

Functional diversity in a subtropical forest based on anatomical and morphological species traits

Dissertation

zur Erlangung des akademischen Grades
doctor rerum naturalium (Dr. rer. nat.)

vorgelegt der
Naturwissenschaftlichen Fakultät I
Biowissenschaften
der Martin-Luther-Universität Halle-Wittenberg



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Verteidigt in Halle (Institut für Biologie/Geobotanik & Botanischer Garten) am 20.12.2011

Meinem Bruder gewidmet

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Every tree is numbered, but who can count them ?!

(The RZA of Wu-Tang Clan in *Sunlight*)

SUMMARY

Trait-based approaches have become an essential field in biodiversity research. In this dissertation, anatomical and morphological leaf and wood traits were measured with the objective to investigate, on the one hand, trait-environment relationships of community mean trait values, and on the other hand, trait variation among species within communities.

Along a succession series it was analysed which traits were correlated with successional stage and it was asked which traits and which environmental factors were particularly important for the trait-environment relationship. Furthermore, this dissertation presents a new trait-based approach to disentangle the effects of species richness, species identity and trait identity on *functional diversity* (FD) in communities using null models. Thus, FD assessed by Rao's Q (quadratic entropy), was partitioned into trait *dissimilarity* (TD = mean distance between all traits in the community) and *functional evenness* (FE = the ratio of the observed FD value to a FD value that is obtained by assuming equal distances among all traits). It was also the aim of this thesis to relate mean responses and plasticity indices to species characteristics such as leaf habit, ontogenetic stage and local frequency in forest communities.

In a subtropical broadleaved forest in Zhejiang Province (S-E China), a series of plots in a secondary forest was established, stratified by successional stages. On a total of 27 plots, all tree and shrub individuals taller than one meter were recorded and 16,120 individuals of 148 species representing 46 families encountered. In total, a dataset of 26 leaf and 29 wood traits was generated. Additionally, a greenhouse experiment with 36 deciduous and 35 evergreen tree and shrub species was carried out to test the influence of light and nutrient availability on trait expression and plasticity of the species. Furthermore, to analyse the impact of ontogenetic stage and local frequency, the greenhouse responses were compared with adult individuals of 46 species that also occurred in the field.

A Fourth Corner Analysis revealed that many leaf and wood traits were tightly related to the successional gradient. Most relationships to leaf traits followed the leaf economics spectrum with decreasing specific leaf area and leaf nutrient contents with successional time. Compared to biotic community characteristics (e.g. plant density), abiotic environmental variables (e.g. inclination of the plots) showed only marginal correlations to leaf and wood traits. In addition, it was found that the link between the communities and traits was less important in explaining trait-environment relationships than the link between environment and the species.

Concerning FD, the analyses of this dissertation failed to detect any successional trend. Instead, trait dissimilarity decreased. The community compensated the loss in TD by distributing the remaining traits more evenly among the resident species, seen in increasing FE values. The null models revealed equivalence among species in trait space. Thus, it seems to be irrelevant which species were present in the different successional stages, which provides an explanation why the species richness increases in these subtropical forests with time.

In the greenhouse experiment, mean trait values and plasticity indices showed significant differences between full shade and full light treatments as well as between low and high nutrient supply. Moreover, it was encountered that leaf habit had a strong impact on mean responses and on phenotypic plasticity. These results contribute to the current debate of distinctions in characteristics of deciduous and evergreen species and to the differentiation between passive and active adjustment of the phenotype, as active responses to decreasing light availability were best captured by allocation variables such as node density. Concerning ontogenetic stage, no significant correlation in growth rates between young individuals in the greenhouse and adults trees in the field could be detected. In contrast, significant relationships of species abundance in the field were encountered with mean responses of dry weight of total biomass as well as with number of nodes per unit shoot length. Furthermore, phenotypic plasticity of dry weight of total biomass tended to decrease with increasing abundance.

In summary, this dissertation fully confirmed the role of traits associated with the leaf economics spectrum in subtropical forests as being the most responsive ones to environmental gradients. Furthermore, the here presented results support the hypothesis that most of the species in the subtropical forest are functionally equivalent. Although certain trait values are clearly filtered during succession, environmental filtering is mainly brought about by biotic interactions rather than by abiotic site conditions. In addition, the weak correlations between greenhouse and field data imply ontogenetic trait shifts of the woody species in this subtropical forest, whereas the linkage to abundance suggests that species that are locally abundant tend to be less “plastic” than locally rare species.

ZUSAMMENFASSUNG

Studien, die auf Pflanzenmerkmalen beruhen, sind zu einem essentiellen Bestandteil der Biodiversitätsforschung geworden. In der vorliegenden Dissertation wurden anatomische und morphologische Blatt- und Holzeigenschaften gemessen, zum einen mit dem Ziel, die Beziehungen solcher über eine Pflanzengesellschaft gemittelten Merkmale zu Umweltvariablen zu ermitteln, und zum anderen, um die Merkmalsvariation zwischen Arten innerhalb einer Pflanzengesellschaft zu bestimmen.

Entlang einer Sukzessionsreihe wurde analysiert, welche der Merkmale mit dem Sukzessionsgrad korrelieren und welche der Pflanzen- und Umweltcharakteristika besonders wichtig für den Merkmal-Umwelt-Zusammenhang sind. Darüber hinaus präsentiert diese Dissertation einen neuen, auf Pflanzenmerkmalen basierenden Ansatz, um den Einfluss von Artenreichtum, Arten- und Merkmalsidentität auf *funktionelle Diversität* (FD) in Pflanzengemeinschaften zu bestimmen. FD wurde dabei auf Grundlage von Rao's Q (quadratische Entropie) berechnet und in Nullmodellen in *Merkmalsunterschiedlichkeit* (TD = mittlerer Abstand zwischen allen Arten in der Pflanzengemeinschaft) und *funktionelle Gleichmäßigkeit* unterteilt (FE = das Verhältnis von beobachteten FD-Werten mit solchen FD-Werten, die auf gleichen Abständen zwischen den Merkmalen beruhen). Ein weiteres Ziel dieser Arbeit war, die durchschnittlichen Pflanzenreaktionen und Plastizitätsindizes in Relation zu anderen Charakteristika (z.B. Laubtyp, ontogenetisches Stadium und Arthäufigkeit) zu setzen.

Betrachtet wurden dafür Untersuchungsflächen, die in einem subtropischen Laubwald in der Zhejiang Provinz (S-O China) entlang eines Sukzessionsgradienten eingerichtet wurden. In diesen 27 Flächen erfolgte eine Inventur aller über ein Meter großen Individuen. Dabei wurden insgesamt 16.120 Individuen und 148 Arten (aus 46 Pflanzenfamilien) vorgefunden und ein aus 26 Blatt- und 29 Holzmerkmalen bestehender Datensatz erstellt. Zusätzlich dazu wurden in einem Gewächshausexperiment 36 sommer- und 35 immergrüne Baum- und Straucharten benutzt, um den Einfluss von Licht- und Nährstoffverfügbarkeit auf die Merkmalsausbildung und die Plastizität der Arten zu ermitteln. Um darüber hinaus den Einfluss des ontogenetischen Stadiums und der lokalen Häufigkeit zu analysieren, wurden an 46 Arten, die sowohl im Gewächshaus als auch in den Untersuchungsflächen vorkamen, Merkmale bestimmt und miteinander verglichen.

Eine *Fourth Corner*-Analyse zeigte, dass viele Blatt- und Holzmerkmale eine enge Verbundenheit zum Sukzessionsgradienten kennzeichnete. Die meisten Beziehungen innerhalb der Blattmerkmale folgten dem ökonomischen Spektrum von Blättern, wobei mit zunehmender Sukzession die spezifische Blattfläche und der Nährstoffgehalt in den Blättern abnahmen. Verglichen mit den biotischen Eigenschaften der Pflanzengemeinschaften (z.B. Individuendichte)

zeigten die abiotischen Umweltvariablen (z.B. Neigung der Flächen) nur marginale Korrelationen mit Blatt- und Holzmerkmalen. Die Verbindung zwischen den Gemeinschaften und den Artenmerkmalen scheinen zudem weniger wichtig für die Erklärung von Merkmal-Umwelt-Beziehungen zu sein als die Verbindungen zwischen Umwelt und den Arten.

Kein Zusammenhang wurde für FD mit der Sukzession gefunden. Die Gemeinschaft kompensiert jedoch sinkende TD-Werte, indem sie die verbliebenen Merkmale gleichmäßiger innerhalb der ansässigen Arten verteilt, was sich wiederum in steigenden FE-Werten zeigte. Die Nullmodelle offenbarten darüber hinaus eine Äquivalenz unter den Arten im Merkmalsraum. Daher scheint es irrelevant, welche Arten in den unterschiedlichen Sukzessionsphasen vertreten sind, was eine Erklärung dafür wäre, warum der Artenreichtum in den subtropischen Wäldern mit der Zeit steigt. Im Gewächshausversuch wiesen die durchschnittlichen Merkmalswerte und Plastizitätsindizes signifikante Unterschiede zwischen starker Schattierung und vollem Lichtgenuss sowie geringer und ausgewogener Nährstoffversorgung auf. Des Weiteren wurde gefunden, dass die sommer- bzw. immergrüne Lebensform einen starken Einfluss auf die durchschnittliche Merkmalsausbildung und phänotypische Plastizität hatte. Diese Resultate tragen zur aktuellen Debatte zu Merkmalsunterschieden zwischen sommer- und immergrünen Arten und zur Differenzierung zwischen passiven und aktiven Anpassungen des Phänotyps bei. Aktive Reaktionen auf sinkenden Lichtgenuss wurden dabei am besten von Allokationsvariablen, wie z.B. der Dichte an Sprossknoten erfasst. Hinsichtlich der Ontogenese konnte keine signifikante Korrelation zwischen den Wachstumsraten von jungen Individuen im Gewächshaus und adulten Bäumen im Gelände gefunden werden. Im Gegensatz dazu wurden signifikante Zusammenhänge zwischen Artenhäufigkeiten im Gelände und Durchschnittswerten für das Trockengewicht der absoluten Biomasse und der Zahl an Sprossknoten pro Einheit Sprosslänge entdeckt. Außerdem neigt die phänotypische Plastizität des Trockengewichts der gemessenen absoluten Biomasse dazu, mit steigender Häufigkeit der Arten im Gelände zu sinken.

Zusammenfassend bestätigt diese Dissertation, dass Pflanzenmerkmale, die das ökonomische Spektrum des Blatts widerspiegeln, die deutlichste Reaktion auf Umweltgradienten zeigen. Des Weiteren unterstützen die hier präsentierten Resultate die Hypothese, dass die meisten Arten in subtropischen Laubwäldern funktionell äquivalent sind. Obwohl bestimmte Ausprägungen von Pflanzenmerkmalen während der Sukzession eindeutig gefiltert werden, beruht diese Filterfunktion mehr auf biotischen Interaktionen als auf abiotischen Umweltbedingungen. Zusätzlich implizieren die schwachen Korrelationen zwischen Gewächshaus- und Geländedaten ontogenetische Merkmals-Verschiebungen der Gehölzarten in diesem subtropischen Wald. Hingegen weist die Verbindung der Gewächshausdaten zur Häufigkeit der Arten im Gelände darauf hin, dass abundante Arten dazu tendieren weniger „plastisch“ zu sein als selten auftretende Arten.

总记

在过去十年中，性状为基础的方法已成为多样性研究中的一个重要领域。在本论文中，作者汇集了大量叶片和木材的结构和形态学性状，一方面，以此调查性状与环境的关系，另一方面，调查性状特征本身的变化。

作者使用演替系列分析了哪些性状与演替阶段相关，并调查哪些性状和哪些环境因素对于性状与环境的关系尤为重要。此外，作者提出一种新的基于性状的研究途径，在近自然的群落中运用虚无模型，进而分辨物种丰富度，物种身份和性状身份对功能多样性的影响。功能多样性被区分为功能均匀度和性状差异性。后者被定义为群落中所有性状的平均距离。功能均匀度可表示为功能多样性的观测值与基于所有性状的平均距离之上的功能多样性的设定值之间的比值。此外，本论文还将平均响应和可塑性指数与叶的性状特征相关联，例如叶的习性，个体发育阶段以及在当地森林群落的出现频度。

在浙江省（中国东南部）亚热带次生阔叶林中，由于过去的伐木活动，不同地块根据演替阶段在次生林中形成不同的等级。作者在2008年7月和10月之间，建立了27个样地，并记录样地内所有超过1 m的乔木和灌木。所有个体被鉴定到种的水平。记录结果包括了46个科，148个物种，共16120个个体。所建立的数据库总共包括26种叶的和29种木材的性状特征。此外，作者还开展了包括36种落叶和35种常绿亚热带乔灌木的温室实验，以测试光线和养分利用率对物种性状表达和可塑性的影响。为了分析个体发育阶段和当地频度的影响，作者选择了同时包括在27个野外永久样地和温室中的46个物种，比较它们在温室和野外的不同响应。

四角模型分析（Fourth Corner Analysis）结果表明，许多叶和木材的性状与演替梯度紧密相关。叶片性状的最大转移遵循经济型谱，伴随演替序列比叶面积和叶片养分含量下降。此外，作者发现木材孔隙度、生长年轮的可视性、导管分布和演替梯度有很强的相关性。除演替外，一些其它的环境变量也会导致显著的性状相关关系，如土壤碳和氮含量、土壤湿度以及地形变量。下降的海拔显示与增加的常绿树种比例相关。然而，相对于生物群落特征（如植物密度），非生物环境变量（如样地的土壤特性，坡向和坡度）只显示与叶和木材性状边际相关。通过比较四角分析不同的排列模型，作者进一步发现，在解释性状-环境相关关系中，环境和森林群落的连接性比群落和物种性状的连接性更重要。

作者未发现任何关于功能多样性的演替趋势。相反，性状差异性呈下降趋势。群落通过更均匀的分配居留种其它的性状，以补偿性状差异的损失，由此引发功能均匀度进一步增加。虚无模型显示物种性状空间之间的平衡，比如性状间类似的差异性。由此可推测某个物种出现在不同演替阶段是不确定的。这也可解释随着时间的推移，亚热带森林的物种丰度增加。

在温室试验中，在全阴处理($10 \mu\text{E m}^{-2} \text{s}^{-1}$)和全光照处理($250 \mu\text{E m}^{-2} \text{s}^{-1}$)对比，以及高营养和低营养供给处理对比中，性状平均值和可塑性指数显示显著性差异。这一结果强调光量作为一个关键因

子，对于解剖性状可塑性，以至于群落中物种组成的重要性。此外，作者发现，叶习性对物种平均响应（如落叶树种生物量的积累比常绿树种高20%以上）和表型可塑性（落叶树种高于常绿树种）具有强烈的影响。然而，有关落叶和常绿树种的特点以及物种表型之间的被动和主动调整的分化（节点密度能最好的捕获减少光可用性的积极响应）依然存在争议，我们的结果为此提供了新的研究素材。作者未发现任何关于个体发育阶段的显著相关关系。反之，作者发现总生物量的平均响应以及单位幼枝长度节点数量与野外物种多度有显著相关性。此外，总生物量的表型可塑性随着物种多度增加呈下降趋势。

总之，作者验证了性状与叶片经济型谱的相关性，以及环境敏感性最强的亚热带森林的环境过滤作用。我们的研究结果支持假设：亚热带森林的大多数物种在功能上是等价的。此外，温室实验和野外数据之间的较弱相关性揭示了大型物种的个体变化，同时与物种多度的相关性表明：本地丰富的物种往往比本地稀有物种的可塑性差。

FUNCTIONAL DIVERSITY IN A SUBTROPICAL FOREST BASED ON ANATOMICAL AND MORPHOLOGICAL SPECIES TRAITS – INTRODUCTION AND OVERVIEW

General introduction to the project

This thesis is part of the Chinese-European research project “BEF China¹”, which established a forest Biodiversity and Ecosystem Functioning (BEF) experiment in Xingangshan (Jiangxi Province, China) with the topic: *The role of tree and shrub diversity for production, erosion control, element cycling and species conservation in Chinese subtropical forest ecosystems*. The aim of the project is to analyse the impact of tree and shrub species diversity on ecosystem functioning and services. Forest communities in the subtropics provide an ideal setting for this aim. They are rich in vascular plant species (Mutke & Barthlott 2005; see also Fig. 1) and linked to highly structured, geodiverse areas (Legendre *et al.* 2009).

The first phase of the project has been divided into nine subprojects with the focus on primary production, plant growth and demography, plant traits and functional diversity, plant genetics, carbon storage and nitrogen cycling, soil properties and soil erosion, mycorrhiza, soil macrofauna and invasibility. Additionally, two central subprojects were established for coordination and data management. There was not only a close link between all subprojects, but also a tight intercultural cooperation of Chinese and European institutes representing different disciplines such as botany, ecology, forestry, genetics, mycology, soil science, and zoology as well as informatics and statistics. The joint research will help to resolve one of the most central issues in ecology and global change biology: how plant diversity may be used to establish forests that stabilize the environment and maintain vital ecosystem services in the face of multiple stresses.

¹ The “BEF China” is funded by the German Science Foundation (DFG FOR 891/1). For further details see also www.bef-china.de.

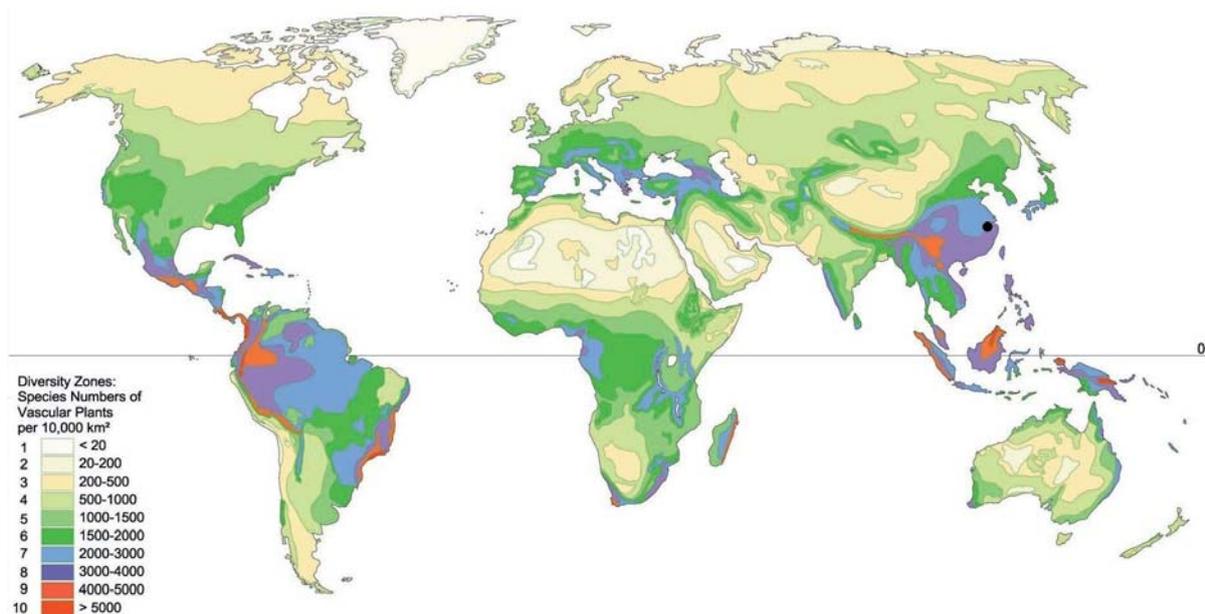


Figure 1: Global phytodiversity. Black dot showing the position of “BEF China”. From Barthlott *et al.* (2005).

Plant traits and functional diversity

This dissertation is the first one of Subproject 3 (SP3) that has the aim to investigate the functional diversity based on species traits. Over the last decade, trait-based approaches have grown exponentially in diversity research. For example, Lavorel & Garnier (2002) as well as Eviner & Chapin III (2003) presented frameworks using concepts and results from ecosystem ecology, community ecology and evolutionary biology to predict multiple plant effects, changes in ecosystem functioning and community composition from plant traits. Furthermore, Stubbs & Wilson (2004) measured 23 functional characters on plant species of a New Zealand sand dune community to prove that limiting similarity controls the ability of species to coexist. Wright *et al.* (2004) brought together leaf trait data spanning over 2,500 species and 175 sites. At a global scale, they described a universal spectrum of leaf economics consisting of key structural, physiological and chemical properties. Petchey & Gaston (2006) reviewed the ability of functional diversity to predict and explain the impact of organisms on ecosystems and provide a mechanistic linkage between the two. Ackerly & Cornwell (2007) presented a trait-based approach in woody plant communities of coastal California to show a decomposition of species’ trait values into alpha and beta components: alpha values are the difference between the mean of co-occurring species and species’ trait values; beta components refer to a species’ position along a gradient determined by community-level mean trait values. 2008, Schamp *et al.* investigated in an old-field plant community patterns in the dispersion of species’ characteristics that are frequently associated with competitive ability. Aside from that, Jung *et al.* (2010) used trait-based approaches to investigate the effect

of environmental filters and intraspecific variability on species assembly. A further study concerning a trait based community assembly analysis was presented by Lebrija-Trejos *et al.* (2010) who measured species traits, environmental conditions, and structure of secondary forests in a species-rich tropical system. Additionally, Webb *et al.* (2010) presented a dynamic and structured framework to improve trait-based prediction and theory in ecology.

In the context of this thesis, the term *trait* is defined as a measurable biological feature that in total represent the phenotype of an individual. At the onset of the project, very little was known about the species in the “BEF China” experiment. Furthermore, it was unidentified which of the traits are *functional* and impact fitness indirectly via their effects on survival, growth and reproduction (Violle *et al.* 2007). Thus, anatomical and morphological leaf and wood traits were collected with the aim to investigate, on the one hand, the mean trait-environment relationship and, on the other hand, the trait variation.

Concerning the trait-environment relationship, these traits are used as response and/or predictor for functioning variables that have been measured in other subprojects. The latter is especially necessary regarding “complementarity effects”, which describe processes that increase the performance of a community of different species compared to the performance of individuals of single species (Loreau & Hector 2001).

Regarding the trait variation, it can be expected that biodiversity-ecosystem functioning relationships are fundamentally affected by the degree of trait divergence or convergence (Hector *et al.* 2002). Thus, trait matrices were prepared to estimate Functional Diversity (FD), which is defined as the range of functional differences among the species in a community (Tilman 2001). To ensure that my calculated FD is unaffected by the measurement units and or the by the number of species, the index provided by Rao (1982) termed quadratic entropy (Q) was chosen (for further details see Chapter IV). In addition to species richness, FD is an alternative explanatory variable for effects of biodiversity on ecosystem functions. Tilman *et al.* (1997) varied plant species diversity and FD in a grassland experiment and showed already that FD was the principal factor explaining plant productivity. Also for grassland community, Hector *et al.* (1999) additionally demonstrated that communities with more functional groups were more productive.

A further aim was the linkage of trait-environment relationships and trait variation to analyse trade-offs and inter-relationships between traits. For example, it is well known that specific leaf area (SLA, leaf area per dry mass) is positively correlated with leaf nitrogen content (LNC, leaf nitrogen per dry mass), leaf stomatal conductance and net photosynthetic capacity (A_{\max}), but negatively correlated with leaf lifespan (e.g. Reich *et al.* 1999, Wright *et al.* 2001).

Regarding leaf lifespan and the obvious linkage to leaf habit, Reich *et al.* (1998) also determine that deciduous species tend to have a different A_{\max} -LNC-relationship than evergreen species. Nevertheless, it can be expected that differences between evergreen and deciduous species are smaller than variation among families (Villar *et al.* 2006). However, for many other traits there are no clear ideas which types of relationship are to be expected.

Concerning the linkage of trait-environment relationships and trait variation, it was also of peculiar interest how an individual plant with a given genotype is able to react to a changing environment by adjusting its phenotype. The magnitude of this adjustment is defined as plasticity (e.g. Bradshaw 1965). The plasticity is governed by key traits like the species' leaf habit. For example, Lusk *et al.* (2008) showed that plasticity in leaf mass per area differed between deciduous and evergreen species. However, a major challenge is the disconnection of passive reduction in growth because of low resource supply and active responses to different environmental settings (e.g. van Kleunen *et al.* 2000). Nevertheless, any knowledge about species-specific responses to different resource conditions will help to understand a community's functional composition. For example, communities composed of species representing low plasticity might perform as well in different environments compared to those composed of mixtures of different species.

A further objective of this work was to analyse ontogenetic trait shifts from juveniles to adults. For long-lived tree and shrub species, which also attain large size, trait measurements indicate the problem of ontogeny-dependent shifts because of allometric limits (Cornelissen *et al.* 2003). In the example of SLA the values of seedlings were found to differ from those of adults by a factor of four (Cornelissen *et al.* 2003). In total, knowledge about ontogenetic influences on traits will allow to analyse to which degree FD measures delivered by juveniles can be assigned to mature plants and vice versa. This knowledge will play an essential role for the whole project because the complementarity of the saplings planted may change with time.

In summary, the trait-based approaches presented here will lay the foundation for further studies to predict niche complementarity between species in the “BEF China” experiment. Furthermore, the results also allow first interpretations of complementarity effects. For example, a found ontogenetic trait shift would raise the question if all species are equally affected. If that is the case, ontogenetic trait shifts should have no impact on the chronological differences in complementarity. Also it could be the case, that trait shift is higher for a specific group of species, e.g. evergreen compared to deciduous species. Following this, these species would be differently adapted to young or late successional stages, thus a sampling along a successional gradient (see below) would be particularly advantageous.

Study area

In the first phase of “BEF China”, a central issue has been the integration of observations in natural established vegetation into an experimental approach to test for mean trait-environment relationships and trait convergence and to provide a database that allows an eventual linkage of variables measured under experimental and natural conditions. Such existing forests were found in the Gutianshan National Nature Reserve (GNNR) in the western part of Kaihua County, Zhejiang Province, China (29°8'18"-29°17'29" N, 118°2'14"-118°11'12" E; see Fig. 2). The forest reserve is located close to the county capital Kaihua (about 30 km) and near to the border triangle of the three provinces Zhejiang, Jiangxi and Anhui. The two experimental sites of the main project of “BEF China”, where the corresponding artificial stands of defined tree species diversity levels have been planted, are located nearby (see Fig. 2C). On a total area of about 70 ha, experimental forest stands were planted there, representing a species pool of about 100 native tree and shrub species and varying in both tree and shrub species richness. A range of ecosystem and biodiversity variables will be investigated to assess community dynamics and its relationship to nutrient cycling, primary productivity, nitrogen and carbon storage, and prevention of soil erosion.

As part of the subtropics, the study area is characterized by an annual average precipitation of 1963 mm and a mean annual temperature of 15.1 °C (Fig. 3). Maximum temperature is 38.1 °C in July and minimal temperature is -6.8 °C in January (Bruelheide *et al.* 2011). The prevailing soil type is Cambisol with a generally sandy-loamy texture. At some locations, the stone content can exceed 90 %-Vol. Soil depth varies between shallow soils less than 50 cm and deeply developed soils of more than 120 cm thickness. The soil parent rock is mainly granite or deeply weathered granite (saprolite) (Geißler *et al.* 2010).

The reserve of Gutianshan was initially established as a National Forest Reserve in 1975 and became a National Nature Reserve in 2001 (Bruelheide *et al.* 2011). It has a size of about 8000 ha and involves elevations between 250 m and 1200 m above sea level (Kröber *et al.* 2011). Maximum tree ages of only about 180 years (Hu & Yu 2008), relicts of agricultural terraces and the presence of charcoal in the soil (Geißler *et al.* 2010) indicate that the stands of the Gutianshan NNR are mainly secondary forests (Bruelheide *et al.* 2011). As a result of the very high pressure of land use in China (Wang *et al.* 2007), deforestation within the reserve and the surrounding areas has occurred during the Great Leap Forward in the 1950s. Anyhow, mostly because of the steep slopes (many of them exceeding 30°), the area in the Gutianshan mountains was only hardly usable for agriculture, and in consequence, an extraordinary intact forest has been preserved that can be considered representative of the

formerly widespread Chinese mixed broad-leaved vegetation type² (Wu 1980, Hu & Yu 2008, Legendre *et al.* 2009). In total, 1426 seed-plant species of 648 genera and 149 families occur in the reserve, making this region a global hot spot of phytodiversity (Mutke & Barthlott 2005, see also Fig. 1). Dominant species are the evergreen tree species *Schima superba* Gardn. et Champ. (Theaceae) and *Castanopsis eyrei* (Champ. ex Benth.) Tutch. (Fagaceae) (Yu *et al.* 2001). Nevertheless, in terms of species number the proportions of evergreen and deciduous species are almost balanced (Lou & Jin 2000).

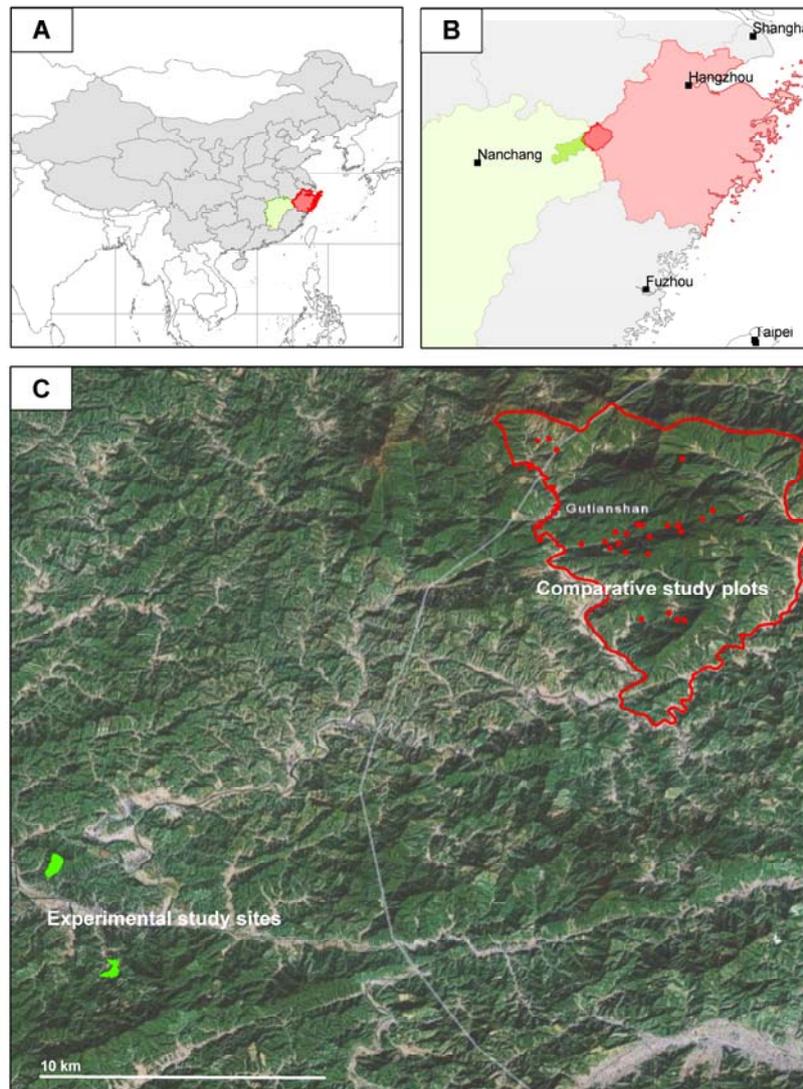


Figure 2: **A** Location of the two provinces Jiangxi (green) and Zhejiang (red) in China. **B** Location of Kaihua county in Zhejiang Province (red = area of the 27 Comparative Study Plots) and Dexing county in Jiangxi Province (green = area where the associated forest biodiversity–ecosystem functioning experiment (“BEF-China”) has been set up). **C** Landsat image of the study site. The red line represents the border of the Gutianshan National Nature Reserve. Red dots show all 27 Comparative Study Plots. From Bruelheide *et al.* 2011.

² However, younger successional stages occur as well, primarily plantations of the economically important timber species *Pinus massoniana* Lamb., *Cunninghamia lanceolata* (Lamb.) Hook and, characteristically for elevated sites, *Pinus taiwanensis* Hayata (Bruelheide *et al.* 2011).

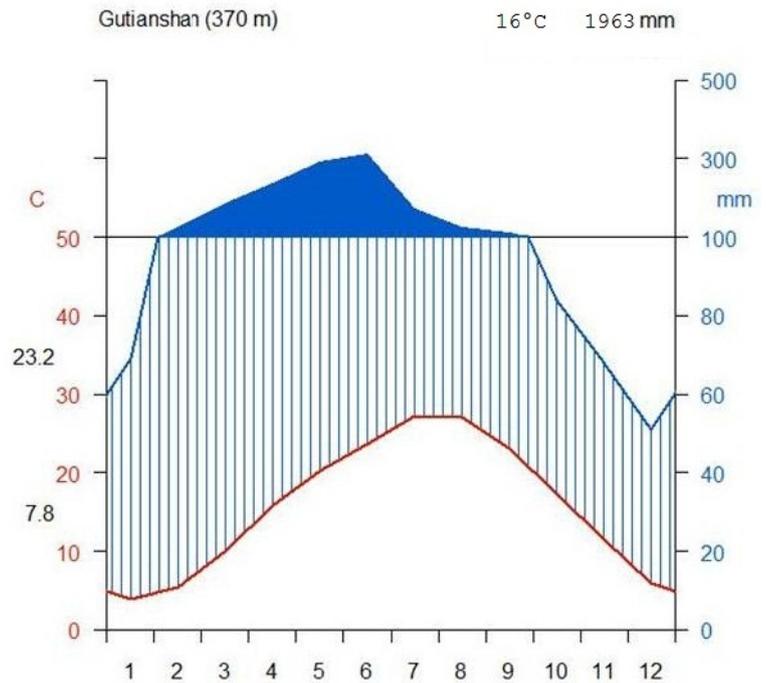


Figure 3: Climate diagram of the Gutianshan NNR. Data based on Hijmans *et al.* (2005). From Kröber 2010.

Study design

Site selection

A set of 27 so called Comparative Study Plots (CSPs) was established in the Gutianshan National Nature Reserve between May and July 2008. Each CSP measures 30 m x 30 m on the ground. All plots were placed randomly, orientated north and stratified by successional age. However, due to extremely steep slopes ($> 50^\circ$), inaccessibility and the highly variable relief (even at a small scale), many parts of the reserve had to be excluded from sampling. The result is a patchy spatial distribution of some of the CSPs (see Fig. 2C). Regarding the age of plots, five successional stages were distinguished, determined by the age of the oldest tree individuals and supported by additional local knowledge of the last logging and status as *feng shui* forest (1: < 20 yrs, 2: < 40 yrs, 3: < 60 yrs, 4: < 80 yrs, 5: > 80 yrs). This classification was confirmed by measurements of diameter at breast height (dbh) of all trees with > 10 cm dbh in the plots and by age determination of stem cores taken from 159 individuals of 64 different tree species across all CSPs. Diameter at breast height was well related to tree age (Fig. 4A). The problem occurred that few old trees were encountered in all age classes, irrespective of the age of the majority of trees because these trees were remnants of the forest before the logging event. Therefore, Bruelheide *et al.* (2011) introduced the idea of choosing the fifth largest tree in a CSP as being representative for the plot age. As shown in Fig. 4B,

the age of the fifth largest tree is closely correlated to the defined successional stage³. The numbers of plots per successional stage were 5, 4, 5, 6 and 7, respectively.

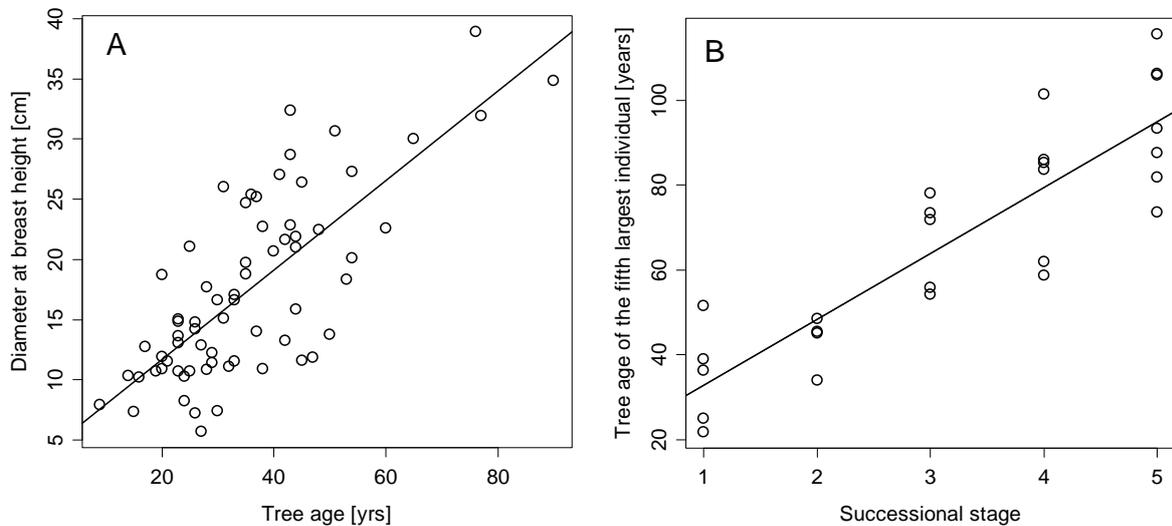


Figure 4: Definition of successional stages: **A** Diameter at breast height (dbh) as a function of tree age, across all Comparative Study Plots (CSPs) and species. The line shows the significant linear regression: $dbh = 4.25 + 0.37 * age$, $r = 0.753$, $p < 0.001$. **B** Age of the fifth largest tree in the plot as a function of successional stage⁴. The line shows the significant linear regression: $age = 17.39 - 15.52 * successional\ stage$, $r = 0.880$, $p < 0.001$. Mean ages (\pm standard deviation) per successional stage: 1 = 34.7 (\pm 11.9), 2 = 43.2 (\pm 6.3), 3 = 66.3 (\pm 10.9), 4 = 79.4 (\pm 16.2) and 5 = 94.8 (\pm 15.0) years. From Bruelheide *et al.* 2011.

Plot characteristics

Species recording of all tree and shrub individuals taller than one meter was performed between July and October 2008 with up to seven visits per plot. Individuals were identified to the species level by the invaluable support of the botanist Teng Fang and the help of local forestry workers and already correctly identified herbarium samples. In total, 16,120 individuals of 148 species representing 46 families were encountered. Only 87 of these individuals (0.53 %) could not be identified explicitly to species level. Consequently, these individuals were not included in any data analysis of this thesis. The number of individuals ranged from only 207 (CSP 12, successional stage 4) to 1233 (CSP 19, successional stage 1) and, regarding the number of species, from 25 (again CSP 12) to 69 (CSP 2, successional stage 5) (see Fig. 5). For a total of 21 species only one individual was found in all CSPs and further 14 species were found only in one plot. Additionally, the only species that occurred in all 27 CSPs were the Theaceae *Schima superba* and *Eurya muricata* Dunn.

³ This dissertation has essentially contributed to this found relationship. However, the study of Bruelheide *et al.* (2011) was not included in this thesis.

⁴ The fact that in some plots five or more old trees survived harvesting (e.g. CSP 16 with eleven trees > 20 cm dbh) results in the comparably high age of successional stage 1.

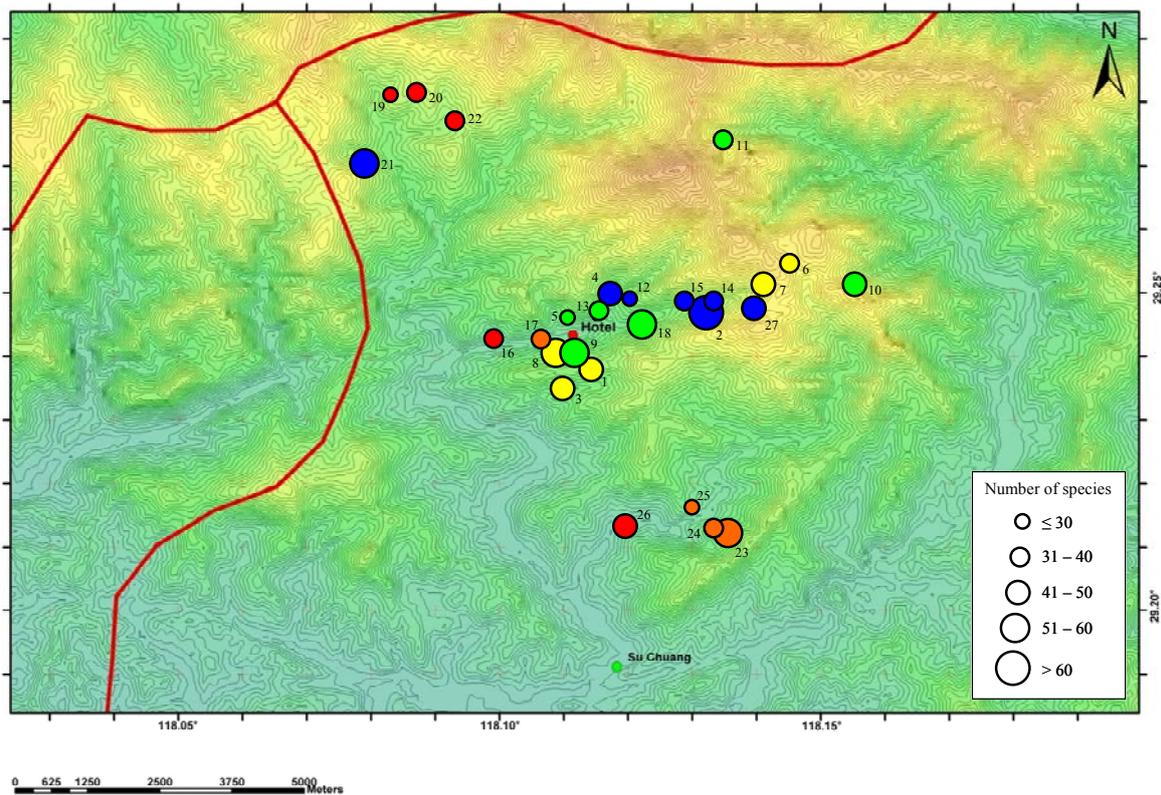


Figure 5: Location of all 27 Comparative Study Plots in the Gutianshan National Nature Reserve. Width of the circles representing species richness encountered in the plots (see inlet in the corner) and colours indicating the successional stages: red: < 20 yrs, orange: < 40 yrs, yellow: < 60 yrs, green: < 80 yrs, blue: > 80 yrs.

Fidelity analysis of Bruelheide *et al.* (2011) showed that rare species were not concentrated in older successional stages. Only one species (*Photinia glabra* Maxim.) was significantly concentrated in the oldest CSPs and only two species (*Glochidion puberum* (Linn.) Hutch. and *Platycarya strobilacea* Sieb. et Zucc.) in the youngest plots. Furthermore, the proportion of rare tree and shrub species was neither related to successional stage nor to the age of the fifth largest tree (see Bruelheide *et al.* 2011).

Additionally, data sets of abiotic environmental variables (e.g. aspect, elevation, slope, soil moisture and pH) as well as sets of biotic structural variables (estimations of cover and height of layers) were collected for each CSP. These data sets were key components for the trait-environment relationships used in the different parts of this dissertation. Aspect was expressed as eastness and northness, using sine and cosine of aspect, respectively. For soil characteristics⁵, in each CSP soil samples were taken from the topsoil (depth increment 0-5 cm) for soil C and soil N analysis in June/July 2008, November 2008 and March 2009. Soil moisture ranged between 0.21 to 0.55 $\text{g}_{\text{water}} \text{g}_{\text{dry soil}}^{-1}$.

⁵ Soil characteristics were determined by Christian Geißler, Peter Kühn and Thomas Scholten of the Institute of Geography, Physical Geography and Soil Science, Eberhard Karls University Tübingen.

The first paper on the CSPs (Bruehlheide *et al.* 2011) had the objective to relate species composition and species richness to successional age. The results showed that none of the measured abiotic variables were significantly correlated with species richness. Nevertheless, they found evidence for a significant turnover of species, and thus (after Jongman *et al.* 1995) a comparably high β -diversity among all plots. Furthermore, Bruehlheide *et al.* (2011) showed that structural characteristics (such as height of shrub and tree layers) changed in the course of the succession. Beyond that, they also present significant correlations with successional stage, e.g. the number of individuals per plot as well as the proportion of deciduous species decreased significantly with increasing successional stage.

Structure of the thesis

This dissertation is divided in chapters, representing independent papers⁶, arranged in a non-chronological order, only with regards to the topics. Thus, Chapters II and III focus on the trait-environment relationship, Chapter IV on trait variations and Chapter V on both. The aims and objectives of the chapters in detail are presented in the following.

CHAPTERS II & III

These two chapters deal with the mean trait-environment relationship. Accordingly, they both provide the methods of the collection of leaf and wood traits in the CSPs, respectively. These traits were used to investigate trade-offs and trait-environment correlations along successional gradients in a subtropical broadleaved forest. I asked which traits were most responsive to the environment and which environmental characteristics had dominant influence on mean trait values in the community. Furthermore, I tested which of the trait-environment links were stronger: those between communities and traits or those between communities and environment. On the basis of the hypothesis that the trait composition is linked to species identities, which should be differ in moderately diverging communities, I expected that leaf as well as wood traits of shrub and tree species are tightly correlated with successional stage. Successional stage itself was expected to be less strongly linked to the abiotic environment because it was assumed that the community composition was mainly shaped by biotic interactions. Consequently, the linkage between traits and species composition should be more important for explaining the encountered trait-environment relationships than the link between species composition and the environment.

⁶ The journals to which the papers have been submitted are mentioned on the title page of each chapter. The style of the manuscripts has been edited to follow the format of this thesis. For headlines, short titles are used.

CHAPTER IV

This chapter aims at the second main topic: trait variation. On that account, a selection of 26 traits for 120 species introduced in previous chapters was used to estimate functional diversity expressed as FD_Q , based on Rao's Q, with the aim to quantify the species' distribution in niche space. An important advantage of FD_Q is that the range of traits and the abundance of the species with those characters in the community are represented. Furthermore, to investigate the impact of species and traits on FD_Q and to capture different aspects of niche complementarity, I used null models and separated FD_Q into functional evenness FE_Q and trait dissimilarity TD_Q . FE_Q can be expressed as the ratio of the observed value of FD_Q to a value of FD that is obtained by assuming equal distances among all traits, whereas TD_Q is defined as the mean distance of all traits in the community. I hypothesised that FD_Q and TD_Q increase with increasing successional stage whereas FE_Q remains constant. Furthermore, I expected that any relationship of FD_Q with successional stage disappears if a subset of traits is randomly selected out of the total number of analysed traits, if species in the community are randomly assigned a trait set from the species pool or if a certain number of species in the community is randomly chosen from all species in the community.

CHAPTER V

This chapter addresses environmental and ontogenetic influences on traits. In addition, it also focusing on the within-species variation and therefore I investigated the ability of an individual plant to react plastic to a changing environment by adjusting its phenotype. Thus, I established a greenhouse experiment with 71 tree and shrub species, naturally occurring in the study area, and tested the influence of light and nutrient availability on trait expression. Additionally, I tried to differentiate between passive and active plasticity. Further, I related mean values and estimated plasticity indices to the species' characteristics such as abundance, ontogenetic stage and leaf habit. To this approach, a set of field data for 46 species that occurred in the CSPs was added. I expected that the traits of the species are differently affected by varying light and nutrient conditions. With regard to leaf habit, I hypothesized that evergreen species are less plastic than deciduous species. With respect to ontogeny, I further hypothesized that plasticity of juveniles are related to plasticity of adults. Finally, I expected that species which showing a higher plasticity in the greenhouse are also more abundant in the field.

CHAPTER VI

The dissertation ends up with a comprehensive conclusion that briefly outlines the findings of chapters II, III, IV and V.

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LEAF TRAIT-ENVIRONMENT RELATIONSHIPS IN A SUBTROPICAL BROADLEAVED FOREST IN SOUTH-EAST CHINA

Submitted to *Journal of Ecology*

Abstract

Although trait analyses have become more important in community ecology, trait-environment correlations have rarely been studied along successional gradients. We asked which environmental variables had the strongest impact on mean trait values in the community and which traits were most responsive to the environment. A further aim was to analyse the different components of the trait-environment relationship to gain insight into community assembly rules.

We established a series of plots in a secondary forest in the Chinese subtropics, stratified by successional stages that were defined by the time elapsed since the last logging activities. On a total of 27 plots all woody plants were recorded and a set of individuals of every species was analysed for leaf traits, resulting in a trait matrix of 26 leaf traits for 122 species.

A Fourth Corner Analysis revealed that many leaf traits were tightly related to the successional gradient. Most shifts in traits followed the leaf economics spectrum with decreasing specific leaf area and leaf nutrient contents with successional time. Besides succession, few additional environmental variables resulted in significant trait relationships, such as soil moisture and soil C and N content as well as topographical variables. Not all traits were related to the leaf economics spectrum, and thus, to the successional gradient, such as stomata size and density as well as leaf area. In addition, stomata density showed a trade-off with stomata size.

By comparing different permutation models in the Fourth Corner Analysis, we found that the trait-environment link was more based on the association of species with the environment than of the communities with species traits, brought about a clear gradient in species composition along the succession series, while communities were not well differentiated in trait composition.

Synthesis: The study confirmed the role of environmental trait filtering in subtropical forests, with traits associated with the leaf economics spectrum as being the most responsive ones. The finding of a weak link between communities and species traits can be either explained by having missed important traits or by a general low importance of trait differences for community assembly in this subtropical forest.

Key words

BEF-China | Determinants of plant community diversity and structure | Environmental filtering | Fourth Corner Analysis | Functional traits | Leaf economics spectrum | Plant community assembly rules | Secondary succession | Specific leaf area | Stomata density

WOOD TRAIT-ENVIRONMENT RELATIONSHIPS IN A SECONDARY FOREST SUCCESSION IN SOUTH-EAST CHINA

Submitted to *Trees – Structure and Function*

Abstract

Concerning forest communities, not much is known about the relationship between wood traits and environmental conditions. Using a succession series, we analysed which wood anatomical traits were correlated with successional stage and asked which traits and which environmental factors were particularly important for the trait-environment relationship.

An extensive dataset of 29 wood traits was generated for 93 woody species that occurred in 27 permanent plots in a secondary subtropical broadleaved forest in Zhejiang Province (SE-China) and subjected to Fourth Corner Analyses, using different permutation models.

We encountered a strong relationship of wood porosity, visibility of growth rings and vessel arrangement to the successional gradient. Compared to biotic community characteristics such as density of plants, abiotic environmental variables such as soil characteristics, aspect and inclination of the plots showed only marginal correlations to wood anatomical traits. Furthermore, the link between environment and the forest communities was found to be more important in explaining trait-environment relationships than between the communities and species wood traits.

In addition, our results supporting the idea that most of the species in the subtropical forest might be functionally equivalent.

Key words

BEF-China | Comparative Study Plots (CSP) | dendroecology | Fourth Corner Analysis | Gutianshan National Nature Reserve (GNNR) | qualitative and quantitative wood traits | paratracheal parenchyma | wood vessel arrangement

MAINTENANCE OF CONSTANT FUNCTIONAL DIVERSITY DURING SECONDARY SUCCESSION OF A SUBTROPICAL FOREST IN CHINA

Submitted to *Ecology*

Abstract

We present a new trait-based approach to disentangle the effects of trait identity, species identity and species richness on functional diversity in natural communities using null models. Functional diversity was partitioned into trait dissimilarity and functional evenness. The approach was applied to secondary succession in a subtropical forest, using a matrix of 26 traits for 120 species. Against expectation, we failed to detect any successional trend in functional diversity. Instead, the mean distance of all traits in the community (i.e. trait dissimilarity) decreased. The community compensated for a loss in trait dissimilarity by distributing the remaining traits more evenly among the resident species, thus increasing functional evenness. The null models revealed an equivalence among species in trait space, i.e. similar differences among traits, thus making it irrelevant which species were present in the different successional stages and providing an explanation why these subtropical forests become more species-rich with time.

Key words

BEF-China | chronosequence | functional evenness | Gutianshan National Nature Reserve (GNNR) | partitioning of functional diversity | null models | random assembly | secondary forest succession | trait dissimilarity

HOW DO EVERGREEN AND DECIDUOUS SPECIES RESPOND TO SHADE ? TOLERANCE AND PLASTICITY OF SUBTROPICAL TREE AND SHRUB SPECIES OF S-E CHINA

Submitted to *Ecological Research*

Abstract

A key strategy of long-lived plants to overcome heterogeneity of essential resources is plasticity. Thus, the main objective of this study was to relate mean responses and plasticity indices, to species characteristics such as leaf habit, ontogenetic stage and local frequency in forest communities. A greenhouse experiment with 36 deciduous and 35 evergreen subtropical tree and shrub species was carried out to test the influence of light and nutrient availability on trait expression and plasticity of the species. The ontogenetic impact was analysed by comparing the greenhouse responses with adult individuals in the field, based on a set of 46 species that occurred also in the 27 permanent plots in a secondary subtropical, broadleaved forest in Zhejiang Province (SE-China). In the greenhouse experiment, most variables showed significant differences between full light ($250 \mu\text{E m}^{-2} \text{s}^{-1}$) and full shade ($10 \mu\text{E m}^{-2} \text{s}^{-1}$) treatments as well as between high and low nutrient supply. Moreover, we found that leaf habit had a strong impact on mean responses and mean phenotypic plasticity. Concerning ontogenetic stage, no significant correlations were detected. In contrast, relationships with mean responses and plasticity were encountered for abundance.

In summary, our results contribute to the debates concerning characteristics of deciduous and evergreen species and the differentiation between passive and active adjustment of the phenotype. In addition, the presented data implies ontogenetic shifts for species of large size, whereas the linkage to abundance suggests that species that are locally abundant tend to be less “plastic” than locally rare species.

Key words

BEF China | greenhouse experiment | Gutianshan National Nature Reserve (GNNR) | phenotypic plasticity | shade tolerance

COMPREHENSIVE CONCLUSIONS

This thesis provides a huge amount of fundamental knowledge on traits of shrub and tree species of subtropical forests in S-E China that were not well known to science yet. In detail, the here presented data set of anatomical and morphological leaf and wood traits was used to investigate the mean trait-environment relationship and the trait variation.

Main results

The four different studies of this thesis were either directly carried out in the 27 Comparative Study Plots in the Gutianshan Nature Reserve or refer to the patterns observed in these plots. They revealed the following five main results:

1. *As expected, leaf and wood traits were tightly related to the successional gradient.*
2. *Contrary to what was expected, the link between species composition and the environment was more important than the link between leaf and wood traits and species composition for explaining mean trait-environment relationships.*

The first two here presented studies (Chapters II & III) on trait-environment relationships fully confirmed the existence of environmental filters. This linkage of leaf and wood traits to environmental conditions is the consequence of the filtering effect of biotic and abiotic conditions that determine which species of a given pool are assembled into local communities (Díaz *et al.* 1998). In addition, the results also supply fundamental knowledge of the co-variation of environmental variables and of the leaves' economics spectrum (Table 1 A & B). Finally, it also provides a more substantial understanding of the role of traits in community assembly, irrespective of the species involved (Keddy 1992). The two studies were able to assess the importance of the different components in the trait-environment relationships, showing that the link between species composition and leaf and wood traits was less important than the link between environment and species composition.

3. *Against expectation, no successional trend in functional diversity could be detected. Instead, trait dissimilarity decreased and functional evenness increased with time.*
4. *Null models of functional diversity revealed equivalence among species in trait space, i.e. similar differences among traits, thus making it irrelevant which species were present in the different successional stages.*

The third study presented in Chapter IV has pointed out the usefulness of partitioning functional diversity (FD) expressed as FD_Q , based on Rao's (1982) quadratic entropy (Q), into trait divergence (TD_Q) and functional evenness (FE_Q) and combining these FD measures with null models. For example, Mason *et al.* (2005) also deliver a definition of functional diversity based on species richness, evenness and divergence and Villéger *et al.* (2008) equally proposed three indices to quantify functional diversity: functional richness, functional evenness, and functional divergence. Compared with these similar procedures, the here presented approach relies on parsimony, only using a single, but powerful index. Furthermore, it allows new insight into identity and complementarity effects in observational studies in other communities. However, it was shown that the patterns in FD did not differ by randomly reshuffling traits or species (Table 1 C). The encountered increase in species richness with time might be caused by this finding, and thus, the maintenance of a constant FD in this forest community has important ecological consequences.

5. *Weak correlations between greenhouse and field data implies ontogenetic shifts, whereas the linkage to abundance suggests that species that are locally abundant tend to be less “plastic” than locally rare species.*

Regarding to this unexpected result of the fourth study (Chapter V), a constant immigration of new species during succession, as suggested by Bruelheide *et al.* (2011), seems to be only possible if the colonizing potential for plastic species is limited and if there are equalizing mechanisms, as suggested by Chesson (2000), for a stable coexistence of species. These mechanisms would allow diversity maintenance and prevent abundance of plastic species. In detail, this chapter also demonstrated that the phenotypic plasticity of the species in this forest community is greatly affected by leaf habit (Table 1 D).

Table 1: Objectives and main results of this dissertation.

Objectives	Results
A Leaf trait-environment relationships (CHAPTER II)	
Analysis of the relationship between environmental variables and leaf traits of shrub and tree species.	Fourth Corner Analysis revealed that many leaf traits were tightly related to the successional gradient. Additionally, further significant trait relationships for soil moisture and soil C and N content as well as topographical variables were found.
Co-variation of environmental variables with the successional gradient, elevation, aspect and slope.	Successional stage was positively related to rarefied species richness. An inverse relationship was encountered to number of individuals and the proportions of deciduous individuals in a plot. Soil moisture, N and C content as well as pH formed a second gradient that was quite unrelated to successional time. Additionally, increasing elevation was found to be associated with decreasing proportion of evergreen species. Aspect and slope displayed only weak relationships to other environmental variables.
Investigation of traits reflecting the leaves' economics spectrum.	Most shifts in traits followed the leaf economics spectrum with decreasing SLA and LNC with successional time. No relationships were found for stomata size and density as well as leaf area. In addition, stomata density showed a trade-off to stomata size.
Relevance of the link between leaf traits and species composition and species composition and the environment for explaining the encountered trait-environment relationships.	Three different permutation models in the Fourth Corner Analysis showed that the environment community link was more important, while traits were rather homogeneously distributed among species.
B Wood trait-environment relationships (CHAPTER III)	
Analysis of the relationship between wood anatomical traits of shrub and tree species and successional stage.	A strong relationship was encountered of wood porosity, vessel arrangement and visibility of growth rings to successional stage.
Analysis of the relationship between successional stage and abiotic and biotic plot characteristics.	Compared to biotic community characteristics such as density of plants, abiotic environmental variables of the plots were less related to successional stage.
Relevance of the link between wood traits and species composition and species composition and environmental characteristics for explaining the encountered trait-environment relationships.	The link between species composition and the environment was more important than the link between wood traits and community for explaining the encountered trait-environment relationships.
C Maintenance of constant functional diversity (CHAPTER IV)	
Analysis of the relationship of successional stage and functional diversity, trait dissimilarity and functional evenness.	Against expectation, no successional trend in functional diversity could be detected. Instead, trait dissimilarity decreased and functional evenness increased with successional time.
Investigation of the equivalence of traits for the relationships encountered.	Choosing eight traits randomly out of the 26 measured traits gave principally the same results for FD, TD and FE as for the full trait set, and thus, certain traits seem not to be responsible for the observed patterns.
Investigation of the impact of particular species contributing specific trait sets for the relationships encountered.	Assigning random trait sets to the species within the community resulted in the same relationships to successional age for FD and FE as the original sets. No species identity effects were observed.
Investigation of the impact of species richness for the relationships encountered, irrespective of the traits involved.	Randomization of trait sets across the whole pool of trait sets only within a particular successional stage resulted in dissolving the observed trend in trait space and in the increase of FD and FE.

D Plasticity of evergreen and deciduous species (CHAPTER V)

Assessment of the effect of varying light and nutrient conditions on different traits of shrub and tree species.	In a greenhouse experiment, most variables showed significant differences between full light and full shade treatments as well as between high and low nutrient supply. In addition, effects of different shade treatments on phenotypic plasticity were large for most species and observed traits.
Detection of the impact of leaf habit on mean responses and phenotypic plasticity.	Leaf habit had a strong impact on mean responses. For example, mean biomass accumulation of deciduous species was 20% higher than that of evergreen species. Furthermore, leaf habit had a significant influence on mean phenotypic plasticity, which was higher for deciduous species than for evergreen species.
Analysis of the relationship of trait values measured on seedlings in the greenhouse to values measured on individuals of the same species growing in the field.	Concerning ontogenetic stage, no significant correlations were detected.
Analysis of the relationship of abundance and mean responses and phenotypic plasticity of species.	Significant relationships with species' abundance in the field were found for mean responses of dry weight of total biomass and from number of nodes per unit shoot length. Additionally, phenotypic plasticity of dry weight of total biomass tended to decrease with increasing abundance.

Prospects

This thesis laid the important groundwork for the other subprojects of “BEF China” and for analysing processes that increase the performance of a community of different species compared to the performance of individuals of single species (Loreau & Hector 2001), so called “complementarity effects”. However, I have conceived traits only in their response function to the environment but not their role as effect traits (*sensu* Suding *et al.* 2008). Regarding the main objective of the whole project, the investigation of the impact of biodiversity on ecosystem functioning, the next steps will have to be the analysis of the effect of traits on ecosystem processes (Hillebrand & Matthiessen 2009), combining the results of the subprojects dealing with productivity, invasion resistance erosion control or herbivory susceptibility. The latter, for example, can be assumed to be one of the dominant interactions in species-rich forests and to have crucial impact on plant diversity and thus ecosystem functions via effects on plant recruitment, growth and mortality (Coley and Barone 1996; Eichhorn *et al.* 2006). In the scope of “BEF China”, Schuldt *et al.* (2010) already analysed insect herbivory on saplings of ten understorey shrub and tree species and demonstrated that plant traits are a potentially confounding factor. For instance, they included leaf habit in their analysis and showed that herbivory increased with plant species richness irrespective the ratio of evergreen and deciduous species. Nevertheless, they suggested a comparison of their findings to coming results of “BEF China”. In addition, Geißler *et al.* (2010) investigated

(also in the framework of “BEF China”) the importance of selecting specific species for reforestation projects considering the prevention of soil erosion. They used sand-filled splash cups to study the erosive power of rainfall and found that the erosion potential and the spatial heterogeneity of throughfall are species-specific. However, for future approaches considering the prevention of soil erosion it would be interesting to test also the impact of specific leaf traits (e.g. leaf area, leaf pinnation or leaf margin) to modify drop size distribution.

In the two studies of this thesis that concern trait-environment relationships, important response traits are at the same time important effect traits, for example specific leaf area (SLA) as a driver of nutrient cycles (Kurokawa & Nakashizuka 2008). Thus, the subproject of “BEF China” concerning the topic *carbon storage and nutrient cycling* (SP5) already used measured SLA-values to test for correlations between leaf traits and decomposition rates. For instance, Stefan Trogisch (PhD student of SP5) placed litter bags on the ground of the permanent plots to determine *in situ* decomposition rates of single-species leaf litter for a subset of 20 species found in the plots. The species of the subset were preselected to represent the entire range of species according their SLA-values and first results imply that increasing SLA values led to higher decomposition rates (unpublished data). However, further experimental approaches that deliberately manipulate trait compositions of communities (such as in the main experiment of “BEF China”, where the corresponding artificial stands of defined tree species diversity levels have been planted in two experimental sites near to the Gutianshan National Nature Reserve) have to be developed.

In summary, this work could demonstrate that constant FD and the equalizing mechanisms (*sensu* Chesson 2000) might be some of the requirements that allow this forest community to become richer with time based on constant immigration. However, immigration of non-resident species can be considered a type of invasion into the community, although they might belong to the same regional species pool. The hypothesis that species-rich communities are less susceptible to invasions is a popular assumption in studying diversity–invasibility relationships (e.g. Levine 2000; Fargione & Tilman 2005), explained by a decreasing level of unused resources in communities of low levels of diversity. However, the mechanism behind is not caused by diversity per se but by FD (Pokorny *et al.* 2005; Hooper & Dukes 2010), and thus, a constant FD over succession means that the communities remain equally invasible by new colonizing of species. On the one hand, this means that the accumulation of species described by Bruelheide *et al.* (2011) does not slow down with ongoing succession. On the other hand, this represents a further possible starting point for the subproject of “BEF China” concerning the topic *invasion* (SP11).

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SUPPLEMENT

Erklärung über den persönlichen Anteil an den Publikationen

The following list shall give an overview of my own contribution and the share of the co-authors and assistants, respectively. I also highly appreciate the suggestions and corrections made by all the reviewers of the journals.

Böhnke M., Kröber W., Welk E., Wirth C. & Bruelheide H. (submitted) Maintenance of constant functional diversity during secondary succession of a subtropical forest in China. *Ecology*.

Field: **Martin Böhnke** (50 %) | Wenzel Kröber (40 %) | Martin Baruffol, Sabine Both, Teng Fang, Anne C. Lang, Andreas Schuldt, Stefan Trogisch, Bo Yang & Xueqin Zeng (together 10 %)

Lab: Wenzel Kröber (45 %) | **Martin Böhnke** (35 %) | Anja Hallensleben, Sebastian Hammer & Juliane Schatz (together 20 %)

Analysis: Helge Bruelheide (50 %) | **Martin Böhnke** (40 %) | Christian Wirth, Erik Welk & Wenzel Kröber (together 10 %)

Writing: **Martin Böhnke** (45 %) | Helge Bruelheide (40 %) | Christian Wirth, Erik Welk & Wenzel Kröber (together 15 %)

Böhnke M., Kreißig N., Kröber W., Fang T. & Bruelheide, H. (submitted) Wood trait-environment relationships in a secondary forest succession in South-East China. *Trees – Structure and Function*.

Field: **Martin Böhnke** (80 %) | Teng Fang (10 %) | Christian Geißler (5 %) | Wenzel Kröber & Andreas Schuldt (together 5 %)

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Writing: **Martin Böhnke** (70 %) | Helge Bruelheide (30 %) | corrections by Wenzel Kröber & Sebastian Hammer

Böhnke M. & Bruelheide H. (submitted) How do evergreen and deciduous species respond to shade? - Plasticity of subtropical tree and shrub species of South-East China. *Ecological Research*.

Greenhouse: **Martin Böhnke** (40 %) | Sebastian Hammer (20 %) | Juliane Schatz (20 %) | Anja Hallensleben (10 %) | Wenzel Kröber, Eva Bremer & Felix Berthold (together 10 %)
Lab: **Martin Böhnke** (60 %) | Sebastian Hammer (15 %) | Juliane Schatz (15 %) | Anja Hallensleben (10 %)
Analysis: **Martin Böhnke** (80 %) | Helge Bruelheide (20 %)
Writing: **Martin Böhnke** (80 %) | Helge Bruelheide (20 %)

Kröber W., **Böhnke M.**, Welk E., Wirth C. & Bruelheide H. (submitted) Leaf trait-environment relationships in a subtropical broadleaved forest in South-East China. *Journal of Ecology*.

Field: Wenzel Kröber (55 %) | **Martin Böhnke** (30 %) | Teng Fang (10 %) | Christian Geißler (5 %)
Lab: Wenzel Kröber (55 %) | Anja Hallensleben, Juliane Schatz, Ullrike Gosdzinski, Sebastian Hammer & **Martin Böhnke** (together 45 %)
Analysis: Wenzel Kröber (50 %) | Helge Bruelheide (30 %) | **Martin Böhnke** (20 %)
Writing: Helge Bruelheide (70 %) | Wenzel Kröber (15 %) | **Martin Böhnke**, Erik Welk & Christian Wirth (together 15 %)

Curriculum Vitae

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- 2001: Abitur at the Wilhelm-von-Siemens-Gymnasium in Berlin, Germany
- 2002-2005: Prediploma at the TU Darmstadt, Germany
- 2005-2008: Studies at the MLU Halle-Wittenberg, Germany (subjects: geobotany, zoology, nature conservation and soil sciences)
- 2008: Diploma: „Invasive *Acer negundo*-Populationen im Stadtgebiet Halle (Saale): Gibt es eine Habitat-abhängige Differenzierung?“
- 2008-2011: PhD student within the framework of DFG project "BEF China" (FOR 891), subproject 3: plant traits and functional diversity

Field trips

- 2007: Three weeks field course *Pollination Ecology* in Mongolia, led by PD Dr. habil. Karsten Wesche and Dr. Peggy Seltman in cooperation with the National University of Mongolia, Ulan Bator
- 2008: Four month field work in the Gutianshan National Nature Reserve (Zhejiang)
- 2009: Two month field work in Xingangshan (Jiangxi) and one month field work in the Gutianshan National Nature Reserve
- 2010: Three month field work in Xingangshan / Gutianshan National Nature Reserve

Publications of this dissertation

(by chronological order)

Böhnke M., Kröber W., Welk E., Wirth C. & Bruelheide H. (submitted) Maintenance of constant functional diversity during secondary succession of a subtropical forest in China. *Ecology*.

Böhnke M., Kreißig N., Kröber W., Fang T. & Bruelheide H. (submitted) Wood trait-environment relationships in a secondary forest succession in South-East China. *Trees – Structure and Function*.

Kröber W., **Böhnke M.**, Welk E., Wirth C. & Bruelheide H. (submitted) Leaf trait-environment relationships in a subtropical broadleaved forest in South-East China. *Journal of Ecology*.

Böhnke M. & Bruelheide H. (submitted) How do evergreen and deciduous species respond to shade? - Plasticity of subtropical tree and shrub species of South-East China. *Ecological Research*.

Additional publications

(by alphabetical order)

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Contributions to conferences

Böhnke M., Kröber W., Welk E., Wirth C. & Bruelheide H. (2010) Maintenance of constant functional diversity in a secondary succession of a subtropical forest in China. Talk at the 40th annual GfÖ-meeting 2010: “The future of biodiversity”, Aug 30 to Sept 3 in Giessen, Germany.

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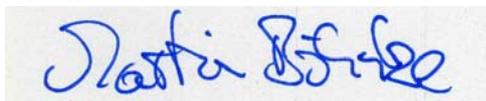
Eigenständigkeitserklärung

Hiermit erkläre ich, dass diese Arbeit bisher weder der Naturwissenschaftlichen Fakultät I (Biowissenschaften) der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Des Weiteren möchte ich festhalten, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe. Die den benutzten Werken wörtlich oder inhaltlich entnommen Textstellen wurden von mir als solche kenntlich gemacht.

Zusätzlich bestätige ich, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Gauting, den 19.01.2012

A handwritten signature in blue ink, reading "Martin Birkel". The signature is written in a cursive style and is contained within a light blue rectangular box.

It was all a dream !!!

(The Notorious B.I.G. in *Juicy*)

Danksagung

This thesis would not have been realized without the framework of the “BEF China” project, which is funded by the German Science Foundation (DFG FOR 891/1) and by the National Science Foundation of China (NSFC 30710103907 & 30930005). Further, travel grants to prepare the project were financed by the Sino-German Centre for Research Promotion in Beijing (GZ 524, 592, 698 & 699).

Prof. Helge Bruelheide and the two other referees are greatly acknowledged for being reviewers of this thesis.

Helge möchte ich darüber hinaus auch von Herzen für seine hervorragende Betreuung während der ganzen Zeit hier am Institut danken. Ich konnte mich immer auf deine Hilfe verlassen und weiß all die Überstunden, die du meinerwegen hattest, mehr als zu schätzen. Jetzt liegt diese Arbeit vor dir und ich bin mir sicher, dass du dich darüber fast genauso freust wie ich. Danken möchte ich auch deiner Familie und das bestimmt nicht nur für das Glas selbstgemachte Mayonnaise.

Im gleichen Atemzug möchte ich mich bei **allen** anderen Kolleginnen und Kollegen, die aus den unterschiedlichsten Gründen in China zusammengekommen sind, bedanken. Besonders herausnehmen möchte ich dabei Wenzel Kröber (mein SP3 Tag-Team-Partner – seit der Mongolei war vieles auch ohne großer Worte klar: Danke, dass du es mir immer so einfach gemacht hast), Dr. Andreas Schuldt (N.D. Long – es war mir eine *great* Ehre mit dir das Zimmer + Taxi zu teilen: In tha city of Gutian Shan - In tha city of Mr. Fang! SPIGGEBIB!!), Dr. Sabine Both (Labina – dich kenne ich am längsten hier in Halle, wir haben schon so vieles gemeinsam erlebt und grüßen uns trotzdem noch freundlich: Danke dafür und für deine Hilfe!), Martin Baruffol (Ma Ting Ba – du bist sicher einer der angenehmsten Menschen überhaupt, hast viele unangenehme Situationen gerettet und mir bewiesen, dass man besser keine chinesischen Trinkspiele mit Kolumbianern spielt: *Gracias por todo! ...también a Juliana*), Anne C. Lang (Enna – auch du hast vieles erleichtert und ich freue mich nach wie vor über Musik von dir), Xueqin Zeng (Schürze – now that you’re almost German I shouldn’t write this in English, however, I really like to thank you for your help and for showing me the real *chinese way!*), Stefan Trogisch (Stiefel – Sachsen waren, sind und bleiben mir halt immer sympathisch: Danke für deine einmalige und unermüdliche Art), Bo Yang (Yang Bo – thank you very much for all the translation / organisation stuff and your smiling face) und Teng Fang (Mr. Fang lǎoshī – you are my personal chinese hero, no talking!). Ich denke, zusammenfassend war das wirklich eine sehr eingeschworene erste „*BEF China*“ Generation und ich bin froh ein Teil davon zu sein.

Ebenfalls großen Dank gilt **allen** Diplomandinnen und Diplomanden, Doktorandinnen und Doktoranden, sowie Mitarbeiterinnen und Mitarbeitern des Bereichs für Geobotanik und Botanischer Garten am Institut für Biologie der Martin-Luther-Universität Halle-Wittenberg. Besonders erwähnen möchte ich dabei die folgenden Personen: Anja Hallensleben, Felix Berthold, Christine Voigt, Anne Piel, Alexandra Erfmeier, Eva Bremer, Heike Heklau, Erik Welk, Isabell Hensen, David Eichenberg, Nadine Kreißig, Maria Hock und Alrun Siebenkaes. Für ihre große Hilfe bei Statistikproblemen, wichtigen Hinweisen bei Manuskripten und viele aufmunternder Worte möchte ich mich außerdem ausdrücklich bei Henrik von Wehrden und Christian Wirth bedanken.

Ganz persönlich gilt mein Dank vor allem meiner einzigartigen Familie, ganz egal ob Böhnke oder Raabe Seite. Danke für eure wirklich immer bedingungslose Liebe und euer großes Vertrauen in mich. Ich weiß, dass ihr alle stets für mich da sein werdet und nicht nur deshalb habe ich immer massig Platz für euch in meiner Brust! Hier schließen sich nun nahtlos die Kammerlanders und Pletzers an. Vielen Dank für die entspannten Stunden und eure Unterstützung, von Anfang an. Ich freue mich auf alles, was da noch so kommen mag. Stellvertretend möchte ich mich besonders bei Judith bedanken, die mir immer das Gefühl gab/gibt dazu zu gehören und mir (trotz *vogelwuidem Start*) auf eine sehr liebevolle Art und Weise ihr Vertrauen schenkt. Danke!

Sebastian, du hast mir hier in so vielerlei Hinsicht geholfen. Schön, dass wir nun schon so lange gemeinsam diesen Weg gehen. „Ein Freund ist ein Mensch, vor dem man laut denken kann“... daher mein spezieller Dank an Sven, Patrick, Gregor, Martin, Martin, Matthias, Jens, Tobias, Jan, Dominic und dem Rest von VmL & friends... und den Frauen an ihrer Seite!!!... ich glaube, wir vergessen manchmal vielleicht, wie gut wir es doch alle im Großen und Ganzen erwischt haben... oder um bei Christopher George Latore Wallace zu bleiben:

To all my friends in the struggle, you know what i’m sayin’ ?

Ah-ha, it’s all good baby bay-bee, uh !

...und Julia? *I can see your halo. You know you’re my saving grace. ...wir beede!!!*