also increase resource diversity and therefore support specialized species depending on particular deadwood types or decay stages (McClain et al. 2016). Alternatively, higher detritivore diversity in the higher-elevation plots may also be related to the lower predator richness and predation pressure (sensu Siemann et al. 1998, Roslin et al. 2017).

Apart from successional age, deadwood mass may in the GNNR be interwoven with elevation by a further factor: the susceptibility to ice storms (Nadrowski et al. 2014). In subtropical China, rare but detrimental ice storms dramatically increase deadwood mass, as observed in early 2008. Such storms occur on average every 50 to 100 years and are important for natural succession in evergreen broadleaved Chinese forests (King et al. 2005, Zhou et al. 2011). Under the load of snow and ice, branches and entire stems break, which increases deadwood mass. Breakage is higher in cooler and more exposed high elevation sites that are also characterized by older trees (Nadrowski et al. 2014). In combination, this contributes to the positive relationship between elevation and deadwood likely explaining the unusual increase of detritivores. However, elevation effects might be partially confounded by the degree of anthropogenic disturbance, which is almost invariably the case in Chinese forests and elsewhere. The higher-elevation plots in our study region tend to be more remote from settlements and have, compared to lower-elevation plots, historically been less influenced by anthropogenic activities such as logging (Bruelheide et al. 2011, see also López-Pujol et al. 2006). Thus, the positive relationship between elevation and detritivores cannot be extrapolated for elevation gradients in general, but it exemplifies the importance to consider specific characteristics of the local environment when studying the response of organism groups or trophic guilds to elevation.
Our study is one of the first to analyse the diversity of soil microorganisms in relation to elevation. While former studies found various patterns of fungal richness along elevation gradients, which were mostly caused by changes in soil characteristics (e.g. Siles and Margesin 2016), we found a positive relationship via tree age, similar to detritivores. However, in contrast to detritivores, the main effect of tree age on fungi richness was not mediated by deadwood. Rather, fungi were probably related to the higher habitat heterogeneity and biomass in older forests (Bachelot et al. 2016). With the exception of the expected higher plant individual numbers in the relatively younger low elevation plots, we found no associations with elevation for plants, herbivores and bacteria (compare Fierer et al. 2011). The effects of aspect on trophic groups indicate that in subtropical China topographic orientation can be important for understanding elevation gradients. This is potentially related to the monsoon climate, which is strongly shaped by the north-easterly trade winds, making slope exposition an important habitat property.

Recently, Schuldt et al. (2015) demonstrated that in topographically heterogeneous regions relations among the species richness of different organism groups are nonlinear across spatial scales and we offer further insight into these findings. The larger an area is, the more likely it is to encompass habitat at different elevations, and, as shown by our study, trophic guilds can be non-uniformly related to elevation-associated changes of the environment. In mountainous regions, as opposed to topographically homogenous ecosystems (e.g. Basset et al. 2012), such differing elevational diversity might contribute to the often observed non-linearity in taxonomic diversity congruence (Staunton et al. 2011, Westgate et al. 2014, Schuldt et al. 2015), to which abundance driven changes in species richness at small spatial scales might

‘This article is protected by copyright. All rights reserved.’
contribute. Furthermore, our study demonstrates the necessity to perform comprehensive case-by-case assessments of individual organism groups (see also Kitching et al. 2011, Nakamura et al. 2016) and to include trophic ecology when studying elevation gradients. This is particularly important considering the many threats (including climate change) organisms in mountainous areas are facing (McCain & Colwell 2011). Otherwise evaluating possible threats may be biased by taxon-specific elevation patterns, which may not be representative for entire guilds and the entire ecosystem.

Acknowledgements

We thank the administration of the Gutianshan National Nature Reserve for generously granting research permissions and for enabling BEF-China. Gathering such a comprehensive dataset would not have been possible without the help of numerous students and local assistants; Fang Teng is particularly acknowledged for sharing his extensive knowledge. Bernhard Schmid, Werner Härdtle, Christian Wirth, Jürgen Bauhus, Sabine Both, and Xiaojuan Liu provided a great deal of intellectual and logistic support. The manuscript text benefited considerably from constructive input by the subject editor, an anonymous reviewer and Roger Kitching. We are grateful to Charles Nock for English language editing. This study was funded by the German Research Foundation (DFG FOR 891/1, 891/2), the Sino-German Centre for Research Promotion (GZ 524, 592, 698, 699, 785 and 1020), and the National Science Foundation of China (NSFC 30710103907 and 30930005). JB was supported by equality funds of the German Research Foundation.

‘This article is protected by copyright. All rights reserved.’
References


'This article is protected by copyright. All rights reserved.'


'This article is protected by copyright. All rights reserved.'


‘This article is protected by copyright. All rights reserved.’


Nadrowski, K. et al. 2014. Tree species traits but not diversity mitigate stem breakage in a subtropical forest following a rare and extreme ice storm. - PLOS ONE 9: e96022.


‘This article is protected by copyright. All rights reserved.’


Schuldt, A. et al. 2015. Multitrophic diversity in a biodiverse forest is highly nonlinear across spatial scales. - Nat. Commun. 6: 10169.


'This article is protected by copyright. All rights reserved.'


‘This article is protected by copyright. All rights reserved.’


Table Legends

**Table 1** Results of linear regressions showing raw (neither standardised nor scaled) results of the correlation between elevation and species richness/abundance as well as environmental variables chosen for their potential relevance for trophic guilds.

<table>
<thead>
<tr>
<th>Richness, abundance and environmental variables</th>
<th>Slope ± SE</th>
<th>Intercept ± SE</th>
<th>t</th>
<th>df</th>
<th>p</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Richness</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total richness incl. microorganisms</td>
<td>0.223 ± 0.173</td>
<td>2362.546 ± 97.369</td>
<td>1.291</td>
<td>25</td>
<td>0.209</td>
<td>0.062</td>
</tr>
<tr>
<td>Total richness excl. microorganisms</td>
<td>0.019 ± 0.021</td>
<td>173.39 ± 11.714</td>
<td>0.918</td>
<td>25</td>
<td>0.368</td>
<td>0.033</td>
</tr>
<tr>
<td>Richness predators</td>
<td>-0.029 ± 0.008</td>
<td>100.503 ± 4.72</td>
<td>-3.411</td>
<td>25</td>
<td><strong>0.002</strong></td>
<td>0.318</td>
</tr>
<tr>
<td>Richness detritivores¹</td>
<td>0.038 ± 0.009</td>
<td>13.238 ± 4.738</td>
<td>4.487</td>
<td>22</td>
<td><strong>&lt;0.001</strong></td>
<td>0.478</td>
</tr>
<tr>
<td>Richness herbivores</td>
<td>0.002 ± 0.004</td>
<td>16.192 ± 2.346</td>
<td>0.558</td>
<td>25</td>
<td>0.581</td>
<td>0.012</td>
</tr>
<tr>
<td>Richness plants</td>
<td>0.013 ± 0.013</td>
<td>42.181 ± 7.592</td>
<td>0.970</td>
<td>25</td>
<td>0.341</td>
<td>0.036</td>
</tr>
<tr>
<td>Richness bacteria</td>
<td>0.105 ± 0.133</td>
<td>1785.025 ± 74.825</td>
<td>0.790</td>
<td>25</td>
<td>0.437</td>
<td>0.024</td>
</tr>
<tr>
<td>Richness fungi¹</td>
<td>0.103 ± 0.057</td>
<td>404.539 ± 31.591</td>
<td>1.810</td>
<td>22</td>
<td>0.084</td>
<td>0.130</td>
</tr>
<tr>
<td><strong>Abundance</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abundance predators²</td>
<td>&lt;0.001 ± &lt;0.001</td>
<td>7.477 ± 0.187</td>
<td>-2.326</td>
<td>25</td>
<td><strong>0.028</strong></td>
<td>0.178</td>
</tr>
<tr>
<td>Abundance detritivores¹,²</td>
<td>0.003 ± 0.001</td>
<td>4.537 ± 0.579</td>
<td>2.746</td>
<td>22</td>
<td><strong>0.012</strong></td>
<td>0.255</td>
</tr>
<tr>
<td>Abundance herbivores²</td>
<td>&lt;0.001 ± &lt;0.001</td>
<td>4.208 ± 0.437</td>
<td>-1.099</td>
<td>25</td>
<td>0.282</td>
<td>0.046</td>
</tr>
<tr>
<td>Abundance plants²</td>
<td>&lt;0.001 ± &lt;0.001</td>
<td>7.066 ± 0.421</td>
<td>-0.809</td>
<td>25</td>
<td>0.426</td>
<td>0.026</td>
</tr>
<tr>
<td><strong>Environment</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MAT</td>
<td>-0.004 ± &lt;0.001</td>
<td>19.215 ± 0.211</td>
<td>-10.787</td>
<td>25</td>
<td><strong>&lt;0.001</strong></td>
<td>0.823</td>
</tr>
<tr>
<td>MAA</td>
<td>-0.331 ± 0.016</td>
<td>273.357 ± 8.786</td>
<td>-21.259</td>
<td>25</td>
<td><strong>&lt;0.001</strong></td>
<td>0.948</td>
</tr>
<tr>
<td>Deadwood mass¹,²,³</td>
<td>8.965 ± 1.114</td>
<td>80.427 ± 40.260</td>
<td>2.675</td>
<td>22</td>
<td><strong>&lt;0.001</strong></td>
<td>0.262</td>
</tr>
<tr>
<td>Soil pH</td>
<td>&lt;0.001 ± &lt;0.001</td>
<td>4.228 ± 0.151</td>
<td>-2.566</td>
<td>25</td>
<td><strong>0.017</strong></td>
<td>0.209</td>
</tr>
<tr>
<td>Soil C:N ratio</td>
<td>-0.001 ± 0.002</td>
<td>18.733 ± 1.157</td>
<td>-0.547</td>
<td>25</td>
<td>0.589</td>
<td>0.012</td>
</tr>
<tr>
<td>Northness</td>
<td>&lt;0.001 ± &lt;0.001</td>
<td>-0.547 ± 0.472</td>
<td>1.043</td>
<td>25</td>
<td>0.307</td>
<td>0.042</td>
</tr>
<tr>
<td>Eastness</td>
<td>&lt;0.001 ± &lt;0.001</td>
<td>0.258 ± 0.455</td>
<td>-1.015</td>
<td>25</td>
<td>0.320</td>
<td>0.040</td>
</tr>
<tr>
<td>Tree age</td>
<td>0.035 ± 0.030</td>
<td>48.717 ± 17.006</td>
<td>1.149</td>
<td>25</td>
<td>0.261</td>
<td>0.050</td>
</tr>
</tbody>
</table>

Significant p-values (p<0.05) are indicated in bold.

¹ Based on a dataset from which three plots were removed (for details see Materials and Methods).

² Based on log-transformed data.

This article is protected by copyright. All rights reserved.'
Statistics are based on a Michaelis-Menten model (see text); column slope represents $V_{\text{max}}$ and column intercept $K_{\text{m}}$. 

"This article is protected by copyright. All rights reserved."
**Table 2** Summary results of minimal linear models for each trophic guild after AICc-based model selection. Shown are model estimates ± SE of environmental variables included as predictors in the minimal models, t-values, p-values and adjusted $R^2$ of the model. All reported analyses are based on scaled response (between 0 and 1) and standardized environmental variables (mean=0, SD=±1).

<table>
<thead>
<tr>
<th>Best predictors of trophic guild richness and abundance</th>
<th>Estimate ± SE</th>
<th>t</th>
<th>p</th>
<th>adj. $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Predators</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Richness</td>
<td>MAT</td>
<td>0.049 ± 0.015</td>
<td>3.371</td>
<td><strong>0.002</strong></td>
</tr>
<tr>
<td>Abundance</td>
<td>MAT</td>
<td>0.013 ± 0.008</td>
<td>1.724</td>
<td>0.097</td>
</tr>
<tr>
<td><strong>Detritivores</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Richness</td>
<td>Tree age</td>
<td>0.079 ± 0.030</td>
<td>2.599</td>
<td><strong>0.017</strong></td>
</tr>
<tr>
<td></td>
<td>Eastness</td>
<td>-0.052 ± 0.025</td>
<td>-2.053</td>
<td>0.053</td>
</tr>
<tr>
<td></td>
<td>Deadwood mass</td>
<td>0.063 ± 0.032</td>
<td>1.987</td>
<td>0.061</td>
</tr>
<tr>
<td>Abundance</td>
<td>Deadwood mass</td>
<td>0.084 ± 0.021</td>
<td>3.925</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><strong>Herbivores</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Richness &amp; Abundance</td>
<td>none</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td><strong>Plants</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Richness</td>
<td>Northness</td>
<td>0.058 ± 0.038</td>
<td>2.096</td>
<td><strong>0.046</strong></td>
</tr>
<tr>
<td>Abundance</td>
<td>Tree age</td>
<td>-0.047 ± 0.011</td>
<td>-4.208</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Eastness</td>
<td>0.026 ± 0.011</td>
<td>2.343</td>
<td><strong>0.028</strong></td>
</tr>
<tr>
<td><strong>Bacteria</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Richness</td>
<td>none</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td><strong>Fungi</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Richness</td>
<td>Tree age</td>
<td>0.052 ± 0.013</td>
<td>3.901</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Eastness</td>
<td>-0.033 ± 0.013</td>
<td>-2.452</td>
<td><strong>0.024</strong></td>
</tr>
<tr>
<td></td>
<td>Northness</td>
<td>0.029 ± 0.013</td>
<td>2.171</td>
<td><strong>0.042</strong></td>
</tr>
</tbody>
</table>

Significant $p$-values ($p<0.05$) are indicated in bold.

1 Based on a dataset from which three plots were removed (for details see Materials and Methods).

2 Based on log-transformed data.

'This article is protected by copyright. All rights reserved.'
Figure legends

Figure 1 Relationships between species richness and abundance and elevation. Predator (a, c) and detritivore (b, d) species richness and abundance changed along an elevational gradient in the GNNR in subtropical China. Shown are linear regression lines (significant at $p<0.05$) and 95% CI. The open points in (b) and (d) indicate three plots, which were removed from the dataset when analysing detritivores (for details see Materials and Methods). Note that the y-axes in (c) and (d) are log-scaled and that species richness and abundance within both trophic guilds were significantly related (predators: $p=0.006$, Fig. 3a; detritivores: $p<0.001$, Fig. 3b).
**Figure 2** Relationships between environmental variables and elevation. MAT (a) decreased with elevation, whereas deadwood mass (b) increased with higher elevations, saturating around 500 m a.s.l. \(p<0.05\). Shown are a linear regression line with 95% CI (a) and a Michaelis-Menten curve (b). The open points in (b) indicate three plots, which were removed from the dataset when analysing detritivores (for details see Materials and Methods). Note that the y-axis in (b) is log-scaled.
Figure 3 Relationships between species richness and abundance and environmental variables. Predator (a) and detritivore (b) species richness increased each with the abundance of the respective trophic guild. Furthermore, predator species richness (c) increased with MAT as did predator abundance (e, albeit not significantly). In turn, detritivore species richness (d) and abundance (f) were positively related to deadwood mass. Lines show linear regressions with 95% CI (only for $p<0.05$; based on variables retained in the respective most parsimonious models for (c), (d), (e) and (f)). The open points in (b), (d) and (f) indicate three plots, which were removed from the dataset when analysing detritivores (for details see Materials and Methods). Note that the y-axes in (e) and (f) and the x-axes in (a), (b), (d) and (f) are log-scaled.
**Figure 4** Path models showing how elevation affects species richness of predators (a) and detritivores (b) directly via mean annual temperature (MAT), mean available area (MAA), and other environmental variables, or indirectly via the effects of the environment on abundance. Numbers next to arrows give the standardized path coefficients. Significant causal paths are indicated with full arrows, non-significant paths with dashed arrows. Green arrows indicate positive relationships, blue arrows negative relationships. Guild-specific predictor variables are shown in unfilled boxes. Path model (b) is based on a reduced data set from which three plots were removed (for details see Materials and Methods). Significances were obtained from z-tests and are *** $p<0.001$, ** $p<0.01$, * $p<0.05$, and (.) $p<0.1$. 

This article is protected by copyright. All rights reserved.