Towards the determination of fundamental plant strategies and plant climate range limits by functional traits

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

vorgelegt dem Rat der Biologisch-Pharmazeutischen Fakultät
der Friedrich-Schiller-Universität Jena

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geboren am 10.04.1976 in Jena

Summary

It has long been known that plants differ in form and function (i.e. plants' functional traits) which reflect their adaptation to the environment globally and locally. Thus, functional traits provide a functional understanding of plants' geographical distribution but also of their co-existence at local scales. Since plants are subjected to fundamental eco-physiological, bio-mechanical and evolutionary tradeoffs, not all combinations of traits are possible but traits co-vary. Sets of co-varying traits – so called trait spectra – represent general plant strategy axes which can be quantified exploring the relationships among many traits for many plants distributed in different environments. Thus, the exploration of how and why functional plant traits vary among plants and among sites sheds light on two fundamental questions in plant ecology and functional plant geography:

1) *What are fundamental trait spectra and which general plant strategies do they reflect corroborating the prevalence of functional tradeoffs?*
2) *Which functional traits limit plants to distribute towards certain climates and which functional processes can be inferred driving large-scaled distribution patterns?*

This research attempted to answer these two questions for North American forest ecosystems. For the majority of shrub and tree species distributed across the whole North American continent, from the boreal to the subtropics as well as from arid to humid regions, 23 functional traits were explored.

To quantify fundamental trait spectra and to explore which general plant strategy axes they reflect, a distance based ordination method (Principle Coordination Analysis) was performed. Identified trait spectra were correlated with species specific shade, drought, water logging, fire tolerance and growth potential. These tolerances represent general strategies in forests because they are measures of whole plant performance in dependence on key environmental drivers among which woody species do trade off. Wood density, seed mass, maximum height, specific leaf area and life span were identified as key traits of partially independent trait spectra which were mainly correlated to species specific shade and drought tolerance and growth potential, respectively. The trait spectra identified here quantify the tradeoffs among fundamental plant strategies providing thus a more mechanistic understanding of plant functioning with respect to light and water availability. As seed mass, maximum height and specific leaf area belong to independent trait spectra, it supports additionally a conceptual trait-based plant strategy scheme which assumes these three traits *per se* as independent tradeoff axes. These findings confirm the use of the five key traits in order to quantify their limiting effect on species climate range limits.

To explore the limiting effects on species’ climatic distribution, linear quantile regression was performed predicting species’ climatic range limits derived from distribution ranges. Quantile regression is the preferred method to analyze the effect of a limiting factor on a response. It was found that traits reflecting adaptation to regional factors like drought (e.g. wood density and maximum height) limit species’ climatic distribution while traits reflecting adaptation to local factors such as shade (e.g. specific leaf area) did not show a clear effect. Quantifying limiting effects gives insights into the mechanistic processes underlying climate niche occupation of species and thus of large scale distribution pattern. Mapping the limiting effects of traits back into the geographical space ‘no-go’ areas and areas ‘unconstrained’ to occupy for a species could be determined. Such maps can be finally used to derive ‘species exclusion maps’ which might be useful when evaluating predictions of species distribution models for climate change scenarios. Furthermore, dynamic vegetation models which use these traits already as predictors of plant functioning could be easily improved when implementing their effects also on range limits, i.e. serving a dual purpose.

In summary, the results of both studies provide on the one hand side a deeper understanding of plant functioning in relation to their environment; on the other hand they have the potential to improve dynamic vegetation models and thus predictions under climate change scenarios.

Zusammenfassung

Es ist eine alte Erkenntnis, dass Pflanzen sich in Form und Funktion (d.h. in ihren funktionellen Merkmalen) unterscheiden und dass entsprechende Merkmale ihre Anpassung an die Umwelt widerspiegeln - sowohl auf globaler als auch auf lokaler Ebene. Funktionelle Pflanzenmerkmale sind somit der Schlüssel, um geographische Verbreitungsmuster sowie lokale Koexistenz von Pflanzen funktionell zu verstehen. Da Pflanzen im Zuge der Anpassung an die Umwelt ökophysiologischen, biomechanischen und evolutionären Kompromissen unterliegen, sind nicht alle Kombinationen von Merkmalen möglich, sondern bestimmte Merkmale korrelieren miteinander. Funktionelle Merkmale, die miteinander korrelieren – so genanntes Merkmalsspektrum – , repräsentieren ein Spektrum von verschiedenen Pflanzenstrategien. Generelle Merkmalsspektren können quantifiziert werden, wenn die Korrelationsstruktur vieler Merkmale von vielen Pflanzen aus unterschiedlichen Habitaten untersucht wird. Die Erforschung, wie und warum funktionelle Pflanzenmerkmale sich zwischen Pflanzen und zwischen ihren Verbreitungsorten unterscheiden, wirft Licht auf zwei fundamentale Fragen in der Pflanzenökologie und funktionellen Pflanzengeographie:

1) *Wie sehen grundlegende Merkmalsspektren aus, welche grundlegenden Pflanzenstrategien spiegeln sie wider und welche verschiedenen Funktionsweisen lassen sich somit spezifizieren?*
2) *Welche funktionellen Merkmale limitieren die klimatischen Verbreitungsgrenzen von Pflanzen und erlauben diese Limitationen Rückschlüsse auf grundlegende Funktionsweisen, die maßgeblich die Verbreitung von Pflanzen auf kontinentaler Ebene bestimmen?*

Diese Studie versucht diese zwei Fragen für nordamerikanische Wälder zu beantworten. Für die Mehrheit der über den ganzen nordamerikanischen Kontinent verbreiteten Busch- und Baumarten wurden 23 funktionelle Merkmale erhoben und analysiert. Um grundlegende Merkmalsspektren zu quantifizieren und um zu evaluieren, ob diese generelle Pflanzenstrategien widerspiegeln, wurde eine Hauptkoordinaten-Analyse (Principle Coordination Analysis) durchgeführt. Dazu wurden die quantifizierten Merkmalsspektren mit artspezifischen Schattentoleranz-, Trockentoleranz-, Überflutungstoleranz-, und Feuertoleranzzeigerwerten sowie Werten für Wachstumspotential korreliert. Diese Zeigerwerte reflektieren grundlegende ökologische Strategien in Wäldern, da sie ein Maß für die Gesamtfitness der Arten in Anhängigkeit von wichtigen Umweltfaktoren darstellen. Holzdichte, Samenmasse, maximale Pflanzenhöhe, spezifische Blattfläche und Lebensalter wurden als Schlüsselmerkmale z.T. unabhängiger

Merkmalsspektren identifiziert, die jeweils mit den artspezifischen Werten für Schattentoleranz, Trockentoleranz und potentiellem Wachstum korrelieren. Somit quantifizieren und validieren die identifizierten Merkmalsspektren die unterschiedlichen funktionellen Kompromisse zwischen verschiedenen Anpassungsstrategien an unterschiedliche Wasser- und Lichtverfügbarkeiten und geben so einen tieferen Einblick in die generellen Funktionsweisen von Pflanzen. Da Samenmasse, maximale Pflanzenhöhe und spezifische Blattfläche jeweils unabhängige Merkmalsspektren repräsentieren, stützen diese Ergebnisse zusätzlich konzeptionelle merkmalsbasierte Pflanzenstrategieschemata. In diesen Schemata repräsentieren diese drei Merkmale essentielle unabhängige Funktionsachsen, die selbst grundlegende biomechanische oder ökophysiologische Kompromisse widerspiegeln. Aufgrund dieser Ergebnisse wurde für die 5 Schlüsselmerkmale der limitierende Effekt auf die klimatischen Verbreitungsgrenzen der Strauch- und Baumarten quantifiziert. Lineare Quantilsregression wurde benutzt, um den limitierenden Effekt der Merkmale auf die klimatischen Verbreitungsgrenzen der Arten zu quantifizieren, welche von geographischen Verbreitungskarten abgeleitet wurden. Quantilsregression ist eine geeignete Methode, um den Effekt eines limitierenden Faktors auf eine biologische Auswirkung zu quantifizieren. Merkmale, die Anpassungen an regional wirksame Umweltfaktoren wie Trockenheit widerspiegeln (z.B. maximale Pflanzenhöhe) zeigen einen limitierenden Effekt auf die klimatischen Verbreitungsgrenzen, wohingegen Merkmale (z.B. spezifische Blattfläche), die Anpassungen an lokal wirksame Umweltfaktoren widerspiegeln (z.B. Schattentoleranz), keine deutlichen Effekte zeigen. Die Quantifizierung von limitierenden Effekten erlaubt eine Sicht auf Funktionsweisen von Pflanzen, die es ihnen ermöglicht bestimmte Klimanischen zu besetzen. Es können somit Pflanzenverbreitungsmuster grundlegender erklärt werden. Die Rückkartierung dieser Effekte in den geographischen Raum visualisiert dann Gebiete, die von Arten mit bestimmten Merkmalsausprägungen nicht besiedelt werden können (‚verbotene‘ Gebiete) und solche, wo es keine Einschränkungen gibt (‚uneingeschränkte‘ Gebiete). Solche Karten können beispielsweise genutzt werden, um ‚Artenabstinenzkarten‘ abzuleiten, mit denen man die Vorhersagen von Verbreitungsmodellen für zukünftige Klimaszenarien evaluieren kann. Weiterhin könnte die Vorhersagekraft dynamischer Vegetationsmodelle verbessert werden, wenn für jene Merkmale, die im Modell wichtige Pflanzenfunktionsprinzipien beschreiben, zusätzlich ihr limitierender Effekt auf klimatische Verbreitungsgrenzen implementiert wird, d.h. eine Mehrzwecknutzung der Merkmale.

Zusammenfassend tragen die Ergebnisse beider Studien einerseits zu einem tieferen Verständnis der Funktionsprinzipien von Pflanzen in Abhängigkeit von der Umwelt bei, andererseits haben sie das Potential Modelle, und somit deren Vorhersagen für zukünftige Klimaszenarien, zu verbessern.

Acknowledgements

In 2008 I started my PhD in the group “Organismic Biogeochemistry” headed by Christian Wirth at the Max-Planck-Institute of Biogeochemistry in Jena. He offered me scientific research on highly relevant questions using large data on plant functional traits – a great opportunity to do substantial work. I am very thankful for the many inspiring discussions, for introducing me to a nice scientific community and supporting me in scientific writing, making the publications of this thesis possible. I also thank Winfried Voigt and Gottfried Jetschke who co-supervised this thesis. I am very grateful for your interest, helpful comments and discussions and for careful reviewing this thesis.

I especially thank Björn Reu and Jens Kattge for exchanging ideas, critical questions and their careful proof-reading of many manuscript versions. Björn I thank for his strong support in the second paper, especially for providing data and for visualizing the results in attractive maps which made them more suitable for model evaluations. His straight-forward way to work was very helpful to structure and clarify the two papers of the thesis. Jens I thank for his carful proof reading of the first paper and his help requesting data from TRY. Many thanks to both of you for pushing and motivating me the whole time and for your immediate willingness to help whenever I asked for it.

I thank Kiona Ogle and John Dickie for their support on the first paper. Kiona Ogle’s extensive text editing clearly improved the first paper and John Dickie helped with the identification of taxonomic synonyms for the 305 tree species analyzed. I want to especially thank Gerhard Bönisch who helped me in all sorts of questions regarding databases and data downloading and who always had easy practical solutions for difficult problems.

Many scientists I have met during the last 5 years supported me and enriched my life in many different ways. Especially with my office mates Lee Miller and Fabian Gans I ran easily into philosophical discussion which I really enjoyed. Uli Weber provided me consistently with coffee which made thinking possible in the first place but made it also homelike. I thank Kristin Bohn, Jannis v. Buttlar, Dorothea Frank, Angela Günther, Myroslava Khomik, Axel Kleidon, Mario Liebergesell, Miguel Mahecha, Karin Nadrowski, Stefanie Nöllert, Katharina Pietsch, Raphael Proulx, Tanja Rheinhold, Sophia Ratcliffe, Markus Reichstein, Micha Rzanny, Franziska Schrodt, Carolin Seele, Susanne Tautenhahn, Kirsten Thonike and many others.

Finally, I thank my parents Sylvia Bartke and Klaus Bartke and my brother Steffen Bartke for their mental support and trust throughout my life and that they always encouraged me to go my own way. An enormous thankyou goes to my family – my husband Volker and my children Florian and Karoline. Thank you very much for your support, your love and endless patience and sympathy.

I thank the Max Planck society and the University of Leipzig for their financial support.

List of manuscripts included

This thesis consists of a published and an accepted manuscript which are the content of chapter 2 and 3, respectively. I am the first author of both manuscripts and contributed essentially to the conceptional design, statistical analysis and writing (see details below).

Stahl, U., J. Kattge, B. Reu, W. Voigt, K. Ogle, J. Dickie, and C. Wirth. 2013. Whole-plant trait spectra of North American woody plant species reflect fundamental ecological strategies. *Ecosphere* **4**:art128. http://dx.doi.org/10.1890/ES13-00143.1. This manuscript is inserted as copied pages of the journal.

Content:
This manuscript quantifies fundamental plant trait spectra and explores how they relate to plants' ecological performances corroborating the prevalence of general plant strategy axes and their underlying eco-physiological tradeoffs. The study is based on 23 different traits and 5 species-specific ecological performance measures for the majority of North American woody species (305 trees and shrubs).

Own contribution (in percent per content feature):
I contributed to the conceptual idea and the statistical design of the manuscript (70%) and edited and cleaned the data (100%). I did all of the statistical analyses (100%), made all the figures (100%) and interpreted and discussed the results together with Christian Wirth (80%). I wrote the manuscript and improved it by implementing text editing und suggestions from Jens Kattge, Björn Reu, Kiona Ogle, Winfried Voigt and Christian Wirth (80%) and was responsible during the whole publication process. I collected part of the data by myself from the literature (10%) while the main part was already stored in group intern data bases which were provided by Angele Nüske, Sabine Rensch, Kiona Ogle and Stefanie Nöllert or requested from the TRY database (see acknowledgements of this manuscript for details). The taxonomic information of considered species was provided by John Dickie (0%).

Stahl, U., B. Reu, C. Wirth. Predicting species' range limits from functional traits for the tree flora of North America, *PNAS, Special Feature Functional Biogeography* accepted 8.1.2014. This manuscript is inserted as manuscript.

Content:

This manuscript quantifies the limiting effect of 5 functional plant traits — seed mass, wood density, maximum height, specific leaf area and longevity — on climate range limits of 250 North American woody species and discusses the functional mechanisms behind it. It thus gives insight into mechanistic processes of plants' adaptations to the environment which govern species distribution patterns on a continental scale.

Own contribution:

I contributed to the conceptual idea and the statistical design of the manuscript (80%) and provided and organized the trait data (100%) while Björn Reu provided the climate and species distribution data (0%). I did all of the statistical analyses (100%) and made most of the figures (80%); I interpreted and discussed the results together with Christian Wirth and Björn Reu (80%). I wrote the manuscript and improved it by implementing text editing und suggestions from both co-authors (90%) and was responsible during the whole publication process.

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CHAPTER 1

1 General introduction

The recognition that plants' different form and function (i.e. plants' traits) reflect their adaptation to the environment and thus explain their distribution dates back to the end of the 19th century (Schimper 1898, Warming and Vahl 1909). Schimper was the first to explain the 'oecology of plant distribution' by relating plant traits to functional responses to environmental factors such as water, temperature and light. His thoughts about the relationships between temperature, precipitation and plant distribution were included in global vegetation models until the mid 1990s (Prentice et al. 1992, Box 1995). Raunkiaer (1934) and Box (1981) defined plant traits which are required for plants' existence in a particular site and thus laid the foundation of trait-based functional plant geography on a global scale. Parallel to the trait-based approaches at a global scale, trait-based approaches focusing on local scales, where species interact directly amongst each other, were developed. With the development of niche theory in the middle of the 20th century (Hutchinson 1957, MacArthur and Levins 1967), trait environment relations and plants' intrinsic tradeoffs expressed by traits were seen as paramount for species co-existence at local scales (reviewed in Chase and Myers (2011)) because they quantify fundamental ecological strategies. One important reason for intrinsic tradeoffs is that the amount of carbon a plant can allocate to different functions or processes is limited. Thus, a plant cannot do *everything equally well* but rather does *some things very well*. That means, investing carbon in certain structures (e.g. shoot biomass) to be well adapted to a certain environment comes at the cost of other structures (e.g. root biomass), i.e. the plant has to trade off between eco-physiological alternatives. Beside this there are also biomechanical tradeoffs (i.e. conduit size versus conductivity) and evolutionary tradeoffs plants have to deal with.

Today, it is widely accepted that functional traits are the key to quantify the different processes operating on local to global spatial scales (McGill et al. 2006, Weiher et al. 2011, Wiens 2011) and thus are suited to link the different trait-based approaches. The exploration of how and why functional plant traits vary among plants and among sites sheds light on fundamental questions in plant ecology and functional plant geography: 1) What are plants' fundamental adaption mechanisms to the environment and what are the intrinsic tradeoffs plants are subjected to? 2) What are the functional mechanisms behind species distribution patterns on continental scales?

These two questions are the overarching topic of the chapters 2 and 3 which contain two research arcticles, respectively (see list of manuscripts). The following chapter 1 consists of an overview of how plant traits are currently defined and used to determine fundamental plant strategies and tradeoffs. Furthermore, it reviews different niche concepts and explaines how plant traits are related to them. At the end of this chapter the relevance of plant trait research with respect to the two research questions is described, including a short introduction of the research arcticles presented in chapters 2 and 3. Chapter 4 contains an overall discussion of the used methods and results of the articles, respectively and ends with general conclusions including future perspectives.

1.1 Definition of plant functional traits

To explore these questions, a unified definition of functional plant traits, plant performance and fitness are necessary. Violle et al. (2007) provide definitions of these terms and explain how they relate to each other. Their concept is widely accepted and used in recent plant trait research (Kattge et al. 2011).

Violle et al. (2007) defined a functional trait as *“any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization […] which impacts fitness indirectly via its effects on growth, reproduction and survival”.*

This definition is suited to investigate trait variation among plants and to explore trait-environment relationships because 1) a functional trait is a measurement on the smallest unit (i.e. the individual) which is actually subjected to evolution by natural selection, 2) a trait is based on the performance idea of Charles Darwin (1859) who realized that functional traits are proxies of an individual’s fitness in a given environment and 3) a functional trait is free of environmental or organizational descriptors which allows correlation with these without circular reasoning. As the functional traits impact plant fitness indirectly, Violle et al. (2007) defined the linkage between functional traits and plant fitness via three performance measures which they called *“performance traits”*. According to their concept, vegetative biomass is a performance trait which is linked to growth as is a fitness measure. Analogous plant survival and reproduction output are performance traits which are linked to the fitness measures mortality rate and fecundity respectively. Furthermore, Violle et al. (2007) separate the term *“ecological performance”* (e.g., species’ shade tolerance) from functional traits (e.g., seed mass) and define it as an optimum and/or breadth of at least one of three mentioned performance traits along an environmental gradient. This means that for instance shade, drought and frost tolerance are reflected by a set of correlated functional traits covering morphological, anatomical and demographic traits, which impact the three fitness components growth, reproduction and survival rather than a single trait.

When using plant functional traits for global species and vegetation modeling they must fullfill additional requirements (Cornelissen et al. 2003, Lavorel et al. 2007): the traits should 1) be linked to a certain function (e.g. nutrient resorption, light interception, dispersal and recruitment), 2) show a consistent ranking across species when environmental conditions vary (e.g. CO_2, soil resources, disturbance, climate, competitive strength and plants' defense against herbivores and pathogens) and 3) be easily measureable for many plants.

1.2 Plant functional traits with respect to plant strategy concepts, tradeoffs and species' niche differentiation

In the most general sense, plant strategies are the units or entities of functional classification schemes which try to classify plants on functional grounds and not on taxonomy (Cornelissen et al. 2003) with functional plant traits being used to describe them. However, the concept of 'plant strategy' is used from different perspectives: 1) plants' different functions or 2) plants' different responses to the environment and their underlying tradeoffs or 3) plants' intrinsic tradeoffs to which they are subjected to (Cornelissen et al. 2003, Reich et al. 2003a). An example for the first perspective is the classification of plants into separate groups based on qualitative traits (e.g. C3 vs C4 plants or tree vs shrub vs herb). These traits are largely used in large scale vegetation models to determining plant functional types (PFTs). Examples for the second perspective are conceptual strategy schemes which determine integrated whole plant behavior with respect to important environmental drivers (e.g. tradeoffs between plants' ability to tolerate shade and drought discussed by Smith and Huston (1989), or the CSR scheme of Grime (1977, 1979)). In these schemes three tradeoff axes are distinguished along which the different plant strategies are separated. However, these schemes are difficult to verify using many different species from diverse environments, because complex whole plant performance measures are necessary to determine the strategies. Moreover, the functional adaptation of plants (i.e. the prevalence of certain traits) enabling these strategies cannot be inferred directly. According to the third perspective, single traits are assumed to reflect meaningful causal tradeoffs plants are subjected to and are thus suggested to describe together the main axes of plant functioning (Westoby 1998, Westoby et al. 2002, Westoby and Wright 2006). In such trait-based plant strategy schemes, the position of a taxon in the trait space determines its functional strategy. This scheme could be easily verified when analyzing the respective traits for many taxa from many different habitats. Since plant functional traits reflect plants' adaptation to the environment but also eco-physiological, biomechanical and evolutionary tradeoffs a plant has to deal with, they do not vary independently but are correlated with each other (Lavorel et al. 2007). This motivates a number of studies which try to identify co-varying sets of traits by analyzing trait correlation structure among many species, i.e. identification of so called 'trait spectra' or 'trait syndromes' (Grime et al. 1997, Reich et al. 2003a, Diaz et al. 2004). Such trait spectra are then thought to reflect 'general plant strategy axes' or 'axes of general plant specialization'. The position of a taxon along these 'axes' relates to how a species "makes a living" (Wright et al. 2007) and represent therefore species' niche differentiation. Prominent examples are the leaf economic spectrum (Wright et al. 2004) and the wood economic spectrum (Chave et al. 2009), which both reflect fundamental eco-physiological and biomechanical tradeoffs. Two to four such 'strategy axes', which themselves reflect tradeoffs and are independent to each other are determined (Diaz et al. 2004, Wright et al. 2007, Baraloto et al. 2010) exploring species trait matrices containing many species but few traits.

However, the explanation of high species diversity failed using only few 'tradeoff axes' as in nature many species co-exist without obvious niche differentiation along few axes (Clark et al. 2007). On the other hand, assuming multiple tradeoff axes could explain high species diversity (Clark et al. 2007). Thus, a major aim is to identify 'general plant strategy axes' and to determine their underlying fundamental tradeoffs. This is the basis to understand species' niche differentiation, species coexistence and species sorting across large gradients and hence patterns of biodiversity. However, to capture the different tradeoffs which are suggested to pre-requisite species co-existence on local and regional scales (see for instance, Chase and Leibold 2003, Kneitel and Chase 2004) it requires a large set of traits for many different species. For example traits reflecting tradeoffs to resource use, uptake or storage strategies are different to traits reflecting tradeoffs to stress tolerances like herbivory or frost and those are again different to traits reflecting tradeoffs to reproduction strategies. To quantify trait spectra with respect to their underlying tradeoffs one could relate them to vital rates (e.g. mortality, growth, survival) which describe together whole plant performance (e.g., Wright et al. 2010). One could also relate trait spectra to whole plant performance measures which reflect adaptation to key environmental drivers (e.g., Hallik et al. 2009).

1.3 The ecological niche concept and its application

To describe, model and understand patterns of plants' distributional areas, plant geographers and vegetation modelers focus on species ranges and their limits. They are especially interested in processes operating on regional to continental scales at low resolution (e.g. at grid cell levels of 10-50 km²) and try to describe species' ecological niche. According to Sexton (2009)*"Species range limits are essentially the expression of a species' ecological niche in space"*. More generally, the ecological niche represents the n-dimensional hyper volume of conditions (i.e. niche axes or dimensions) where a species is positioned where it can grow, reproduce and survive (Hutchinson 1957).

The ecological niche comprises of two different aspects: one operating on population scale and the other one operating on individual scale - both controlling species range limits (Soberon 2007). The first is the 'Grinnelian' niche which is described by non-interacting environmenetal factors like temperature, solar radiation and soil type which control species' eco-physiology on broad scales and are relevant to understand coarse-scale ecological and geographic properties of species. It describes the environmental conditions in which birth rates are higher or equal to death rates. The second is the 'Eltonian' niche which focuses on biotic interaction and resource partitioning like competition, mutualism, predation, pathogens. It describes a species' impact on its surrounding environment and operates on local fine grained spatial scales at which individuals can interact. Both concepts are codified by Hutchinson (1957) into fundamental and realized niches, respectively. Thus, the geographic distribution of a species, i.e. the 'realized' distribution of a species, is classically defined as the 'fundamental' distribution dependent on physical conditions, reduced by biotic factors within the constraints set by historical factors (Morin et al. 2007).

According to the 'fundamental' and 'realized' niche aspects contemporary models predicting plant distribution (focusing on species or PFT level) can be grouped into two classes (Morin and Lechowicz 2008): 1) the mechanistic process based models which model typically the fundamental niche based on general tradeoffs known to affect species' fitness and 2) the correlative models which model the realized niches correlating environmental parameters to species' spatial distribution (e.g. presence/absence). Mechanistic models are limited in the number of species because a lot of species-specific demographic and eco-physiological traits are necessary. On the other hand, they give insight into mechanisms limiting species distribution and are therefore suited for prediction under future climate conditions. By contrast, correlative models can easily predict the ranges of many species based on environmental data by correlating e.g.

species presence/absence information with e.g. climate date (climate envelope models) quantifying the climate niche. However, they do not provide any information on the underlying processes assuming equilibrium with the climate and are thus not suited to make predictions under future climate scenarios. Moreover, history (changes in geology, lineages that reflect phylogenetic conservatism), source-sink dynamics and biotic interaction are essential factors determining species realized niches (Soberon 2007) but are not included in such models (Zimmermann et al. 2010). Recent advances propose a hierarchical modeling framework integrating the different factors and accounting explicitly for the spatial nestedness of processes, i.e. a species undergoes successive filters (Boulangeat et al. 2012). The first filter determines species' presence or absence and is primarily driven by abiotic variables determining species' eco-physiological limitations and by dispersal limitations (history). The second filter is determined by species' dispersal limitations and/or historical legacies. The third filter determines species' local abundance mainly driven by biotic interactions and dispersal in case of source-sink dynamics. Morin and Lechowitz (2008) propose a similar hierarchical approach using different process based models based on the idea of Silverton (2006). They modeled species distribution locally (at a specific location), at landscape/habitat scale (many locations reflecting for instance micro climate and topography) and at the continental/regional scale (many landscapes). From local to continental scale species alpha niche, beta niche and gamma niche is represented, respectively. Thereby each of these niches is defined by certain traits and environmental factors influencing species distribution at each of these scales. However, only few species and vegetation models follow a trait-based niche view (Kearney et al. 2010, Dormann et al. 2012). On of the reasons for this is that community ecologist investigate processes on local scales rather than this more theoretical concept of community ecology (Ackerly and Cornwell 2007, Cornwell and Ackerly 2009, Chase and Myers 2011, Weiher et al. 2011).

1.4 The trait-based niche concept and its application

Whether a species successfully survives, reproduces and growths in a given environment depends on how well its form and function (i.e. its traits) fits with the environment. Because functional traits are related to species' fitness (sensu Violle et al. 2007) a species' niche is determined by its functional traits (Rosenzweig 1987, Chase and Myers 2011). This is the theoretical background of the 'niche-based' filter concepts in community ecology in which local assemblages of species are filtered subsets of a regional species pool because they have certain traits allowing them to pass certain environmental filters (Keddy 1992, Weiher and Keddy 1995, Webb et al. 2010, Götzenberger et al. 2012). Analog to the ‘Eltonian’ and the ‘Grinellian’ niche the authors distinguish between abiotic = ‘fundamental’ and biotic = ‘realized’ niche filters. The abiotic niche filters determine whether a species has the required traits to colonize, establish and persist in a given habitat. The biotic niche filters are imposed by the interactive milieu of competitors, mutualists and consumers reflecting niche differentiation due to different use of resources and adaptation to herbivory and pathogens. The effect of the two filters result in two patterns considering trait variation of coexisting species: 1) abiotic filters result in trait convergence (species are more similar in their trait values compared to randomness) and 2) biotic filters result in trait divergence (species differ more in their trait values compared to randomness). Both filters reflect two different processes which are assumed to occur in a predicted manner with increasing spatial scale (here extant) and along environmental gradients within a study location. At small spatial scales (e.g. at plot level) trait divergence is expected to dominate due to limits in similarity; when the spatial scale increases (e.g. towards landscapes and continents) trait patterns should become first neutral and shift than to convergent trait patterns due to environmental constraints (Weiher and Keddy 1995). The process of trait convergence is also called ‘habitat or environmental filtering’ while the process of trait divergence is called ‘biotic filtering’. Along an environmental gradient from unfavorable to favorable conditions (e.g. along a drought gradient on local scales) ‘habitat filtering’ occurs in the most unfavorable conditions whereas ‘biotic filtering’ occurs in more favorable conditions (Weiher and Keddy 1995, Weiher et al. 1998). These mechanisms seem to operate also on larger scales, e.g. along latitudinal gradients from the poles to the equator, resulting in a shift from trait convergence to trait divergence (Swenson et al. 2011).

To understand patterns of species distribution and mechanisms at species ranges across large scales, the main goal is to identify which environmental factors act on which traits and how those factors filter these traits across gradients in space and time. Thus, quantifying trait-environment relationships can be used to predict the filtered trait distribution at different points in space and time. At at the same time it allows a back calculation from traits to species niche parameters (e.g. lowest tolerable temperature) which might be reflected by species range limits (e.g. species northern range limits). That means certain trait attributes limit a plant to distribute towards certain environments because of constrained trait performance. Hence, the prediction of, for instance, species temperature range limits from traits can provide insight in the functional mechanisms constraining species distribution towards areas of low temperature.

Mac Arthur (1972) proposed that the balance between abiotic and biotic factors explaining species distribution depend on the latitude. Species northern distributional limits were due to physical environmental constrains (e.g. cold tolerance) and species southern distributional limits were due to competition. Abiotic factors have often been identified to set northern range limits but biotic factors do not necessarily set southern range limits (Morin et al. 2007). Thus, to understand the processes operating on the different parts of species ranges ideally, multiple traits responding to abiotic (e.g. temperature, seasonal growth length, water availability) and to biotic factors (e.g. predators, species' interaction) need to be considered. Which traits and which of these factors are important depends on the spatial scale and the ecosystem to be investigated. If investigating for instance species distribution limits along a temperature gradient only temperature sensitive traits impacting performance will show a response while other traits for which temperature does not act as an performance filter will not show any response (Webb et al. 2010).

1.5 On the relevance of the plant functional trait approach

Since plant traits can be measured for any individual worldwide, relationships among traits and between traits and environmental parameters are quantifiable and thus, plants' adapation to the environment and fundamental tradeoffs can be determined. Due to the increasing availability of plant trait data, the analysis of such relationships for many traits and many species from many different environments becomes possible (Kattge et al. 2011). This means, 1) 'general plant strategy axes', their underlying tradeoffs and the key traits reflecting them can be detected (Wright et al. 2004, Wright et al. 2010) and 2) functional processes governing species distribution and diversity patterns across large environmental gradients become quantifiable (Moles et al. 2006, Moles et al. 2009, Swenson et al. 2011). Both findings are useful for modelers whose ultimate goal is to identify a minimal list of traits which together represent key responses and effects of vegetation at various scales from ecosystem, landscape, biome, continent (Cornelissen et al. 2003, Lavorel et al. 2007). As climate can have strong direct and indirect impacts on species distribution (Chen et al. 2011) and therefore on species traits it might alter the composition of communities and can thus change ecosystem processes and biodiversity (Lavorel and Garnier 2002). Therefore a major motivation analyzing large trait-species matrices is the possibility to improve and evaluate models that predict species distribution or vegetation under climate change scenarios. However, current global vegetation models are often simplistic and theoretical, their mechanistic understanding is limited and the lack of valuable data to test and parameterize those models causes high uncertainty when making predictions (McMahon et al. 2011). For instance, in contemporary climate envelope models (also known as habitat or niche models) and in dynamic global vegetation models (DGVMs) the real mechanistic processes determining distribution limits of species or plant functional types are unknown and only fixed bioclimatic limits derived from distribution maps are implemented. Thus, to understand species range limits on a functional basis one ultimate aim is to identify the traits which limit a species to expand its range (Wiens 2011). Furthermore, empirical findings of co-varying traits which reflect general tradeoffs could be used to evaluate contemporary tradeoff based vegetation models (e.g., Reu et al. 2010) and could be directly implemented in future trait-based vegetation models (Scheiter et al. 2013).

1.6 Research questions

In this thesis I focus on two main questions for which the analysis of plant traits has the potential to quantify ‘general plant strategies axes’ deepening consequently the understanding of fundamental tradeoffs and to explore functional mechanisms limiting species distribution:

1) *What are fundamental trait spectra and do they reflect general plant strategies corroborating the prevalence of functional tradeoffs?*

2) *Can functional traits predict species climate range limits and do the relationships give insights into mechanistic processes of plants’ adaptations to the environment governing finally species distribution patterns on continental scale?*

Answering question one will provide key traits which describe ‘general plant strategies’ such as shade and drought tolerance and as such recurrent pattern of plant specialization and their underlying tradeoffs. The key traits themselves and/or their underlying tradeoffs could improve tradeoff-based vegetation models like JeDi (see e.g., Reu et al. 2010) but also vegetation models which go beyond the classical PFT classification scheme (Van Bodegom et al. 2011). Furthermore, theoretical trait based plant strategy concepts can be refined and our understanding of the functional mechanisms how plants are adapted to the environment and how these adaptations reflect fundamental tradeoffs in terms of costs and benefits can be improved.

Answering question two will provide a mechanistic understanding of species sorting across large environmental gradients by linking ‘trait-based’ and ‘ecological-based’ niche concepts. Found trait-climate range limit relationships could be transferred into the geographical space and maps visualizing areas constrained for certain trait values could be used to evaluate future trait based vegetation models (e.g., Scheiter et al. 2013). Furthermore, trait-climate range limit relationships have the potential to be implemented in DGVMs which go beyond PFT classification and to replace for example the fixed bioclimatic limits for PFTs. This would make such models more mechanistic allowing for better prediction under climate change scenarios.

1.7 Overview

The study presented in Chapter 2 quantifies fundamental plant trait spectra and explores how they relate to plants' ecological performances corroborating the prevalence of fundamental eco-physiological tradeoffs. The study is based on 23 different traits and 5 species-specific ecological performance measures for the majority of North American woody species (305 trees and shrubs). The 23 traits are causally related to growth, reproduction and survival (i.e. plant fitness, sensu Violle et al. (2007)) and reflect adaptation to the key environmental factors light, water, disturbance and stress by relevant plant functions (e.g. storage, resource acquisition, dispersal) carried out by different organs (e.g. stem, leaf, seed). Furthermore, they accomplish the additional requirements of modelers, as they are easy to measure for many species and vary with environmental factors. The 305 woody species are distributed across the whole North American continent covering large climate gradients from the boreal to the subtropics as well as from arid to humid regions. The 5 different ecological performance measures (e.g. shade and drought tolerance) used represent whole plant behavior that affects plant performance along key resource gradients such as light and water and important disturbance impacts like fire. Thus, the large species-trait matrix as well as the straightforward approach relating trait spectra to "*ecological performances"* sensu Violle et al. (2007) is suited to determine 'general plant strategy axes' and their underlying tradeoffs predominant in North American forests.

The study presented in Chapter 3 explores the predictive power of 5 functional plant traits — seed mass, wood density, maximum height, specific leaf area and longevity — on climate range limits of 250 North American woody species. The five traits represent key traits which themselves represent general tradeoffs plants have to deal with (e.g. seed mass reflect a seed size versus seed number tradeoff) and which represent an adaptation to key environmental factors like water and light availability. Four of them (seed mass, specific leaf area, maximum height and wood density) are key traits of complex trait spectra reflecting 'general plant strategy axes' (e.g. specific leaf area is a key trait of the leaf economic spectrum, (Wright et al. 2004)). Thus, these five traits together should capture a large amount of tree and shrub strategies and might largely determine woody species' niches. Therefore, they have a large potential to predict species abiotic and biotic niche parameters. In this study only the response of climate niche limits like species' maximum and minimum temperature range limit to the five traits is quantified and functional mechanisms of how woody species control climate range limits are explored.

CHAPTER 2

2 Whole-plant trait spectra of North American woody plant species reflect fundamental ecological strategies

esa ECOSPHERE

Whole-plant trait spectra of North American woody plant species reflect fundamental ecological strategies

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Citation: Stahl, U., J. Kattge, B. Reu, W. Voigt, K. Ogle, J. Dickie, and C. Wirth. 2013. Whole-plant trait spectra of North American woody plant species reflect fundamental ecological strategies. Ecosphere 4(10):128. http://dx.doi.org/10.1890/ES13-00143.1

Abstract. The adaptation of plant species to their biotic and abiotic environment is manifested in their traits. Suites of correlated functional traits may reflect fundamental tradeoffs and general plant strategies and hence represent trait spectra along which plant species can vary according to their respective strategies. However, the functional interpretation of these trait spectra requires the inspection of their relation to plant performance. We employed principle coordinate analysis (PCoA) to quantify fundamental whole-plant trait spectra based on 23 traits for 305 North American woody species that span boreal to subtropical climates. We related the major axes of PCoA to five measures of plant performance (i.e., growth rate, and tolerance to drought, shade, water-logging and fire) for all species and separately for gymnosperms and angiosperms. Across all species a unified gymnosperm-angiosperm trait spectrum (wood density, seed mass, rooting habit) is identified, which is correlated with drought tolerance. Apart from this, leaf type and specific leaf area (SLA) strongly separate gymnosperms from angiosperms. For gymnosperms, one trait spectrum emerges (seed mass, rooting habit), which is positively correlated with drought tolerance and inversely with shade tolerance, reflecting a tradeoff between these two strategies due to opposing trait characteristics. Angiosperms are functionally more diverse. The trait spectra related to drought tolerance and shade tolerance are decoupled and three distinct strategies emerge: high drought tolerance (low SLA, dense wood, heavy seeds, taproot), high shade tolerance (high SLA, shallow roots, high toxicity, opposite arranged leaves), and fast growth/stress intolerance (large maximum heights, soft wood, light seeds, high seed spread rate). In summary, our approach reveals that complex suits of traits and potential tradeoffs underlie fundamental performance strategies in forests. Studies relying on small sets of plant traits may not be able to reveal such underlying strategies.

Key words: drought tolerance; forests; ordinal-scaled traits; plant performance; plant strategies; principle coordinate analysis; shade tolerance; trait tradeoffs; vital rates.

Received 25 April 2013; accepted 23 May 2013; final version received 20 September 2013; **published** 25 October 2013. Corresponding Editor: D. P. C. Peters.

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INTRODUCTION

Plant functional traits reflect adaptations to the environment and affect ecosystem functioning. They are thus the key inferring plant strategies and for predicting ecosystem properties (Cornelissen et al. 2003, McGill et al. 2006, Lavorel et al. 2007). Plant strategies are manifested in a suit of whole-plant performances including e.g., reproduction, growth and survival, each governed by a particular set of morphological, anatomical or physiological traits. Characterizing plant strategies therefore requires the knowledge of many traits. However, we typically lack the complete information on multiple important traits, because plant trait datasets are often biased towards a few traits that are easily measured (e.g., characteristics of leaves, seed weight, plant maximum height), while other traits may only be available for a small subset of plant species (e.g., potential allelopathy, bark thickness) (Kattge et al. 2011).

Functional traits are often grouped as sets of co-varying traits that reflect evolutionary or biophysical tradeoffs and hence jointly represent an axis of trait variation (trait spectrum) along which plant species can vary according to their respective strategies (Reich et al. 2003, Lavorel et al. 2007). Such trait spectra are typically identified with dimension reduction methods that extract lower-dimensional information (orthogonal principle components) from multidimensional trait data sets (Grime et al. 1997, Wright et al. 2007). Two prominent examples are the leaf and the wood economic spectrum (Wright et al. 2004, Chave et al. 2009) each of which described by a characteristic set of co-varying traits. The two spectra appear to be orthogonal to one another (Baraloto et al. 2010). This implies that the number and types of traits that vary independently of each other (i.e., not necessarily the total number of traits) determine unique strategy axes. However, proving the existence of trait spectra per se does not necessarily tell us anything about their relevance for whole-plant performance and for vital rates such as growth, stress tolerance or reproduction. Thus additional information on plant performance must be considered to fully understand their implications. This is challenging because comparative field data on species-specific performances controlled for the biotic and abiotic environment are scarce. Hence, studies relating traits to performances are typically conducted in controlled settings, often with short-lived herbaceous species (Poorter and Van der Werf 1998, Useche and Shipley 2010). Such 'rates and traits' studies for trees are typically restricted to growth and mortality and conducted on well-studied small forest plots with homogeneous environmental conditions (Rüger et al. 2012). Biome-scale studies are lacking. Moreover, there are hardly any studies focusing on more holistic performance measures such as niche preferences or stress tolerances—integrating growth, survival and recruitment—despite the fact that these are critical for understanding vegetation composition and dynamics under global change.

In forest communities, light and water availability are critical drivers of temporal and spatial processes such as succession and zonation (Smith and Huston 1989, Pacala et al. 1996, Poorter and Markesteijn 2008). Species-specific shade and drought tolerances are typically inferred as ordinal indices ('scores') from occurrences and vitality along gradients of light and water availability and are viewed as suitable measures of performance. Niinemets and Valladares (2006) found an inverse relationship between shade and drought tolerance indices among woody species of different plant functional types for all continents that aligns with Smith and Huston's (1989) cost-benefit tradeoff model. This model predicts (1) no viable strategies should exist under both low light and low water due to conflicts between allocation to roots versus shoots, (2) under abundant light and water, the highest growth rates are expected in species deemed intolerant of both stresses, and (3) a tradeoff between high growth under favorable conditions versus low growth under more stressful conditions (Craine 2009). The first two predictions suggest a tight tradeoff between shade and drought tolerance, implying a highly constrained trait space (i.e., limited niche differentiation) for traits underlying these tolerance indices. Independence between these two tolerance indices would indicate a more flexible trait space (Sack 2004). Trait-based analyses, however, have yielded ambiguous results. For instance, Hallik et al. (2009) identified leaf traits underlying the inverse relationship between shade and drought tolerance of temperate tree species, while Markesteijn and Poorter

(2009) found different trait spectra associated with shade and drought tolerance of tropical tree seedlings based on leaf, stem and root traits.

Disturbance events that lead to significant biomass loss can interact with stress tolerance strategies to affect whole-plant performance. This implies the existence of other strategies related to the ability to tolerate or recover from disturbances such as fires, wind-throw, or snow-break. For instance, Loehle (2000) described a tree strategy scheme with four independent axes (shade tolerance, tree height, seed dispersal, capacity to resprout) that was incorporated into a fitness-based model to predict species richness under different disturbance regimes in North American forests. According to Bond and Midgley (2001), three of these four axes align with the traits and tradeoffs defined in Westoby's (1998) LHS scheme (L = specific leaf area [SLA] relates to shade tolerance; H = maximum tree height; S = seed mass relates to seed dispersal). Loehle's fourth axis (capacity to resprout) reflects adaptations to disturbance (Pausas and Lavorel 2003).

In summary, the linkage between plant functional traits and tolerance indices which reflect whole-plant performance as a function of growth, reproduction and survival along environmental and disturbance gradients has yet to be quantified. This quantification requires species-specific information for a potentially large number of traits (Grime et al. 1997, Diaz et al. 2004, Wright et al. 2007) that reflect adaptations to key environmental factors (Cornelissen et al. 2003, Lavorel et al. 2007) and influence whole-plant performance (Violle et al. 2007) ideally for a large number of species.

In this study, we developed a database that contains information on 23 traits for 305 North American woody species that span boreal to subtropical climates. We conducted principle coordinate analyses (PCoA) to identify dominant trait spectra, and we evaluated how these spectra are related to whole-plant performance indices. In doing so, we addressed three sets of questions: (1) What are the dominant trait spectra, what are the traits underlying each spectrum, and how do they relate to whole-plant performance measures, i.e., growth rate and tolerance to shade, drought, water-logging, and fire? (2) Do the relationships between trait spectra and performances differ between major phylogenetic clades, such as gymnosperms versus angiosperms? (3) To what degree do these trait spectra agree with existing plant strategy schemes proposed by Westoby (1998) and Loehle (2000)?

MATERIAL AND METHODS

Selection of species and traits

The primary literature and various existing databases (USDA, NRCS, National Plant Data Team 2007, Kattge et al. 2011) were mined for data on functional traits for the 305 North American woody species (103 gymnosperms, 202 angiosperms) identified by the US Forest Service's Forest Inventory and Analysis (FIA) program (Miles et al. 2001) (see Appendix A: Table A1 for a complete list). The species span a range of habitat types (semi-arid woodlands, mesic temperate, boreal, to sub-tropical forests), and are classified mostly as trees (only 16 shrubs are included, of which 7 are chaparral species). The 305 species are phylogenetically dispersed across 79 genera, 36 families, 16 orders, and the two major clades.

To identify traits that most likely reflect adaptation to key environmental factors and that are likely to be related to whole-plant performance we used the following criteria: (1) traits are causally related to fitness components, i.e., growth, reproduction and survival (Violle et al. 2007), (2) they reflect adaptation to constraints by water and light, (3) they are related to the ability to resist or recover from disturbances, and/or adaptation to competition stress (Lavorel et al. 2007), (4) they reflect relevant functions (storage, defense, resource acquisition, dispersal) carried out by different plant organs (leaf, stem, root, seed) and (5) they are quantifiable for many species spanning a range of resource, climatic, and disturbance gradients. To minimize trait redundancy, we avoided selection of multiple, correlated traits related to the same tradeoff; e.g., only one trait (SLA) was chosen from the leaf economics spectrum (Wright et al. 2004). We focused on 23 traits that fulfilled these criteria (Table 1 and Appendix A: Table A2 for a detailed description).

In case of multiple values per species we averaged across the individual values to obtain one species-specific trait value. All traits were available for at least 70% of the species, except for

Table 1. Traits with their respective units or categorical levels and performance measures compiled including their main sources.

Trait/performance	Data type	Trait levels or units	Abbr.†	Source
Leaf traits				
Leaf composition	nominal	composite vs simple	lcomp	1
Leaf arrangement	nominal	alternate	alt	1
		whorled	lwhorl	
		opposite	lopp	
		spirally	lspir	
		shoots	lshoot	
Leaf type	nominal	evergreen needle leaved	evnd	1
		deciduous needle leaved	dcnd	
		evergreen scaled	evsc	
		evergreen broad leaved	evbr	
		deciduous broad leaved	dcbr	
		evergreen/deciduous broad leaved	evdcbr	
Leaf margin	ordinal	0 = entire, 1 = toothed and/or entire, 2 = toothed , 3 = lobed	lmar	2‡
Specific leaf area	continuous	cm^2/g	sla	3
Reproduction traits				
Dispersal syndrome	multi-choice nominal	dispersal via animals	animal	(4, 5, 6)§
		dispersal unassisted	unass	
		dispersal via water	water	
		dispersal via wind	wind	
Seed mass	continuous	mg	seed	(4,5)§
Seed spread rate	ordinal	0 = none, 1 = slow, 2 = moderate, 3 = rapid	sspr	7
Vegetative spread rate	ordinal	0 = none, 1 = slow, 2 = moderate, 3 = rapid	vspr	7
Resprout ability	binary	able to resprout vs not able to resprout	sprout	7
Root and stem traits				
Rooting habit	nominal	taproot	taproot	8
		shallow root	sha.root	
		variable root habit	var.root	
Bark surface	ordinal	1 = smooth, 2 = between smooth and medium, 3 = medium, 4 = between medium and rugged, 5 = rugged	barksu	1
Bark thickness	continuous	cm	barkth	8
Wood density	continuous	g/cm^3	wood	9, 10
Maximum height	continuous	m	height	8
Conduit type and arrangement (porosity)	multi-choice nominal	vessels ring porous	rp	8, 11, 12
		vessels diffuse porous	dp	
		vessels semi ring porous	sr	
		tracheids	tr	
Plant level traits				
Lifespan	continuous	years	age	7, 12‡
C:N ratio (% carbon/ % nitrogen)	continuous	unitless	CN	7‡
Nitrogen fixation	ordinal	0 = none, 1 = low < 85 lb N/acre/year, 2 = medium = 85-160, 3 = high > 160	Nfix	7
Toxicity	ordinal	0 = none, 1 = slight, 2 = moderate, 3 = severe	tox	7
Potential allelopathy	ordinal	0 = none, 1 = slight, 2 = moderate, 3 = strong	allelo	13
Growth form	nominal	tree	tree	1
		shrub	shrub	
		tree/shrub	tree/shrub	
Fire resistance (flammability)	binary	fire resistant vs not fire resistant	fireres	7
Performance measures				
Growth rate	ordinal	1 = slow, 2 = moderate, 3 = rapid	GROWTH	7
Shade tolerance	continuous	scores from 1 = low to 5 = high	SHADE	14
Drought tolerance	continuous	scores from 1 = low to 5 = high	DROUGHT	14
Water-logging tolerance	continuous	scores from 1 = low to 5 = high	WATER	14
Fire tolerance	ordinal	0 = none, 1 = low, 2 = medium, 3 = high	FIRE	7

Notes: Sources are 1, Flora of North America Editorial Committee (1993); 2, Adams et al. (2008); 3, Ogle et al. (2012); 4, Moles et al. (2005); 5, Royal Botanical Garden KEW (2008); 6, Paula et al. (2009); 7, USDA, NRCS, National Plant Data Team (2007); 8, Appendix B; 9, Zanne et al. (2009); 10, Jenkins et al. (2004); 11, Inside Wood (2004); 12, Dallwitz et al. (1993); 13, Coder (1999); 14, Niinemets and Valladares (2006). For detailed description of traits and their ecological function see Appendix A: Table A2.

† Abbreviations used in Figs. 1-4.

‡ For details regarding how trait scales were adapted see Appendix B.

§ Data were provided via the TRY initiative (Kattge et al. 2011), which includes data from different sources given in brackets.

'dispersal mode', which we included despite that it was only available for 54% of the species (see Appendix A: Table A3). The species-trait matrix that we compiled was 85% complete (15% missing data). The fraction of missing information was further reduced to 4% by replacing missing continuous and ordinal traits with the mean values of the respective genera. The 23 traits included nine nominal traits (e.g., leaf type, root habit), seven ordinal traits (e.g., bark surface, seed spread rate, nitrogen fixation), and seven continuous traits (e.g., SLA, seed mass); see Table 1 for the complete list. Because we are interested in broad patterns across species, variability within a species was not incorporated into the analysis.

Selection of performance measures

We selected five species-specific performance measures: growth rate (USDA, NRCS, National Plant Data Team 2007), shade, drought, waterlogging tolerances (Niinemets and Valladares 2006), and fire tolerance (USDA, NRCS, National Plant Data Team 2007). These indices represent whole-plant behavior that affects plant performance along resource or disturbance gradients and are expected to result from the coordination of multiple functional traits (Reich et al. 2003, Violle et al. 2007, Webb et al. 2010). Shade, drought, and water-logging tolerance are ordinal variables ranging from 1 (intolerant) to 5 (tolerant). These species-specific tolerance indices are based on (1) site characteristics (e.g., annual precipitation and duration of the dry period for drought tolerance) representative for each species' range, (2) the physiological potential that a species can survive long periods of exposure to the associated stress (e.g., 50% of foliage damage for drought tolerance), but to a certain degree also on expert knowledge about morphological and life history traits (Niinemets and Valladares 2006). To reduce the risk of circularity we validated the shade and drought tolerance indices. To validate the shade tolerance classifications of Niienemets and Valladares (2006), we correlated these with the shade tolerance estimates of Lichstein et al. (2010), which are only derived from individual growth versus light-level measurements. Both shade tolerances were significantly correlated ($r = 0.56$, $P < 0.001$, see Appendix A: Fig. A1), and thus, we used one of the indices (Niinemets and Valladares 2006). To validate the drought tolerance classifications, we correlated these with species-specific scores of humidity (annual P minus potential evapotranspiration derived from species' geographic distribution; see Appendix A: Fig. A2) and found a significant correlation ($r = 0.40$, $P < 0.001$). Fire tolerance is also an ordinal variable that ranges from 0 (intolerant) to 3 (high tolerant) and describes the relative ability of a species to resprout, regrow, or reestablish from seeds after a fire. Growth rate is represented on an ordinal scale from 1 (slow) to 3 (fast) and describes the growth potential of a species relative to other species after successful establishment. The imputation of missing values for the performance measures was done in the same manner as for the functional traits (see Appendix A: Table A3).

Data analysis

The data analysis was performed in two steps. First, we quantified trait spectra (sets of co-varying traits) as composite variables by extracting dominant axes of trait variation running a principle coordinate analysis (PCoA) (Gower 1971). We chose PCoA over principal components analysis (PCA) or correspondence analysis (CA) because it is flexible in the choice of distance measures, which was more appropriate for our analysis given the different data types (i.e., nominal, continuous, ordinal, multi-choice nominal); Euclidean (PCA) or chi-square (CA) distances are not appropriate in our setting. PCoA provides a Euclidean representation (i.e., a graphical representation in a Cartesian coordinate system) of the distance relationships between species based on their trait values. Thus, the major PCoA axes extracted from our data represent dominant variation in the traits, i.e., the axes are explained by certain sets of traits (trait spectra). To understand the attributes of the respective trait spectra, we correlated the PCoA axes with the trait values. Second, we explored relationships between the main trait spectra (i.e., major PCoA axes) and the plant performance indices.

PCoA was conducted on a general extension of Gower's distance coefficient (Gower 1971) developed by Pavoine et al. (2009), which accounts for different trait data types by assigning appropriate metrics for the specific data types, has Euclidean properties, and accounts for missing values. Due to missing data (4%), the distance matrix was unbalanced, and thus, the PCoA yielded some negative eigenvalues. We did not correct for these because the largest negative eigenvalues were smaller in absolute magnitude than any of the first three positive eigenvalues of interest, i.e., their interpretation was still meaningful following the rules provided by Legendre and Legendre (1998).

To account for differences between gymnosperms and angiosperms, we repeated the analysis three times: once for all 305 species and 23 traits followed by two analyses that considered gymnosperms and angiosperms separately. The gymnosperm analysis was based on 19 traits (conduit type/arrangement, leaf composition, leaf margin, and nitrogen fixation were excluded because they did not vary within this group). The angiosperm analysis was based on 22 traits (dispersal mode was excluded because of missing values for 46%). If necessary traits were square-root- or log-transformed to approximate normality and to reduce the influence of extremely high values. All continuous-valued traits (original or transformed) were standardized to z-scores by subtracting the mean trait value across species from each species-specific value and by dividing this difference by the standard deviation across species.

To assess the relative contribution of each trait to the trait spectra, we computed linear correlation coefficients (Pearson's r) between all traits and the first three PCoA axes of the species-trait matrix, representing the main trait spectra. To explore the relationship between the main trait spectra and the plant performance indices, we computed linear correlations between the first three PCoA axes and the growth rate and tolerance indices. All statistical analyses were conducted in R (R Development Core Team 2010).

RESULTS

For each of the three analyses (all species, gymnosperms, angiosperms), the first three PCoA axes explain a significant amount of variation (total ~40%) in trait values (Table 2). Each additional axis explains <6 % of the total variation, and we do not include these axes in subsequent analyses.

All 305 woody species

When considering all 305 species, the first axis explains 26% of trait variation (Table 2; Fig. 1). This axis is mainly correlated with leaf traits (leaf type, SLA, leaf margin), resprouting capacity and conduit type (vessel vs tracheids) (Fig. 1A and B, Table 2) and separates angiosperms and gymnosperms. Water-logging tolerance, fire tolerance, and growth rate are the performance indices that are most strongly correlated with this axis (Fig. 1B, Table 2). The second axis explains 9% of trait variation, and is mainly driven by traits representing responses to water availability and reproduction (wood density, root habit, seed mass). Drought tolerance and growth rate are correlated with this axis, but in opposite directions. Drought tolerant, slow growing species are located at the positive end of this axis and are characterized by a growth form intermediate between trees and shrubs (see Appendix A: Table A2 for definition) with heavy seeds, slow seed spread rate, slow vegetative spread rate, dense wood, and a taproot (Fig. 1B, Table 2). Conversely, drought intolerant, fast growing species are located at the negative end of the axis. They exhibit a tree-like growth form and support the opposite trait configuration. The third axis explains 6.9% of the trait variation and is mainly driven by leaf composition, potential for allelopathy and bark surface; it is not significantly correlated with any of the performance measures (Table 2).

Gymnosperms

For the gymnosperm-only analysis, the first axis explains 22% of trait variation and separates species in the Cupressaceae family, characterized by opposite arranged evergreen scale-like leaves, from Pinaceae, Taxaceae, and Taxodiaceae with spirally arranged evergreen needles (Fig. 2A and B, Table 2). Growth rate and drought tolerance indices are correlated with the first axis (Fig. 2B, Table 2). The second axis explains 13% of trait variation and is driven by traits related to water acquisition and reproduction. Drought tolerance and shade tolerance are inversely correlated with this axis (Fig. 2B, Table 2), reflecting the negative relationship between these tolerance strategies. The drought tolerant and shade intolerant species located at the positive end of the second axis exhibit tree/shrub growth forms, animal-

Table 2. Pearson's correlation coefficient (r) between traits and performance indices versus the first three PCoA axes (A1, A2, A3) obtained by analyzing all species, only gymnosperms and only angiosperms.

	All species			Gymnosperms			Angiosperms		
Trait/performance	A1 26.1%	A2 9.1%	A3 6.9%	A1 21.6%	A2 12.6%	A3 11.2%	A1 13.7%	A2 12.0%	A3 8.7%
Leaf traits									
Leaf composition	0.33***	n.s.	−0.65***	. . .	. . .	. . .	n.s.	0.76***	0.27***
Leaves alternate	0.77***	0.27***	0.26***	n.s.	n.s.	0.44***	0.37***	−0.25***	−0.58***
Leaves whorled	n.s.	n.s.	n.s.	. . .	. . .	. . .	n.s.	n.s.	n.s.
Leaves opposite	n.s.	−0.23***	−0.33***	0.92***	n.s.	n.s.	−0.41***	0.28***	0.57***
Leaves spirally	−0.78***	n.s.	n.s.	−0.8***	0.2*	n.s.	n.s.	n.s.	n.s.
Leaves in shoots	−0.17**	n.s.	n.s.	n.s.	n.s.	n.s.	. . .	. . .	. . .
Evergreen needle leaved	−0.84***	n.s.	n.s.	−0.9***	n.s.	n.s.	. . .	. . .	. . .
Deciduous needle leaved	n.s.	n.s.	n.s.	n.s.	n.s.	0.25*	. . .	. . .	. . .
Evergreen scaled	−0.28***	n.s.	n.s.	0.91***	n.s.	n.s.	. . .	. . .	. . .
Evergreen broad leaved	n.s.	0.32***	0.3***	. . .	. . .	. . .	0.43***	−0.4***	0.32***
Deciduous broad leaved	0.85***	−0.17**	−0.19**	. . .	. . .	. . .	−0.47***	0.44***	−0.32***
Evergreen/deciduous broad leaved	n.s.	0.13*	0.13*	. . .	. . .	. . .	0.16*	−0.15*	n.s.
Leaf margin	0.74***	−0.19**	−0.13**	. . .	. . .	. . .	−0.36***	0.26***	−0.3***
Specific leaf area	0.83***	−0.13***	n.s.	n.s.	−0.21*	0.09	−0.44***	n.s.	0.34***
Reproduction traits									
Dispersal via animals	n.s.	0.52***	n.s.	0.48***	0.54***	−0.28*	. . .	. . .	. . .
Dispersal unassisted	0.22**	n.s.	−0.29***	. . .	. . .	. . .	. . .	. . .	. . .
Dispersal via water	n.s.	n.s.	0.29***	n.s.	n.s.	0.36**	. . .	. . .	. . .
Dispersal via wind	−0.26**	−0.58***	n.s.	−0.74***	−0.44***	n.s.	. . .	. . .	. . .
Seed mass	0.22***	0.55***	−0.38***	−n.s.	0.56***	n.s.	0.55***	0.43***	n.s.
Seed spread rate	n.s.	−0.43***	0.13*	0.28**	−0.5***	0.23*	−0.48***	−0.16*	n.s.
Vegetative spread rate	0.19**	−0.39***	n.s.	n.s.	−0.46***	−0.25*	−0.37***	n.s.	−0.17*
Resprout ability	0.83***	n.s.	0.06	n.s.	−0.43***	0.51***	n.s.	n.s.	−0.24**
Root and stem traits									
Taproot	n.s.	0.79***	n.s.	n.s.	0.67***	0.7***	0.71***	0.2*	−0.36***
Shallow root	n.s.	−0.76***	n.s.	n.s.	−0.69***	−0.69***	−0.7***	n.s.	0.37***
Variable root	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Bark surface	−0.35***	0.21***	−0.44***	n.s.	−0.22*	n.s.	0.34***	0.34***	n.s.
Bark thickness	−0.14*	0.15*	n.s.	−0.34***	−0.2*	0.41***	0.31***	n.s.	−0.26***
Wood density	0.4***	0.48***	n.s.	0.23*	0.34**	n.s.	0.58***	n.s.	n.s.
Maximum height	−0.25***	−0.22***	−0.13*	−0.43***	−0.45***	0.34**	−0.22**	0.27***	−0.42***
Ring porous	0.48***	0.34***	−0.38***	. . .	. . .	. . .	0.49***	0.49***	−0.29***
Diffuse porous	0.43***	−0.4***	0.38***	. . .	. . .	. . .	−0.61***	−0.48***	0.21**
Semi ring porous	0.36***	0.16**	n.s.	. . .	. . .	. . .	0.17*	n.s.	n.s.
Tracheids	−0.95***	n.s.	n.s.	. . .	. . .	. . .	. . .	. . .	. . .
Plant level traits									
Lifespan	−0.49***	0.17**	n.s.	0.22*	n.s.	n.s.	0.34***	n.s.	n.s.
C:N ratio	−0.2**	n.s.	−0.18**	n.s.	n.s.	n.s.	n.s.	0.16*	n.s.
Nitrogen fixation	0.14*	n.s.	n.s.	. . .	. . .	. . .	n.s.	n.s.	n.s.
Toxicity	0.16**	n.s.	−0.18**	n.s.	n.s.	n.s.	n.s.	0.16*	0.43***
Potential allelopathy	n.s.	−0.34***	−0.52***	n.s.	n.s.	n.s.	−0.35***	0.5***	n.s.
Tree	n.s.	−0.36***	n.s.	−0.48***	−0.4***	n.s.	−0.38***	0.2**	−0.56***
Shrub	0.16**	n.s.	n.s.	. . .	. . .	. . .	n.s.	−0.16*	0.33***
Tree/shrub	n.s.	0.39***	n.s.	0.48***	0.4***	n.s.	0.39***	n.s.	0.41***
Fire resistance	0.2**	−0.12*	n.s.	0.23*	n.s.	−0.54***	n.s.	n.s.	n.s.
Performance measures									
Growth rate	0.27***	−0.22***	n.s.	−0.38***	n.s.	0.39***	−0.33***	n.s.	n.s.
Shade tolerance	n.s.	−0.15*	n.s.	−0.3**	−0.38***	n.s.	n.s.	n.s.	0.22**
Drought tolerance	−0.12*	0.44***	n.s.	0.44***	0.45***	n.s.	0.49***	n.s.	n.s.
Water-logging tolerance	0.28***	−0.17**	n.s.	n.s.	n.s.	n.s.	−0.22**	n.s.	n.s.
Fire tolerance	0.34***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Notes: r with $p < 0.001$***, $p < 0.01$** and $p < 0.05$*, $p > 0.05$ n.s. (not significant). The explained variance per axis is given in %; in case of no data entry the trait did not occur or did not vary in the specific group or was excluded from the analysis (see Appendix A: Table A3 and *Material and Methods*).

dispersed seeds, heavy seeds, a taproot, low seed spread rate, low vegetative spread rates, and small maximum heights (Fig. 2A and B, Table 2). Drought intolerant and shade tolerant species are located at the negative end of the second axis. They exhibit the opposite trait configuration and a tree-like growth form. The third axis explains 11% of the trait variation, and growth rate is

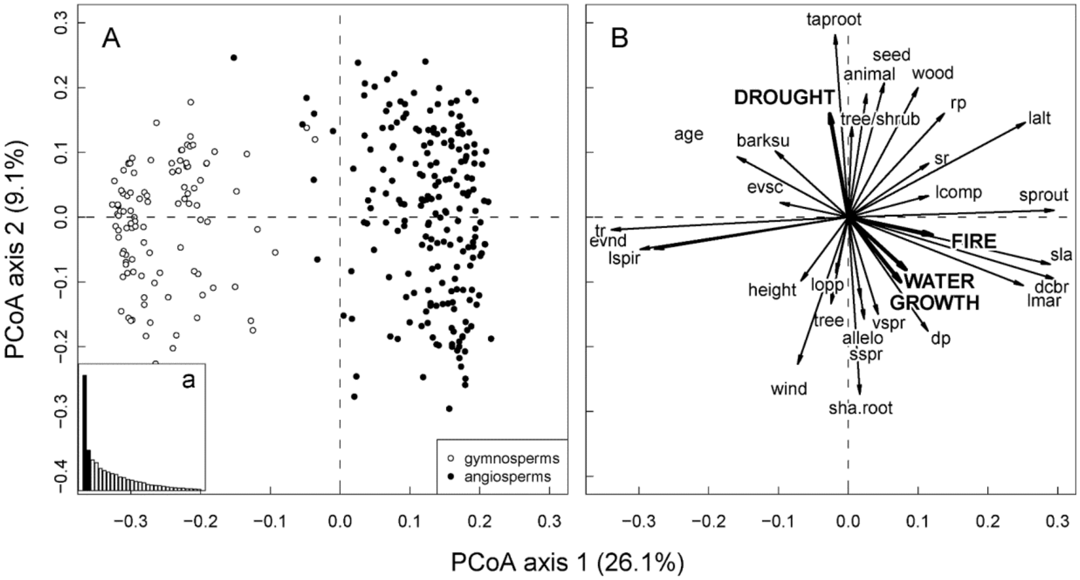

Fig. 1. PCoA ordination plot showing distances among 305 North American woody species based on 23 traits for the first two axes (A) with a histogram (a) showing the first 30 eigenvalues. In (B) significant correlations ($p < 0.001$) of both traits and performance measures (capitals) with the first two PCoA axes are represented as arrows (see Table 1 for abbreviations and Table 2 for respective correlation coefficients); the lengths of the arrows are proportional to their correlation coefficient, and they point in the direction of most rapid change; nominal traits were dummy coded before correlation.

correlated with this axis (Fig. 2C and D, Table 2). Fast growing species are located at the positive end of this axis and tend to have alternate-arranged leaves, a taproot, thick bark, high resprouting capacity, and low fire resistance, compared to the opposite trait configuration for slow growing species at the negative end of this axis. Several genera such as *Pinus*, *Larix*, and *Abies* cover the full range of traits spanned by the third axis.

Angiosperms

In the angiosperm-only analysis, the first axis explains 14% of trait variation and is driven by traits related to water availability and reproduction (Fig. 3A and B and Table 2). This axis is positively correlated with drought tolerance and negatively with growth rate and water-logging tolerance. The second axis explains 12% of the trait variation and is driven by leaf composition and potential for allelopathy; this axis is not notably correlated with any performance measure used (Fig. 3A and B, Table 2). The third axis explains 9% of trait variation and is driven by maximum height and leaf arrangement. This axis is correlated with shade tolerance (Fig. 3C and D, Table 2).

The first and third axes reveal differences between species possessing three different strategies forming a plant strategy triangle with respect to combinations of shade, drought, water-logging tolerance and growth rate (Fig. 3C and D). The corners of this triangle are depicted by (1) species intolerant to shade and drought but with high growth rate and high water-logging tolerance, (2) species tolerant to shade but intolerant to drought and water-logging and no correlation with growth rate, (3) species tolerant to drought but intolerant to shade and water-logging and exhibiting low growth rate (Fig. 3C and D, Table 2). The first strategy is represented by species of the genera *Populus* and *Betula*, which are characterized by low wood density, light seeds, large maximum heights, deciduous leaves, tree-like growth form, short lifespan, low toxicity, high seed spread,

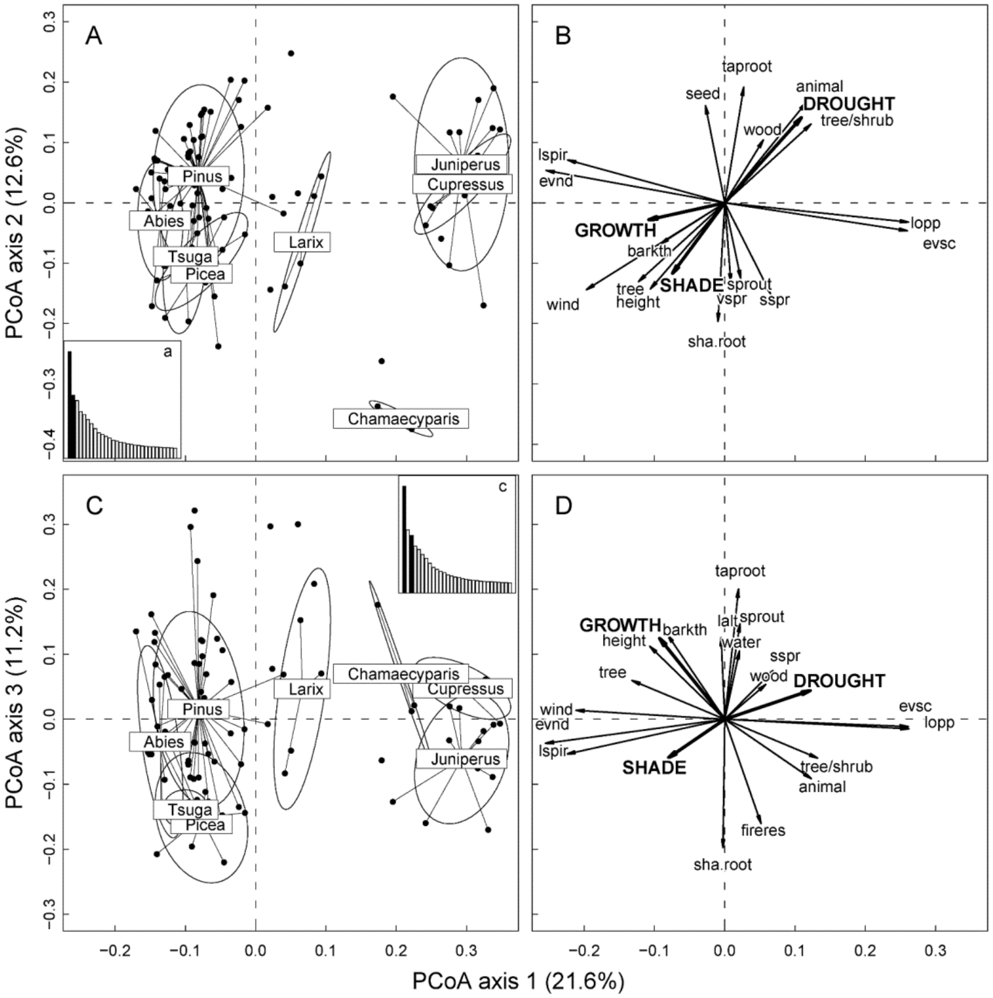

Fig. 2. PCoA ordination plot showing distances among 103 North American woody gymnosperm species based on19 traits for the first two axes (A) and for the first and third axis (C) with histograms (a and c) of the first 30 eigenvalues, respectively. The dispersion of important genera (containing many species or largely explain the axes) are shown as ellipses using standard deviation of the point scores with a confidence limit of 0.7 while the lines connect the species to the genus centroid, respectively. In (B) and (D) significant correlations ($p < 0.01$) of both traits and performances (capitals) with the respective PCoA axes are represented as arrows, see Fig. 1 for detailed description.

high vegetative spread rate, and dissected leaf margins (Fig. 3C and D, Table 2). The second strategy is mainly represented by species of the genera *Acer*, *Aesculus* and *Cercocarpus*, which are characterized by high SLA, opposite-arranged leaves, shallow roots, small maximum heights, diffuse-porous wood, high toxicity, thin bark, and a shrub-like growth form. The third strategy type is mainly represented by species of the genus *Quercus*, which is characterized by low SLA, dense wood, heavy seeds, taproot, thick bark with a rough surface, long lifespan, ring-porous wood, and alternately arranged leaves (Fig. 3C and D, Table 2).

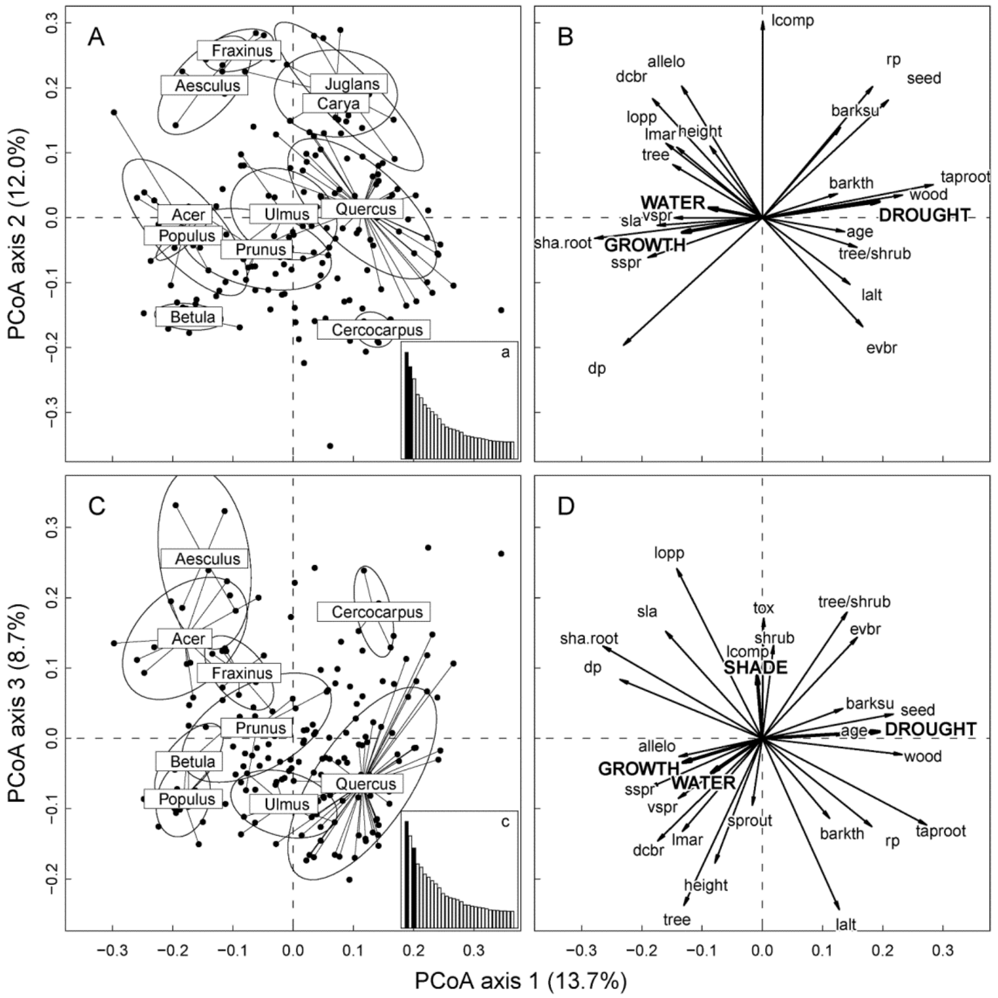

Fig. 3. PCoA ordination plot showing distances among 202 North American woody angiosperm species based on 22 traits for the first two axes (A) and for the first and third axis (C) with histograms of the first 30 eigenvalues (a and c), respectively. The dispersion of important genera are shown as ellipses, see Fig. 2 for detailed description. In (B) and (D) significant correlations ($p < 0.01$) of both traits and performance measures (capitals) with the respective PCoA axes are represented as arrows, see Fig. 1 for detailed description.

Comparison of gymnosperms and angiosperms

Here we compare the PCoA axes obtained from the gymnosperm- and angiosperm-only analyses that are most strongly correlated with shade and drought tolerance (Fig. 4). The axes that are primarily related to drought tolerance (second axis for gymnosperms, first axis for angiosperms, see Table 2) are explained by the same set of traits, which are correlated with each axis in the same direction. That is, regardless of clade association, drought tolerant species tend to have tree/shrub like growth form with a taproot, dense wood, high seed mass, and both low vegetative and low seed spread rates (Fig. 4A, upper right corner); drought intolerant species are characterized by the opposite trait configuration (Fig. 4A, lower left corner). Conversely, the set of traits that are correlated with the axes related to

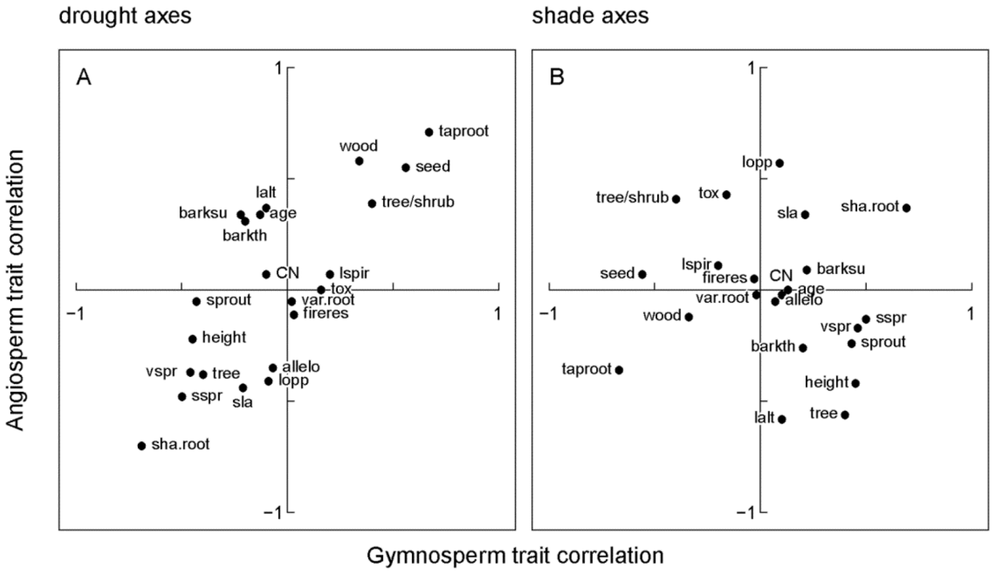

Fig. 4. Comparison of trait spectra reflecting drought (A) and shade tolerance (B) between gymnosperms and angiosperms. Pearson's correlation (r) between traits and those PCoA axes that correlated best with drought tolerance = "drought axes" (A) and best with shade tolerance = "shade axes" (B) in gymnosperm and angiosperm only analysis, respectively (see Table 2 for correlation coefficients and explained variance). If the respective trait spectra of the two clades are similar (i.e., the same traits vary in the same manner) the Pearsons's r values show a linear arrangement along the 1 to 1 line.

shade tolerance (second axis for gymnosperms, third axis for angiosperms) differ between clades (Fig. 4B). These differences occur in two aspects: (1) different traits are correlated with shade tolerance (e.g., leaf arrangement in angiosperms vs. seed mass in gymnosperms), or (2) the same traits are correlated with shade tolerance, but in the opposite direction (e.g., maximum height increased with shade tolerance in gymnosperms but decreased in angiosperms). These clade-level differences in the trait versus shade tolerance associations explain the lack of significant trait correlations with shade tolerance when all species are analyzed together.

DISCUSSION

In this study we quantified major whole-plant spectra for morphological, anatomical and demographic traits for North American woody species and analyzed their relationship to whole-plant performance measures, i.e., growth rate and tolerance to shade, drought, waterlogging and fire (see *Material and Methods* for definition). The results of these analyses confirm that these holistic whole-plant performance measures reflect integrated processes of growth, reproduction and survival involving multiple traits (Reich et al. 2003, Violle et al. 2007, Webb et al. 2010). Furthermore, they support that the major whole-plant trait spectra reflect adaptations to key environmental drivers in temperate forests corroborating the prevalence of fundamental functional tradeoffs defining fundamental plant strategies (Smith and Huston 1989, Pacala et al. 1996, Poorter and Markesteijn 2008) but with substantial differences between gymnosperms and angiosperms. However, we also identified trait spectra which are not related to any of the performance measures used or which reflect clearly the differences between the major clades suggesting that there are also other factors (e.g., evolutionary history) explaining major trait variation.

Whole-plant trait spectra reflect fundamental strategies and differences between basal phylogenetic groups

When all 305 species are considered together, the difference between gymnosperms and angiosperms is captured by the first major PCoA axis. This strong phylogenetic signal essentially reflects the two dominant plant functional types that differ in leaf traits such as SLA, leaf type (evergreen needle-leaved versus deciduous broad-leaved), conduit type (tracheids versus vessels) and resprouting capacity. The strong correlation between SLA and the first major axis highlights its importance as a lineage separating trait in addition to reflecting ecological strategies (Diaz et al. 2004). We also found a weak but significant correlation between growth rate and the first major axis. Overall, this supports the notion that SLA could be used as a weak proxy for growth rate in adult trees (Wright et al. 2010). The correlation of water-logging and fire tolerance with the first axis supports the difference in functionality between the two major clades and indicates phylogenetic conservatism.

In contrast to the first axis, the traits associated with the second major axis are consistent for both clades and are positively correlated with drought tolerance and negatively with growth rate. In our study, the drought tolerant species have a lower growth rate and are characterized by a tree/shrub like growth form with high seed mass, high wood density and a taproot. High seed mass enables the rapid development of a taproot, which allows seedlings to escape dry surface soil conditions and enhances survival rates (Leishman and Westoby 1994). High wood density tends to be associated with low minimum leaf water potentials, deep rooting ability (Brodribb and Feild 2000, Bucci et al. 2004) and increases resistance to drought-induced xylem embolism (Hacke et al. 2001). Thus a complex spectrum of traits involving demographic traits (seed mass), anatomical (wood density) and morphological (taproot) is governing drought tolerance. The fact that the same set of traits governs drought tolerance in the otherwise contrasting gymno- and angiosperms emphasizes their ecological relevance. Our results also suggest that water availability is a key driver of tree growth in North American forests and that the growth rate is low in species adapted to drought. The high wood density associated with drought tolerance could be one indirect factor leading to reduced growth rate—a relationship frequently reported for tropical tree species (Muller-Landau 2004).

Fundamental relationships between drought, shade tolerance, and growth rate are reflected by whole-plant trait spectra within gymnosperms and angiosperms

Shade and drought tolerance are inversely related, but the strength of this relationship differs between gymnosperms (strong correlation) and angiosperms (weak correlation) (Niinemets and Valladares 2006). Our results reveal that different trait spectra underlie the shade versus drought tolerance relationship for gymnosperms and angiosperms, reflecting different trait tradeoffs between these two major clades.

In the gymnosperms, the negative correlation between shade and drought tolerance was reflected by one trait spectrum (large maximum height and shallow roots in shade tolerant species versus small maximum height and taproots in drought tolerant species). This reflects a tradeoff between allocation to roots versus shoots (Fig. 2B). Traits reflecting growth rate are unrelated to the trait spectrum reflecting shade/drought tolerance. This could reflect a true independence, or it may be masking a non-linear, hump-shaped relationship between growth rate and the drought-shade tolerance axis (Smith and Huston 1989, Craine 2009) because the linear methods used here are not suited to identify such non-linearity. However, the very nature of the trait spectrum reflecting high growth rates suggests independent strategies. For example, gymnosperms with high growth rate tend to be trees with large maximum heights and with thick bark that possess the ability to resprout, suggesting a relationship to disturbance strategies, which are expected to be independent of drought/shade tolerance strategies (Loehle 2000).

In the angiosperms, two independent trait spectra imply a difference between the three strategies with respect to shade, drought, and water-logging tolerance (Fig. 3C and D) suggesting different tradeoffs. Shade and drought intolerant angiosperms (e.g., species in *Betula* and *Populus*) are tolerant to water-logging and represent a resource use strategy suited to quickly exploit suitable habitats (tall stature, small wind dispersed seeds, high vegetative spread rates) at the cost of protection and maintenance structures (soft wood)—a typical pioneer trait association. In agreement with Smith and Huston (1989), these species tend to have higher growth rates compared to species that are tolerant to either shade or drought stress. Furthermore, our study agrees with Niinemets and Valladares (2006) in that the deciduous broad-leaved habit is a feature of shade and drought intolerance in North American forests, while evergreen broad-leaved habit tends to be a feature of species able to tolerate these stresses. Shade tolerant species (e.g., species of *Acer*) attain a relatively small stature, and light interception is enhanced by oppositely arranged leaves with a high SLA; these species also support shallow roots and produce toxic defense chemicals. High SLA is typical of winter-deciduous, shade tolerant trees growing in the understory (Lusk and Warton 2007), while the production of toxic defense chemicals might enhance their resistance to herbivores, making such species strong competitors (Kitajima 1994). Drought tolerant angiosperms (e.g., evergreen species of *Quercus*) exhibit a conservative resource use strategy with trait associations aligning with those reported by Markesteijn and Poorter (2009): slow nutrient turnover and long residence times (low SLA), high investment in protection and survival structures (dense wood, thick bark, heavy seeds), combined with features favored under low water availability (taproot and ring-porous wood).

Whole-plant trait spectra independent of growth rate, shade, and drought tolerance

In the angiosperm-only analysis, leaf composition and allelopathy co-vary (composite leaves paired with high potential for allelopathy versus simple leaves paired with low potential for allelopathy) and explain the second major axis. This axis is strongly determined by phylogeny as it separates species in the genera *Fraxinus* (Oleaceae), *Carya*, *Juglans* (Juglandaceae), and *Aesculus* (Sapindaceae) with composite leaves from those with single leaves (Fig. 3A and B); this axis is also independent of growth rate and drought or shade tolerance (Table 2). The fact that leaf composition is not related to shade tolerance has been observed in different deciduous woody floras (Stowe and Brown 1981, Niinemets 1998, Malhado et al. 2010). Species with composite leaves tend to have low branching costs that allow rapid vertical growth during favorable light conditions, which is equally relevant for shade intolerant early successionals (Givnish 1978) and shade tolerant late successionals (Niinemets 1998). Stowe and Brown (1981) and Malhado et al. (2010) showed that leaf composition was related to climatic variables (e.g., spring and summer temperatures and variation in rainfall and water deficits), in such a way that seasonal drought favors composite leaves. Adaptations to episodic drought events are expected to differ from adaptations to persistent drought (Craine 2009), which may explain why we found leaf composition to be independent to trait associations reflecting high drought tolerance. High allelopathic interference more commonly occurs in stressful environments (Blanco 2007), such as under extremes in water and temperature and rapid successional changes. Thus, the co-variation of allelopathy and composite leaves seems to be an indirect relationship that merely emerges from phylogenetic relatedness.

Significance of the results in terms of data and methodological limitations

The results reported in this study could be influenced by the uncertainty caused by intra-specific variability, the choice of traits and by assignment errors in categorical traits and performance indices and the methods used. Our approach to filling-in missing species-level trait data with genus means had little influence on the results (data not shown).

The influence of intra-specific variability is likely to be negligible because we quantified tradeoffs based on 23 traits, with many traits describing morphological features (e.g., leaf arrangement) that are expected to be largely fixed for a given species; however, some traits (e.g., SLA) are likely to varying within a species (Ogle et al. 2012). However, Albert et al. (2010) found that the PCoA solution based on continuous traits exhibiting considerable intra-specific variability remains stable irrespective of whether an analysis was conducted at the species, population, or individual level. Furthermore, in our analysis, species are distributed across large environmental gradients, which is likely to lead to greater inter-species compared to intra-species trait variability (Kattge et al. 2011).

The incorporation of other potentially important traits, such as leaf area, mycorrhiza-associations, fine root diameter, serotiny or twig thickness might have the potential to detect novel tradeoffs (e.g., tradeoffs related to fire tolerance which we could not identify within the major clades), sharpen or slightly modify tradeoffs and strategies found. However, weak correlation between performance measures and the first three major axes might also depend on the resolution and information the indices are based on. Thus, fire tolerance and growth rate should rather be viewed as coarse approximations because they are primarily based on field observations, expert knowledge and estimates from the literature and not on precise measurements or experiments. However, drought tolerance and shade tolerance values used are reliable because they either are directly based on specific plant survival and site condition measurements or correlated well with species-specific values based on such measurements (see *Material and Methods* for details). Thus, the weak correlation of shade tolerance with the third axis analyzing the angiosperms might rather be caused by the complex interactions of functional traits. Moreover, we found a significant strong correlation of shade tolerance with the fifth PCoA axis (data not shown) suggesting that there are several different trait solutions for being shade tolerant (Valladares and Niinemets 2008).

Generally, our analysis is meant to be exploratory and aims to reveal the most important trait spectra in the first part and explores in the second part whether they reflect whole-plant performances describing fundamental ecological strategies or not. In this way it allows the exploration of novel trait spectra (e.g., the second axis in the angiosperm-only analysis) and hypothesis about underlying factors (e.g., adaptation to seasonal drought or phylogenetic constraints), which could be tested in a second step using appropriate designs (e.g., permutations and null-models). However, constrained analyses, e.g., distance-based Redundancy Analysis revealing the trait spectra which are best explained by the performance measures, yielded nearly identical results (analyses not shown), and thus underpins that adaptation to light and water availability are indeed important factors explaining major trait variation in North American woody species.

Phylogenetic signal

An explicit quantification of the phylogentic signal is challenging in this study because we imputed missing species-specific traits with genus means, which could artificially inflate the phylogenetic signal. The analysis involving the complete species pool suggests a trivial phylogenetic signal related to differences in trait strategies between gymnosperms and angiosperms. Thus, performing the separate analyses for these two major clades resulted in a coarse phylogenetic correction (Diaz et al. 2004). Comparison of these three analyses enabled us to identify important trait-performance relationships that differed between these two groups, representing potential adaptations that arose early in the evolution of these two major clades. Niinemets and Valladares (2006) found a significant phylogenetic signal in shade and drought tolerances, which pointed to trait conservatism operating between species within genera. Thus, the trait associations uncovered in this study are potentially not phylogenetically independent at, for example, the genus level. For instance, trait spectra related to drought and shade tolerance often grouped species by genera (Fig. 3); conversely, species are widely spread along the trait spectrum reflecting growth rate, and their position appears to be independent of their genus affiliation (Fig. 2).

Whole-plant trait spectra support plant strategies schemes

Comparing our whole-plant trait spectra with strategy axes of existing plant strategy schemes we found consensus but also insufficiency. For example, the widely used LHS scheme of Westoby (1998) was not sufficient to describe the main axes of trait variation of temperate woody species. The LHS scheme was moderately useful for understanding the trait spectra of angiosperms; for example, SLA (L), maximum tree height (H), and seed mass (S) were independent and contribute to complex spectra reflecting adaptation to shade and drought stress. However, among gymnosperms, SLA was irrelevant for describing inverse adaptations to drought and shade. The differential importance of SLA reflects the contrasting relationship between SLA and leaf life span for evergreen needle-leaved (little variation in SLA and large variation in leaf life span) versus deciduous broad-leaved species (large variation in SLA and little variation in life span, which reflects growing season length). The differential importance of maximum tree height with respect to plant performance indices might reflect different strategies that are controlled by different tradeoffs (Falster and Westoby 2005). In angiosperms, tall stature and fast growth correlate with a stress intolerant strategy, which might trade off with lower productivity (e.g., small stature and slow growth) when shade or drought tolerance increases. Conversely, in gymnosperms, the tall stature of shade tolerant species might be the result of competition for light.

Resprouting and leaf composition might represent additional dimensions reflecting responses to disturbance or periodic stresses that are not captured by the LHS scheme. Thus, the extension to four axes that includes resprouting capacity (Loehle 2000) seems justified for North American forests, but this may still be insufficient. The inclusion of additional traits related to adaptations dealing with disturbance and/or reflecting competitive strength would likely improve upon these existing schemata.

Conclusion

Our study shows that major whole-plant trait spectra of North American woody species are related to performance indices of growth and tolerance to shade, drought and water-logging that reflect whole-plant strategies with respect to growth, reproduction, and survival along environmental gradients in forests (light, water and disturbance). The whole-plant trait spectra related to performance measures are compound of morphological, anatomical and demographic traits and interact with each other, corroborating the assumption of fundamental functional tradeoffs between stress tolerances and growth. Ideal measures of plant performance would include direct observations of vital rates in response to environmental drivers, and a growing number of studies use repeated forest inventories to estimate these rates and relate them to local trait databases (Poorter et al. 2008, Martínez Vilalta et al. 2010, Poorter et al. 2010, Wright et al. 2010). However, this has not been accomplished for a complete continental flora encompassing a wide range of long-lived species and contrasting environments. In this sense, our approach represents a macro-ecological complement to the growing field of the ‘rates and traits’ research. Moreover, it might be an appropriate way to associate the principles of fundamental conceptual strategy schemes (Grime 1977, Smith and Huston 1989, Grubb 1998, Craine 2009) with information on traits to refine current trait-based schemes and to identify underlying tradeoffs.

ACKNOWLEDGMENTS

We would like to thank Stefanie Nöllert, Angela Nüske, and Sabine Rensch for their help with data assembly. Miguel Mahecha provided helpful comments on earlier versions of this manuscript. The study has been supported by the TRY initiative on plant traits (http://www.try-db.org). The TRY initiative and database is hosted, developed and maintained at the Max Planck Institute for Biogeochemistry, Jena, Germany and is/has been supported by DIVERSITAS, IGBP, the Global Land Project, the UK Natural Environment Research Council (NERC) through it's program QUEST (Quantifying and Understanding the Earth System), the French Foundation for Biodiversity Research (FRB), and GIS “Climat, Environnement et Société” France. We thank Hans Cornelissen, Juli Pausas, and Angela Moles for providing valuable data. This research was funded by the Max Planck Institute of Biogeochemistry Jena. K. Ogle was supported a National Science Foundation (NSF) grant (DBI-0850361).

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SUPPLEMENTAL MATERIAL
APPENDIX A

Table A1. List of taxa names used for the analyses and accepted names after name-checking.

Taxa names used for analyses	Comments	Accepted taxa names†
Abies amabilis		Abies amabilis (Douglas ex Loudon) J.Forbes
Abies balsamea		Abies balsamea (L.) Mill.
Abies bracteata		Abies bracteata (D.Don) Poit.
Abies concolor		Abies concolor (Gordon) Lindl. ex Hildebr.
Abies fraseri		Abies fraseri (Pursh) Poir.
Abies grandis		Abies grandis (Douglas ex D.Don) Lindl.
Abies lasiocarpa		Abies lasiocarpa (Hook.) Nutt.
Abies lasiocarpa var. arizonica		Abies lasiocarpa var. arizonica (Merriam) Lemmon
Abies magnifica		Abies magnifica A.Murray bis
Abies magnifica var. shastensis		Abies magnifica var. shastensis Lemmon
Abies procera		Abies procera Rehder
Acer barbatum	synonymy not resolvable without specific authority	Acer (barbatum)
Acer glabrum		Acer glabrum Torr.
Acer grandidentatum	synonym	Acer saccharum subsp. grandidentatum (Torr. & A.Gray) Desmarais
Acer leucoderme	synonym	Acer saccharum subsp. leucoderme (Small) Desmarais
Acer macrophyllum		Acer macrophyllum Pursh
Acer negundo		Acer negundo L.
Acer nigrum	synonym	Acer saccharum subsp. nigrum (F.Michx.) Desmarais
Acer pensylvanicum		Acer pensylvanicum L.
Acer platanoides		Acer platanoides L.
Acer rubrum		Acer rubrum L.
Acer saccharinum		Acer saccharinum L.
Acer saccharum		Acer saccharum Marshall
Acer spicatum		Acer spicatum Lam.
Aesculus californica		Aesculus californica (Spach) Nutt.
Aesculus glabra		Aesculus glabra Willd.
Aesculus glabra var. arguta		Aesculus glabra var. arguta (Buckley) Rob.
Aesculus octandra	synonym	Aesculus flava Sol.
Ailanthus altissima		Ailanthus altissima (Mill.) Swingle
Albizia julibrissin		Albizia julibrissin Durazz.
Alnus glutinosa		Alnus glutinosa (L.) Gaertn.
Alnus rhombifolia		Alnus rhombifolia Nutt.
Alnus rubra		Alnus rubra Bong.
Arbutus menziesii		Arbutus menziesii Pursh
Asimina triloba		Asimina triloba (L.) Dunal
Betula alleghaniensis		Betula alleghaniensis
Betula lenta		Betula lenta L.
Betula nigra		Betula nigra L.
Betula occidentalis		Betula occidentalis Hook.
Betula papyrifera		Betula papyrifera Marshall
Betula papyrifera var. commutata	synonym	Betula papyrifera Marshall var. papyrifera
Betula papyrifera var. subcordata	synonym	Betula papyrifera Marshall var. papyrifera
Betula populifolia		Betula populifolia Marshall
Bumelia lanuginosa	synonym	Sideroxylon lanuginosum Michx.
Calocedrus decurrens		Calocedrus decurrens (Torr.) Florin

Table A1. Continued.

Taxa names used for analyses	Comments	Accepted taxa names†
Carpinus caroliniana		Carpinus caroliniana Walter
Carya aquatica		Carya aquatica (F.Michx.) Nutt. ex Elliott
Carya cordiformis		Carya cordiformis (Wangenh.) K.Koch
Carya glabra		Carya glabra (Mill.) Sweet
Carya illinoinensis		Carya illinoinensis (Wangenh.) K.Koch
Carya laciniosa		Carya laciniosa (F.Michx.) G.Don
Carya myristiciformis		Carya myristiciformis (F.Michx.) Nutt. ex Elliott
Carya ovata		Carya ovata (Mill.) K.Koch
Carya pallida		Carya pallida (Ashe) Engelm. & Graebn.
Carya texana		Carya texana Buckley
Carya tomentosa	synonym	Carya alba (L.) Nutt. ex Elliott
Castanea dentata		Castanea dentata (Marshall) Borkh.
Castanea ozarkensis		Castanea ozarkensis Ashe
Castanea pumila		Castanea pumila (L.) Mill.
Catalpa bignonioides		Catalpa bignonioides Walter
Catalpa speciosa		Catalpa speciosa (Warder ex Barney) Warder ex Engelm.
Celtis laevigata		Celtis laevigata Willd.
Celtis occidentalis		Celtis occidentalis L.
Celtis reticulata	synonym	Celtis laevigata var. reticulata (Torr.) Benson
Cercis canadensis		Cercis canadensis L.
Cercocarpus ledifolius	unresolved name	Cercocarpus (ledifolius)
Cercocarpus ledifolius var. intricatus	synonym	Cercocarpus intricatus S. Watson
Cercocarpus montanus		Cercocarpus montanus Raf.
Cercocarpus montanus var. glaber		Cercocarpus montanus var. glaber (S. Watson) F.L. Martin
Cercocarpus montanus var. paucidentatus		Cercocarpus montanus var. paucidentatus (S. Watson) F.L. Martin
Chamaecyparis lawsoniana		Chamaecyparis lawsoniana (A.Murray bis) Parl.
Chamaecyparis nootkatensis	synonym	Xanthocyparis nootkatensis (D.Don) Farjon & D.K.Harder
Chamaecyparis thyoides		Chamaecyparis thyoides (L.) Britton, Sterns & Poggenb.
Chrysolepis chrysophylla		Chrysolepis chrysophylla (Douglas ex Hook.) Hjelmq.
Cladrastis kentukea		Cladrastis kentukea (Dum.Cours.) Rudd
Cornus florida		Cornus florida L.
Cornus nuttallii		Cornus nuttallii Audubon ex Torr. & A.Gray
Cotinus obovatus		Cotinus obovatus Raf.
Crataegus crus-galli		Crataegus crus-galli L.
Crataegus mollis	synonym	Oxyacantha mollis (Scheele) Lunell
Cupressus arizonica		Cupressus arizonica Greene
Cupressus bakeri		Cupressus bakeri Jeps.
Cupressus guadalupensis var. forbesii		Cupressus guadalupensis var. forbesii (Jeps.) Little
Cupressus macrocarpa		Cupressus macrocarpa Hartw.
Cupressus sargentii		Cupressus sargentii Jeps.
Diospyros virginiana		Diospyros virginiana L.
Elaeagnus angustifolia		Elaeagnus angustifolia L.
Fagus grandifolia		Fagus grandifolia Ehrh.
Fraxinus americana		Fraxinus americana L.
Fraxinus caroliniana		Fraxinus caroliniana Mill.
Fraxinus latifolia		Fraxinus latifolia Benth.
Fraxinus nigra		Fraxinus nigra Marshall
Fraxinus pennsylvanica		Fraxinus pennsylvanica Marshall
Fraxinus profunda		Fraxinus profunda (Bush) Bush
Fraxinus quadrangulata		Fraxinus quadrangulata Michx.
Fraxinus velutina		Fraxinus velutina Torr.
Gleditsia aquatica		Gleditsia aquatica Marshall
Gleditsia triacanthos		Gleditsia triacanthos L.
Gordonia lasianthus		Gordonia lasianthus (L.) Ellis
Gymnocladus dioicus	synonym (spelling variant)	Gymnocladus dioica (L.) K.Koch
Ilex opaca	unresolved name	Ilex (opaca)
Juglans californica	unresolved name	Juglans (californica)
Juglans cinerea		Juglans cinerea L.
Juglans hindsii		Juglans hindsii Jeps. ex R.E. Sm.
Juglans microcarpa		Juglans microcarpa Berland.
Juglans nigra		Juglans nigra L.
Juniperus ashei		Juniperus ashei J.Buchholz

Table A1. Continued.

Taxa names used for analyses	Comments	Accepted taxa names†
Juniperus californica		Juniperus californica Carrière
Juniperus coahuilensis		Juniperus coahuilensis (Martínez) Gaussen ex R.P.Adams
Juniperus communis		Juniperus communis L.
Juniperus deppeana		Juniperus deppeana Steud.
Juniperus monosperma		Juniperus monosperma (Engelm.) Sarg.
Juniperus occidentalis		Juniperus occidentalis Hook.
Juniperus osteosperma		Juniperus osteosperma (Torr.) Little
Juniperus pinchotii		Juniperus pinchotii Sudw.
Juniperus scopulorum		Juniperus scopulorum Sarg.
Juniperus silicicola	synonym	Juniperus virginiana var. silicicola (Small) A.E.Murray
Juniperus virginiana		Juniperus virginiana L.
Larix laricina		Larix laricina (Du Roi) K.Koch
Larix lyallii		Larix lyallii Parl.
Larix occidentalis		Larix occidentalis Nutt.
Liquidambar styraciflua		Liquidambar styraciflua L.
Liriodendron tulipifera		Liriodendron tulipifera L.
Lithocarpus densiflorus		Lithocarpus densiflorus (Hook. & Arn.) Rehder
Maclura pomifera		Maclura pomifera (Raf.) C.K.Schneid.
Magnolia acuminata		Magnolia acuminata (L.) L.
Magnolia fraseri		Magnolia fraseri Walter
Magnolia grandiflora		Magnolia grandiflora L.
Magnolia macrophylla		Magnolia macrophylla Michx.
Magnolia virginiana		Magnolia virginiana L.
Malus fusca		Malus fusca (Raf.) C.K. Schneid.
Melaleuca quinquenervia		Melaleuca quinquenervia (Cav.) S.T.Blake
Melia azedarach		Melia azedarach L.
Morus alba		Morus alba L.
Morus rubra		Morus rubra L.
Nyssa aquatica		Nyssa aquatica L.
Nyssa ogeche		Nyssa ogeche Bartram ex Marshall
Nyssa sylvatica		Nyssa sylvatica Marshall
Nyssa sylvatica var. biflora		Nyssa sylvatica var. biflora (Walter) Sarg.
Olneya tesota		Olneya tesota A.Gray
Ostrya virginiana		Ostrya virginiana (Mill.) K.Koch
Oxydendrum arboreum		Oxydendrum arboreum (L.) DC.
Paulownia tomentosa		Paulownia tomentosa Steud.
Persea borbonia		Persea borbonia (L.) Spreng.
Picea abies		Picea abies (L.) H.Karst.
Picea breweriana		Picea breweriana S.Watson
Picea engelmannii		Picea engelmannii Parry ex Engelm.
Picea glauca		Picea glauca (Moench) Voss
Picea mariana		Picea mariana (Mill.) Britton, Sterns & Poggenb.
Picea pungens		Picea pungens Engelm.
Picea rubens		Picea rubens Sarg.
Picea sitchensis		Picea sitchensis (Bong.) Carrière
Pinus albicaulis		Pinus albicaulis Engelm.
Pinus aristata		Pinus aristata Engelm.
Pinus attenuata		Pinus attenuata Lemmon
Pinus balfouriana		Pinus balfouriana Balf.
Pinus banksiana		Pinus banksiana Lamb.
Pinus cembroides		Pinus cembroides Zucc.
Pinus clausa		Pinus clausa (Chapm. ex Engelm.) Vasey ex Sarg.
Pinus contorta var. contorta		Pinus contorta Douglas ex Loudon var. contorta
Pinus contorta var. latifolia		Pinus contorta var. latifolia Engelm.
Pinus contorta var. murrayana		Pinus contorta var. murrayana (Balf.) S.Watson
Pinus coulteri		Pinus coulteri D.Don
Pinus discolor	synonym	Pinus cembroides var. bicolor Little
Pinus echinata		Pinus echinata Mill.
Pinus edulis		Pinus edulis Engelm.
Pinus elliottii		Pinus elliottii Engelm.
Pinus engelmannii		Pinus engelmannii Carrière
Pinus flexilis		Pinus flexilis E.James
Pinus glabra		Pinus glabra Walter
Pinus jeffreyi		Pinus jeffreyi A.Murray bis
Pinus lambertiana		Pinus lambertiana Douglas
Pinus leiophylla var. chihuahuana		Pinus leiophylla var. chihuahuana (Engelm.) Shaw

Table A1. Continued.

Taxa names used for analyses	Comments	Accepted taxa names†
Pinus longaeva		Pinus longaeva D.K.Bailey
Pinus monophylla		Pinus monophylla Torr. & Frém.
Pinus monophylla var. fallax	synonym	Pinus monophylla Torr. & Frém.
Pinus monticola		Pinus monticola Douglas ex D.Don
Pinus muricata		Pinus muricata D.Don
Pinus nigra		Pinus nigra J.F.Arnold
Pinus palustris		Pinus palustris Mill.
Pinus ponderosa		Pinus ponderosa Douglas ex C.Lawson
Pinus ponderosa var. arizonica	synonym	Pinus arizonica Engelm.
Pinus pungens		Pinus pungens Lamb.
Pinus quadrifolia		Pinus quadrifolia Parl. ex Sudw.
Pinus radiata		Pinus radiata D.Don
Pinus resinosa		Pinus resinosa Aiton
Pinus rigida		Pinus rigida Mill.
Pinus sabiniana		Pinus sabiniana Douglas
Pinus serotina		Pinus serotina Michx.
Pinus strobiformis		Pinus strobiformis Engelm.
Pinus strobus		Pinus strobus L.
Pinus sylvestris		Pinus sylvestris L.
Pinus taeda		Pinus taeda L.
Pinus torreyana		Pinus torreyana Parry ex Carrière
Pinus virginiana		Pinus virginiana Mill.
Pinus washoensis	synonym	Pinus ponderosa Douglas ex C.Lawson
Planera aquatica		Planera aquatica J.F.Gmel.
Platanus occidentalis		Platanus occidentalis L.
Platanus racemosa		Platanus racemosa Nutt.
Populus alba		Populus alba L.
Populus angustifolia		Populus angustifolia E. James
Populus balsamifera		Populus balsamifera L.
Populus deltoides		Populus deltoides W. Bartram ex Marshall
Populus deltoides var. monilifera	synonym	Populus deltoides var. occidentalis Rydb.
Populus fremontii		Populus fremontii S. Watson
Populus grandidentata	synonym	Populus tremula subsp. grandidentata (Michx.) Á. Löve & D. Löve
Populus heterophylla	unresolved name	Populus (heterophylla)
Populus tremuloides		Populus tremuloides Michx.
Populus trichocarpa		Populus trichocarpa Torr. & A. Gray
Prosopis glandulosa var. torreyana		Prosopis glandulosa var. torreyana (L.D.Benson) M.C.Johnst.
Prosopis pubescens		Prosopis pubescens Benth.
Prosopis velutina		Prosopis velutina Wooton
Prunus americana	synonymy not resolvable without specific variety	Prunus (americana)
Prunus emarginata		Prunus emarginata (Douglas) Walp.
Prunus nigra	synonym	Armeniaca dasycarpa (Ehrh.) Borkh.
Prunus pensylvanica	unresolved name	Prunus (pensylvanica)
Prunus serotina		Prunus serotina Ehrh.
Prunus virginiana	synonym	Padus virginiana (L.) M. Roem.
Pseudotsuga macrocarpa		Pseudotsuga macrocarpa (Vasey) Mayr
Pseudotsuga menziesii var. menziesii		Pseudotsuga menziesii (Mirb.) Franco var. menziesii‡
Pseudotsuga menziesii var. glauca		Pseudotsuga menziesii var. glauca (Beissn.) Franco
Quercus agrifolia		Quercus agrifolia Née
Quercus alba		Quercus alba L.
Quercus arizonica		Quercus arizonica Sarg.
Quercus bicolor		Quercus bicolor Willd.
Quercus chrysolepis		Quercus chrysolepis Liebm.
Quercus coccinea		Quercus coccinea Münchh.
Quercus douglasii		Quercus douglasii Hook. & Arn.
Quercus durandii	synonym	Quercus sinuata Walter var. sinuata
Quercus ellipsoidalis		Quercus ellipsoidalis E.J.Hill
Quercus emoryi		Quercus emoryi Torr.
Quercus engelmannii		Quercus engelmannii Greene
Quercus falcata var. falcata		Quercus falcata Michx. var. falcata‡
Quercus falcata var. pagodifolia	synonym	Quercus pagoda Raf.
Quercus gambelii		Quercus gambelii Nutt.
Quercus garryana		Quercus garryana Douglas ex Hook.

Table A1. Continued.

Taxa names used for analyses	Comments	Accepted taxa names†
Quercus grisea		Quercus grisea Liebm.
Quercus hypoleucoides		Quercus hypoleucoides A.Camus
Quercus ilicifolia		Quercus ilicifolia Wangenh.
Quercus imbricaria		Quercus imbricaria Michx.
Quercus incana		Quercus incana Bartram
Quercus kelloggii		Quercus kelloggii Newb.
Quercus laevis		Quercus laevis Walter
Quercus laurifolia		Quercus laurifolia Michx.
Quercus lobata		Quercus lobata Née
Quercus lyrata		Quercus lyrata Walter
Quercus macrocarpa		Quercus macrocarpa Michx.
Quercus marilandica		Quercus marilandica (L.) Münchh.
Quercus michauxii		Quercus michauxii Nutt.
Quercus minima		Quercus minima (Sarg.) Small
Quercus muehlenbergii		Quercus muehlenbergii Engelm.
Quercus nigra		Quercus nigra L.
Quercus nuttallii	synonym	Quercus texana Buckley
Quercus oblongifolia		Quercus oblongifolia Torr.
Quercus oglethorpensis		Quercus oglethorpensis W.H.Duncan
Quercus palustris		Quercus palustris Münchh.
Quercus phellos		Quercus phellos L.
Quercus prinoides		Quercus prinoides Willd.
Quercus prinus	synonym	Quercus michauxii Nutt.
Quercus rubra		Quercus rubra L.
Quercus shumardii		Quercus shumardii Buckley
Quercus stellata		Quercus stellata Wangenh.
Quercus stellata var. margarettiae	synonym	Quercus margarettiae (Ashe) Small
Quercus stellata var. mississippiensis		Quercus similis Ashe
Quercus velutina		Quercus velutina Lam.
Quercus virginiana		Quercus virginiana Mill.
Quercus wislizeni	synonym	Quercus wislizeni A.DC.
Rhizophora mangle		Rhizophora mangle L.
Robinia neomexicana		Robinia neomexicana A.Gray
Robinia pseudoacacia		Robinia pseudoacacia L.
Salix alba		Salix alba L.
Salix amygdaloides		Salix amygdaloides Andersson
Salix discolor var. eriocephala	synonym which itself is unresolved	Salix (eriocephala var. eriocephala)
Salix nigra		Salix nigra Marshall ‡
Sapindus drummondii		Sapindus drummondii Hook. & Arn.
Sapium sebiferum	synonym	Triadica sebifera (L.) Small
Sassafras albidum		Sassafras albidum (Nutt.) Nees
Sequoia sempervirens		Sequoia sempervirens (D.Don) Endl.
Sequoiadendron giganteum		Sequoiadendron giganteum (Lindl.) J.Buchholz
Sorbus americana	synonym	Aucuparia americana (Marshall) Nieuwl.
Sorbus aucuparia		Sorbus aucuparia L.
Taxodium distichum		Taxodium distichum (L.) Rich.
Taxodium distichum var. nutans	synonym not resolvable without specific authority	Taxodium (distichum var. nutans)
Taxus brevifolia		Taxus brevifolia Nutt.
Thuja occidentalis		Thuja occidentalis L.
Thuja plicata		Thuja plicata Donn ex D.Don
Tilia americana		Tilia americana L.
Tilia americana var. caroliniana		Tilia americana var. caroliniana (Mill.) Castigl.
Tilia heterophylla	synonym	Tilia americana var. heterophylla (Vent.) Loudon
Torreya californica		Torreya californica Torr.
Torreya taxifolia		Torreya taxifolia Arn.
Tsuga canadensis		Tsuga canadensis (L.) Carrière
Tsuga caroliniana		Tsuga caroliniana Engelm.
Tsuga heterophylla		Tsuga heterophylla (Raf.) Sarg.
Tsuga mertensiana		Tsuga mertensiana (Bong.) Carrière
Ulmus alata		Ulmus alata Michx.
Ulmus americana		Ulmus americana L.
Ulmus crassifolia		Ulmus crassifolia Nutt.
Ulmus pumila		Ulmus pumila L.
Ulmus rubra		Ulmus rubra Muhl.
Ulmus serotina		Ulmus serotina Sarg.

Table A1. Continued.

Taxa names used for analyses	Comments	Accepted taxa names†
Ulmus thomasii		Ulmus thomasii Sarg.
Umbellularia californica		Umbellularia californica (Hook. & Arn.) Nutt.
Vaccinium arboreum	synonym which itself is unresolved	Batodendron (arboretum)
Vernicia fordii		Vernicia fordii (Hemsl.) Airy Shaw

Notes: All analyses and gap-filling (see *Material and Methods*) were based on the original list of taxa names for which all the traits were collected. In order to identify authority, synonyms and accepted names for the used taxa names we checked them against The Plant List (2010). After name-checking we found two taxa which were synonymous to two other taxa of the list.

† Resolved accepted names are given with authority; for unresolved names the original name is in parentheses with no authority attached to it.

‡ Accepted names are taken from following sources: USDA, NRCS, National Plant Data Team (2007) and Burns and Honkala (1990).

Table A2. Description of traits used for ordination analyses with their main ecological function/proxy.

Trait	Description	Function or proxy for
Leaf traits		
Leaf composition	describes whether a leaf is compound consisting of several leaflets on a rachis or whether it is single-leaved with one leaf on a petiole	branching costs
Leaf arrangement	describes how leaves are arranged at their nodes	light interception
Leaf type	the shape of a leaf in combination whether it is deciduous or evergreen	photosynthetic rate, nutrient turnover time
Leaf margin	the shape of the leaf margin	conductive boundary layer, distributary network, initiation of photosynthesis
Specific leaf area	leaf area per leaf weight	photosynthetic rate, potential relative growth, structural leaf defenses
Reproduction traits		
Dispersal syndrome	the way how the plant disperses its seeds	colonization strategy
Seed mass	seed dry weight	recruitment survival and dispersal
Seed spread rate	the capability of a species to spread through its seed production compared to other tree species	colonization strategy
Vegetative spread rate	the capability of a species to spread compared to other tree species	reproduction strategy, disturbance response
Resprout ability	the ability of a species to resprout after aboveground biomass removal	persisting strategy after major disturbance
Root and stem traits		
Rooting habit	root habit with respect to rooting depth	water and nutrient uptake, fixation in ground
Bark surface	roughness of the bark	stem flow, soil moisture replenishment
Bark thickness	thickness of the bark	protection (e.g. against fire)
Wood density	oven dry mass per fresh volume	durability, mechanic strength, water transport
Maximum height	maximum height observed at a given site	competitive vigor, disturbance frequency
Conduit type and arrangement (porosity)	the arrangement of the vessels (exclusively angiosperms) throughout a growing season or whether there are tracheids (exclusively gymnosperms) instead	water transport, growth period, risk of cavitation and embolism
Plant level traits		
Lifespan	the expected lifespan of a tree species relative to other tree species	general plant strategy
C:N ratio (%carbon/%nitrogen)	the percentage of organic carbon divided by the percentage of total nitrogen in organic material; organic material is specified as the above ground herbaceous material of a woody plant.	general plant strategy, ontogenetic stage
Nitrogen fixation	the amount of nitrogen which is fixed by a species in monoculture	N availability in soil

Table A2. Continued.

Trait	Description	Function or proxy for
Toxicity	the relative toxicity of the plant to either humans or livestock	defense against herbivores
Potential allelopathy	the chemical potential of a species to be considered allelopathic; the relative ranking of species are based upon the completeness of the allelopathic literature, of species' growth strategies, successional position, and conjecture of the author.	direct competition, disturbance /stress response
Growth form	defines a tree as a perennial upright woody plant able to reach at least 6 m in height, a shrub as a woody plant with multiple stems and lower height, usually less than 5–6 m (15–20 ft) tall and intermediate between tree and shrub when both growth forms are combined or even likely.	climate factors, land use, general plant strategy, multi stem vs single stem growth behavior
Fire resistance (flammability)	to the ability of a species to resist burning or alternatively to carry a fire; fire resistant means low flammable	contributor to fire regimes

Table A3. Traits and performances filled for 305 species, 103 gymnosperms and 202 angiosperms, respectively before and after imputing missing values.

	Percentage filled								
	For all species			For gymnosperms			For angiosperms		
Trait	Before	After	Filled	Before	After	Filled	Before	After	Filled
Leaf traits									
Leaf composition	100.0	100.0	0.0	...	...	...	100.0	100.0	0.0
Leaf arrangement	100.0	100.0	0.0	100.0	100.0	0.0	100.0	100.0	0.0
Leaf type	99.7	99.7	0.0	100.0	100.0	0.0	99.5	99.5	0.0
Leaf margin	100.0	100.0	0.0	...	...	...	100.0	100.0	0.0
Specific leaf area	100.0	100.0	0.0	100.0	100.0	0.0	100.0	100.0	0.0
Reproduction traits									
Dispersal syndrome	54.1	54.1	0.0	69.9	69.9	0.0	46.0	46.0	46.0
Seed mass	83.9	97.4	13.4	95.1	100.0	4.9	78.2	96.0	17.8
Seed spread rate	76.1	97.7	21.6	72.8	100.0	27.2	77.7	96.5	18.8
Vegetative spread rate	74.1	96.7	22.6	70.9	100.0	29.1	75.7	95.0	19.3
Resprout ability	76.1	97.7	21.6	72.8	100.0	27.2	77.7	96.5	18.8
Root and stem traits									
Rooting habit	72.5	72.5	0.0	77.7	77.7	0.0	69.8	69.8	0.0
Bark surface	88.9	98.7	9.8	92.2	100.0	7.8	87.1	98.0	10.9
Bark thickness	70.8	93.8	23.0	79.6	100.0	20.4	66.3	90.6	24.3
Wood density	70.5	92.5	22.0	60.2	94.2	34.0	75.7	91.6	15.8
Maximum height	93.4	99.3	5.9	95.1	100.0	4.9	92.6	99.0	6.4
Conduit type and arrangement (porosity)	92.8	92.8	0.0	...	...	...	89.1	89.1	0.0
Plant level traits									
Lifespan	83.6	97.7	14.1	86.4	100.0	13.6	82.2	96.5	14.4
C:N ratio	73.8	96.7	23.0	72.8	100.0	27.2	74.3	95.0	20.8
Nitrogen fixation	100.0	100.0	0.0	100.0	100.0	0.0	100.0	100.0	0.0
Toxicity	75.7	97.4	21.6	72.8	100.0	27.2	77.2	96.0	18.8
Potential allelopathy	100.0	100.0	0.0	100.0	100.0	0.0	100.0	100.0	0.0
Growth form	100.0	100.0	0.0	100.0	100.0	0.0	100.0	100.0	0.0
Fire resistance (flammability)	76.1	97.7	21.6	72.8	100.0	27.2	77.7	96.5	18.8
Performances									
Growth rate	75.4	97.7	22.3	71.8	100.0	28.2	77.2	96.5	19.3
Shade tolerance	73.8	96.1	22.3	73.8	100.0	26.2	73.8	94.1	20.3
Drought tolerance	73.8	96.1	22.3	73.8	100.0	26.2	73.8	94.1	20.3
Shade tolerance	73.8	96.1	22.3	73.8	100.0	26.2	73.8	94.1	20.3
Water tolerance	73.8	96.1	22.3	73.8	100.0	26.2	73.8	94.1	20.3
Fire tolerance	74.4	97.0	22.6	72.8	100.0	27.2	75.2	95.5	20.3

Note: In case of no data entry the trait did not occur or did not vary in the specific group.

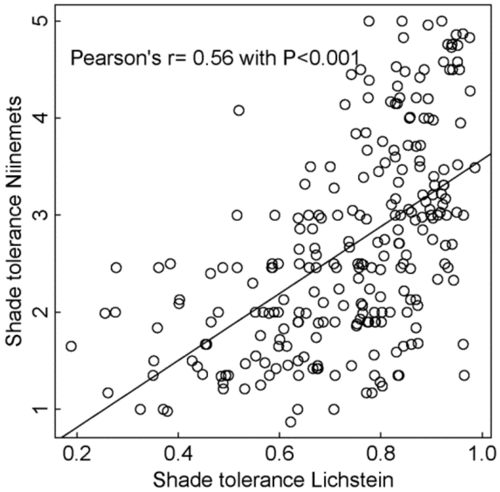

Fig. A1. Relationship between shade tolerance estimates of Lichstein et al. (2010) and shade tolerance values of Niinemets and Valladares (2006) for 261 North American woody species.

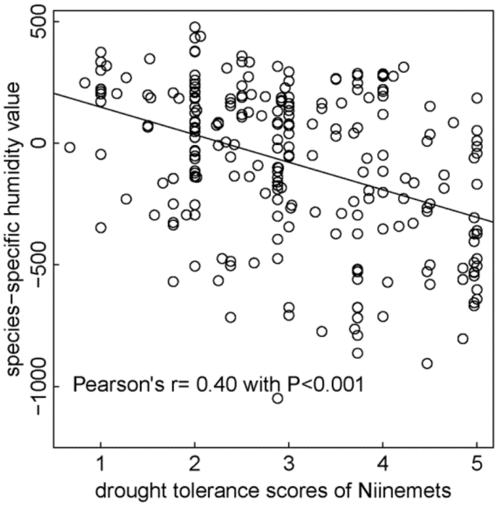

Fig. A2. Relationship between drought tolerance scores of Niinemets and Valladares (2006) and measures of humidity (annual P minus potential evapotranspiration [Willmott and Matsuura 2007]) derived from geographic distribution maps for 247 North American woody species (U.S. Geological Survey 1999) on 0.5 degree resolution. To obtain species-specific measures reflecting species' drought tolerance we used the lower limit (5th quantile) of the humidity measures covering a species range. We used quantiles instead of extreme values (i.e., minimum and maximum values) to minimize the effect of outliers caused by potential mismatches intersecting species range maps with climate.

APPENDIX B

Literature sources of trait entries for maximum height, bark thickness, and rooting habit

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Documentation of the final trait scale for leaf margin, C:N ratio, life span, leaf type and standardization of SLA

For leaf margin we extended the original scale (Adams et al. 2008) of 3 levels (1 = entire, 0.5 = toothed and/or entire, 0 = toothed) to 4 levels (0 = entire, 1 = toothed and/or entire, 2 = toothed, 3 = lobed) to account for species with a pronounced lobed leaf margin. For the C:N ratio we changed the original class based scale (low < 23, medium = 23–59, high > 59) by taking class means instead of class borders (low = 15, medium = 40, high = 65) to account for a realistic upper limit. For life span we combined classed based data (USDA, NRCS, National Plant Data Team 2007) and continuous data (Wirth and Lichstein 2009) as follows: (1) in cases of multiple entries per species continuous data were given priority and (2) first class (short < 100 years), second class (moderate = 100–250 years) and third class (long > 250 years) were converted to 80, 175 and 300 years, respectively. The two traits leaf type with 3 levels (needle-leaved, scale-like, broadleaved) and leaf deciduousness with 3 levels (evergreen, deciduous, evergreen/deciduous) were combined to one nominal trait with 6 levels (called leaf type) to reduce the strong separating effects of the traits with a low number of levels. SLA was a standardized species specific estimate based on a comprehensive meta-analysis for North America which accounts for phylogeny and intra-specific variability (Ogle et al. 2012).

CHAPTER 3

3 Predicting species' range limits from functional traits for the tree flora of North America

3.1 Abstract

Using functional traits to explain species' range limits is a promising approach in functional biogeography. It replaces the idiosyncrasy of species-specific climate ranges with a generic trait-based predictive framework. In addition, it has the potential to shed light on specific filter mechanisms creating large scale vegetation patterns. However, its application to a continental flora, spanning large climate gradients, has been hampered by a lack of trait data. Here, we explore whether five key plant functional traits (seed mass, wood density, specific leaf area, maximum height, longevity of a tree) – indicative of life history, mechanical and physiological adaptations – explain the climate ranges of 250 North American tree species distributed from the boreal to the subtropics. While the relationship between traits and the median climate across a species range is weak, quantile regressions revealed strong effects on range limits. Wood density and seed mass were strongly related to the lower but not upper temperature range limits of species. Maximum height affects the species range limits in both dry and humid climates, whereas specific leaf area and longevity do not show clear relationships. These results allow the definition and delineation of climatic 'no-go' areas for North American tree species based on key traits. As some of these key traits serve as important parameters in recent vegetation models, the implementation of trait-based climatic constraints has the potential to predict both range shifts and ecosystem consequences on a more functional basis. Moreover, for future trait-based vegetation models our results provide a benchmark for model evaluation.

3.2 Keywords

climate niche, plant geography, bioclimatic envelope

3.3 Introduction

In 1895 the Danish plant ecologist Eugen Warming defined for the first time the objectives of a functional plant biogeography, when he expressed the need '*to investigate the problems concerning the economy of plants, the demands that they make on their environment, and the means that they employ to utilize the surrounding conditions…'*. He already envisioned how to tackle this: '*This subject leads us into deep morphological, anatomical, and physiological investigations;[…] it is very difficult, yet very alluring; but only in few cases can its problems be satisfactorily solved at the present time.'*(Warming and Vahl 1909).

Since Warming's days plant science has progressed beyond the study of just a '*few cases*'. For more than a century now, botanists and plant ecologists have collected data on morphological, anatomical, and physiological traits (Violle et al. 2007, Kattge et al. 2011), and have mapped the distributions of tens of thousands of plant species (e.g. GBIF http://www.gbif.org). In addition, climatologists and soil scientists have provided us with high-resolution global maps of the plant's '*surrounding condition'*. With this it has now become feasible to analyze the functional underpinnings of plant distributions for entire regional floras across large-scale environmental gradients (Swenson et al. 2011). It is well established that on regional and global scales, climate determines the distribution not only of plant species but also of form and function (Woodward and Williams 1987, Box 1996) because it constitutes the overall physical constraint under which plants must establish and reproduce, before biotic interactions may modulate plant fitness. Plants have evolved a multitude of adaptations to climatic constraints, which are expressed in the diversity of their functional traits. These allow them to tolerate climate extremes such as summer drought or low winter temperatures. In other words, the climate range occupied by plants should be predictable from their functional traits.

Current species distribution models (SDMs) (McKenney et al. 2007) employ correlations between current climate and species distributions, so-called climate envelopes. Even modern dynamic global vegetation models (DGVMs) (McMahon et al. 2011) capable of representing carbon acquisition, water balance and competitive interactions of plant functional types (PFTs) in great mechanistic detail, still incorporate empirical climate envelopes to constrain PFT distributions. This obvious lack of mechanism is an important limitation when such models are used to predict vegetation shifts under future climate scenarios, especially under novel combinations of climate variables (McMahon et al. 2011). Here, we introduce a new approach – the 'double quantile' approach (see Figure 1 and below) – that allows us to predict species distribution limits from functional plant traits. While still empirical at heart, this approach has distinct advantages: 1) The very nature of the traits emerging as suitable predictors of species distribution limits sheds light on the biological mechanisms. Accordingly, below we are able to put forward concrete hypotheses of the biological underpinnings of trait-climate limit relationships. 2) Functional traits serve as a common currency across species and thus provide the basis for assimilating the behavior of many species into a single generic predictive framework. 3) Because this approach replaces idiosyncrasy by generality, the hand-shake with process-oriented models is greatly facilitated as will be discussed below.

Here, we explore the potential of five functional traits – specific leaf area (SLA), wood density, maximum height, seed mass and tree longevity – to explain the climate range limits and mean climate preferences of 250 North American tree species covering a temperature gradient from the boreal to the subtropics and a gradient from 65 mm to 3000 mm of annual precipitation. While there has been a first attempt to incorporate trait information in SDMs (Pollock et al. 2012), we present here the first study using plant functional traits to predict their limiting effect on species' climate ranges at a taxonomic and climatic scale relevant for DGVMs. We chose to present the relationship between traits and species climate range limits from a trait perspective in order to highlight their potential for predicting species' climate niches as a holistic measure of plant performance in response to climate. Unlike previous studies, our 'double quantile' approach places an emphasis on the responses of species-specific climate ranges at the potentially stressful ends of climate gradients, where strong effects of functional traits on range limits can be expected.

3.3.1 Functional traits – selection and relevance

The five traits represent key functions defining plant strategy axes related to the fundamental tradeoffs of resource acquisition and reproduction (Lavorel and Garnier 2002, Westoby et al. 2002) and are thus indicative of life history, mechanical and physiological mechanisms. Furthermore, some of these traits are frequently used as parameters in DGVMs (Kattge et al. 2011). Because these traits vary across climatic gradients (Wright et al. 2005, Chave et al. 2009), they are ideally suited to gain insight into processes shaping tree distributions at continental scales and at the same time to improve predictions on ecosystem functions under climate change. SLA is a key trait of the leaf economic spectrum (Wright et al. 2004) and defines a species' resource use strategy from acquisitive to conservative. It is related to growth rate under different climatic conditions (Diaz et al. 2004) and reflects tradeoffs in species' shade and drought tolerances (Hallik et al. 2009). Wood density is related to the efficiency and safety of water transport (Sperry et al. 2008) and represents a tradeoff between mechanical strength and vertical growth. It is strongly correlated with growth and mortality rates (Chave et al. 2009). Maximum height describes the maximum recorded height of a species and quantifies species' carbon gain strategy via light capture (Falster and Westoby 2003); it is related to successional status, shade tolerance and responds to gradients in precipitation on a global scale (Moles et al. 2009). Seed mass correlates positively with seedling survival rates under hazardous conditions during seedling establishment (Westoby et al. 2002) and negatively with dispersal distance and the number of seeds produced per unit energy invested (Leishman et al. 2000). Maximum tree longevity determines species responses to disturbance (Loehle 2000), compensates for reduced fecundity or juvenile survival (Lertzman 1995) and relates to defensive investment (Enquist et al. 1999).

3.3.2 Linking traits to climate ranges

We derive a tree species' climate range from its natural geographic distribution (Box 1995). We use a set of eight bioclimatic variables (see Methods) which represent dominant climatic gradients over North America and are widely used in climatic niche modeling (Sitch et al. 2003, McKenney et al. 2007). To define a species' climate range (see Fig.1 A) we estimate for each bioclimatic variable the lower (5th quantile) and upper limits (95th quantile) and the median (50th quantile) across a species' distribution range. Using linear quantile regression analysis (Cade and Noon 2003), we regress across all species the three species-specific range measures against each of the five traits separately estimating the lower (10th, 5th), the upper (90th, 95th) and median (50th) regression quantiles, respectively (Fig. 1B). Thus, the 50th quantile regression lines fit to the medians (black line/black squares; Fig. 1B) and describe how the mean realized climate niche depends on the trait values. The lower and upper quantile regression lines fit to the lower and upper limits (blue line/blue squares and red line/red squares, respectively). In this 'double quantile' approach, the outer regression lines enclose an area corresponding to the climate range the pool of 250 North American tree species can occupy across the range of their trait values (Fig. 1B). At the same time it identifies 'no-go areas' which cannot be occupied by trees with a given trait value. The delineated areas can attain three possible shapes: 1) The area is wedge-shaped when there is a *one-sided* constraint, i.e. only one outer quantile represents a climatic extreme requiring a trait adaptation. 2) The area has the form of an acute-angled triangle, when there is a two-sided constraint leading to *reverse* responses of the outer quantiles. Both triangular shapes, 1) and 2), imply that the possible climate range of the species pool changes with a given trait value (see Fig. 1C for examples). 3) The area can have a rhomboid shape when the two-sided constraints are *aligned*. This implies a shift in the mean climate preference, but no change in the potential climate range per trait value.

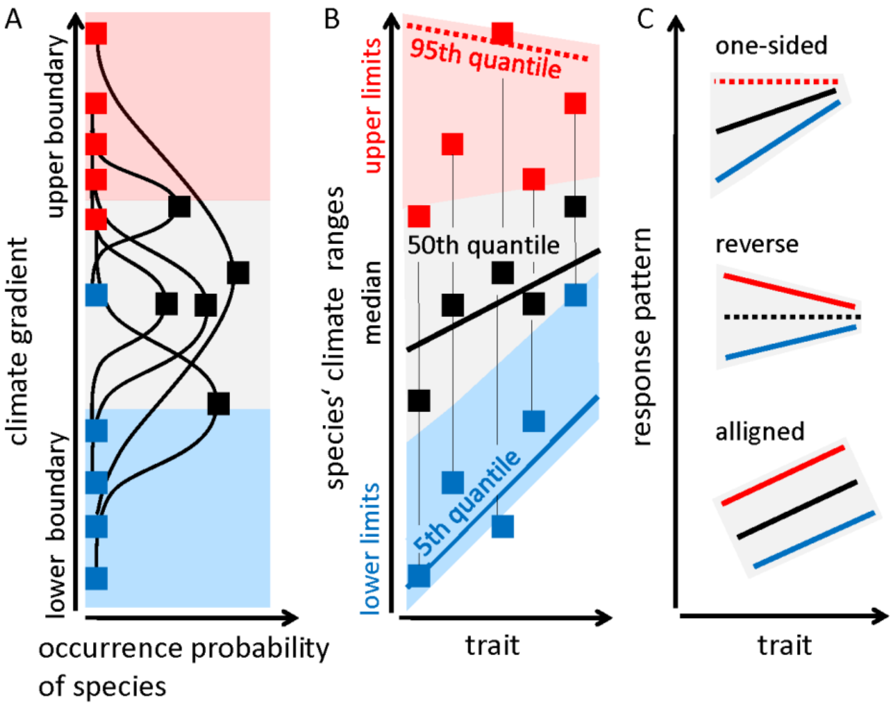

Fig.1. (A) Species are distributed along climatic gradients and occupy species-specific climate ranges, which can be characterized by three measures: the upper (red squares), the lower (blue squares) limit and the median (black squares) for which the highest species' occurrence probability is suggested. (B) To explore the response of the climate range measures to traits we related them separately against the traits using linear quantile regression analysis. We estimated the upper quantiles for the upper, the lower quantiles for the lower limits and the median quantile for the median; a solid line indicates a slope significantly different from zero (increasing or decreasing) and a dotted line a non-significant slope. The area between the outermost regression lines represents the possible climate range species can occupy across their trait values while areas outside these lines describe 'no-go areas'. (C) We distinguish three types of response patterns: 1) *one-sided* constraint, i.e. significant slope at only one limit (the upper or the lower one) 2) two-sided constraint with *reverse* slopes at both limits and 3) constant shift with *aligned* slopes at both limits.

3.4 Results and Discussion

3.4.1 Patterns of trait-climate range relationships

Few significant relationships between functional traits and the median realized climate niche of North American tree species emerge. However, we find strong limiting effects of functional traits on climate range limits estimated as significant upper and/or lower quantile regressions (Fig. 2 and Fig. S1, Table S1). The most *obvious* (see Methods for nomenclature) and dominant response patterns are *one-sided* but we also find significant *aligned* patterns as well as less pronounced *reverse* patterns (Fig. S1). Moreover, there is a clear association between the functional traits and particular response patterns: 1) pronounced *one-sided* patterns are found for wood density (for 2 out of 8 bioclimatic variables) and seed mass (6 out of 8) suggesting an adaptation to harsh climates (e.g. cold and dry). This would indicate a strong climate control at the harsh end but not at the rather benign end where biotic control is suggested; 2) primarily *aligned* patterns are found for maximum height (3 out of 8) suggesting an adaptation to both climatic extremes. This might be an indication of a joint operation of climate control and biotic sorting processes (see also below); 3) no obvious responses are found for SLA and longevity, indicating no climate control. It should be noted that the geographical area of North America fully samples the tree species distribution limits towards dry and cold climates, while it truncates the distributions towards warmer and moister climates in the tropics. Because of this, the observed patterns might change if the region of interest was extended towards the tropics with datasets that are likely to emerge in the near future (e.g. *one-sided* may turn into aligned or reverse patterns).In the following, we will structure the presentation of results according to traits and refer to patterns mentioned above.

3.4.2 Wood density and seed mass – climate-controlled ‘no-go areas’

We observe a *one-sided* response of mean annual temperature (annual T) to wood density, where only the lower limits increase significantly (Fig. 2, Table S1) with increasing wood density. Trees with soft wood can occupy regions covering the complete temperature range of North America but species with high wood density only occur in warmer regions. Trees with wood denser than 0.55 g cm^{-3} do not expand into ‘no-go areas’ with annual T below 0 °C and the species with the hardest wood (> 0.85 g cm^{-3}, e.g. *Rhizophora mangle* and *Quercus virginiana*) are restricted to subtropical climates with annual T > 15 °C. There is also a significant positive relationship between wood density and a species’ annual T preference. The significant *one-sided* pattern also occurs when only angiosperms are considered (Fig. S2) and the more soft-wooded gymnosperms are located well within the triangle formed by the angiosperms (Fig. 2) suggesting a generic response across clades. The mechanism keeping hard-wooded species out of cold regions probably reflects the tradeoff between stability and construction costs (Pittermann et al. 2006). Dense wood lends physical stability and is more resistant to interior decay caused by fungi and insects (Chave et al. 2009). It thus increases longevity particularly in warmer climates where the metabolic activity of decomposers is high. However, the high carbon costs of dense wood slow down growth rates. In cold climates, where carbon gain is limited by short growing seasons, these costs can probably not be met (Pittermann et al. 2006), which is mirrored in the *one-sided* pattern between wood density and temperature seasonality (T seasonality). Species with low wood density are typically fast growing pioneers which are adapted to exploit the increased light and nutrient availability after disturbance. Disturbances occur across the entire climatic gradient and so do the soft-wooded pioneer species.

Seed mass is another important predictor of species' climate range limits. The possible climate range the ensemble of species can jointly occupy generally decreases with increasing seed mass for five bioclimatic variables according to a one-sided pattern (Fig. 2). Trees with low seed mass occupy the whole climate range, while those with seeds heavier than 150 mg (approx. seed mass of *Pinus albicaulis*) do not occur in cold climates (annual T < 0°C) and in regions with high annual precipitation (> 2000 mm). Identical *one-sided* patterns emerge for separate analyses of angiosperms and gymnosperms proving the generic nature of the relationships (Fig. S2 and S3). The functional mechanisms are less clear than for wood density and remain speculative. The short growing season in cold climates might not allow enough time and energy for the development of larger seeds (Moles et al. 2006).

3.4.3 Maximum height –'no-go areas' related to climate and biotic interactions

Species' range limits with respect to annual P and net precipitation (net P, see Methods for definition) are related to maximum height according to an *aligned* pattern (Fig.2, Table S1). With increasing maximum height the medians and limits increase for annual P and net P (Fig. 2). Thus short trees tend to be rare in regions with high absolute annual P and high net P, while tall trees tend to be absent from regions with opposite conditions. Similar patterns emerge when analyzing angiosperms and gymnosperms separately suggesting a generic response across clades (Fig. S2, S3). Hydraulic limitation of height growth (Ryan and Yoder 1997) and competition for light (Falster and Westoby 2005) are the most likely mechanisms driving these patterns. For water to move vertically, the leaf water potential must decline with height (Koch et al. 2004). As the required gradient is a linear function of tree height, any reduction in soil water potential has to be met by a parallel reduction in leaf water potential. Because the latter cannot sink below a certain physiological limit, drought translates directly into shorter tree heights (Stegen et al. 2011). Thus tall trees are missing from dry climates because of physiological constraints which are in agreement with the findings that precipitation controls plant maximum height at the global scale (Moles et al. 2009). The absence of small trees from very humid climates may be under biotic control, e.g. via selection pressure for tall heights in the race for light under otherwise favorable conditions. The upper T seasonality limits seem to follow a bell-shaped right skewed response with a mode at 22m, i.e. 20% of the height range. We capture this by applying linear quantile regression to tree species with maximum heights larger than the mode (Fig. 2, Table S1). Above this threshold, the upper T seasonality limits sharply decrease with maximum height following a *one-sided* pattern. This relationship keeps trees with large maximum heights out of continental boreal climates with high T seasonality, most likely due to short growing season combined with a high risk of frost-drought during spring.

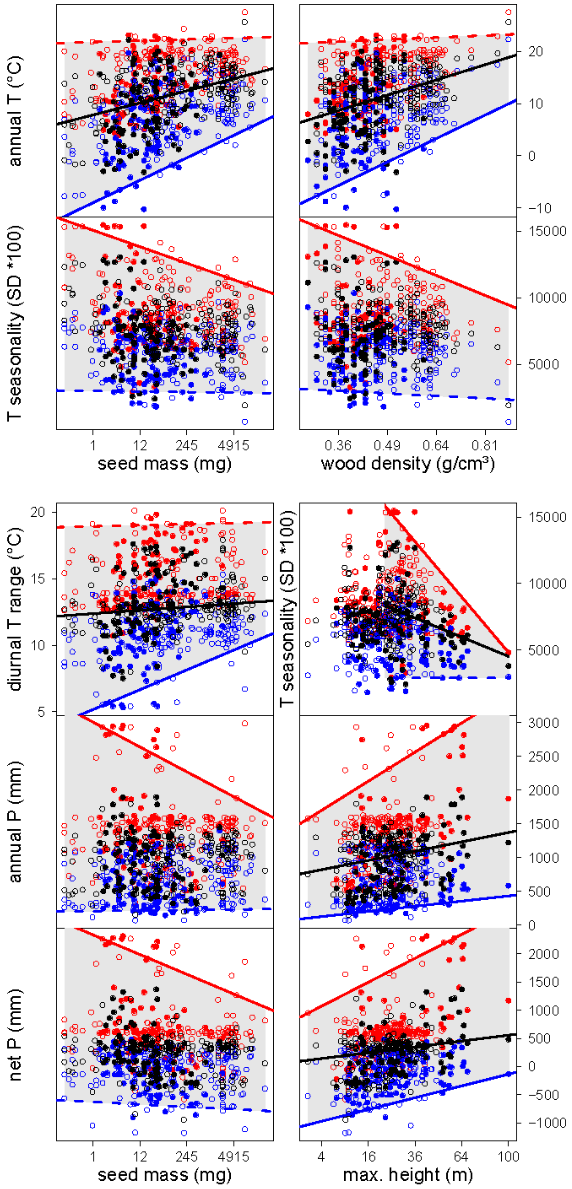

Fig.2. *Obvious* significant trait–climate range relationships (see Methods for rules) matching the proposed response patterns in Fig.1 C based on climate ranges of 250 North American tree species (166 angiosperms= open circles and 84 gymnosperms=filled circles) or 146 species in case of maximum height vs. T seasonality (see text). For each trait–climate combination the responses of the species-specific upper limits (red circles), lower limits (blue circles), and the median (black circles) to the traits are quantified applying linear quantile regression; the 95th quantile (upper limits), the 5th (lower limits) and the 50th quantile (median) is shown; solid lines indicate slopes significantly different from zero ($P<0.05$), dashed lines non-significant slopes of the 95th and 5th quantiles and no line is drawn when slopes of the 50th quantile are non-significant. The grey shaded areas between the outermost quantiles correspond to the climate range the species can jointly occupy across the range of their trait values while the white areas correspond to the ’no-go areas’.

3.4.4 SLA and longevity

For SLA and longevity we find only weak *reverse* and *one-sided* responses (Fig. S1 and Table S1). This might be due to the fact that both traits reflect processes operating at local scales, most notably nutrient use efficiency and shade tolerance, responding to strong local heterogeneity in nutrient and light availability, respectively (Reich et al. 1997). Also temporal changes in these resources and differences in successional niche occupation by species may decouple SLA and longevity from the regional climate. This implies that the differentiation into acquisitive and conservative resource use strategies (high SLA and short tree lifespan vs. low SLA and long tree lifespan) occurs in all climates.

3.4.5 Continental patterns of trait variation and potential functional richness

Having identified obvious patterns (Fig. 2) and discussed the underlying functional mechanisms of how traits constrain climate limits of North American trees, we are able to map climatic ‘no-go areas’ for trees of a given wood density, seed mass and maximum height by applying the quantile regression equations (Table S2) in a reverse mode to gridded climate data. This allows for the identification of maximum attainable trait values in geographic space (Fig. 3, Fig. S4, data SI) and describes how trait variation will change in response to climate. When trait variation changes in response to climate, the color gradient in Fig. 3 depicts how the maximum trait values decline in the direction of the climate factors. In contrast, dark red depicts regions where trait variation is unconstrained. For wood density and seed mass dark red regions mean that any trait value within the spectrum defined by the North American species pool (Fig. 3A and Fig. S4; dark red regions) is possible. For maximum height, however, the dark red colored area in Figure 3B contains some locally humid climates (e.g. The Pacific North West) where some low maximum heights tend to be excluded (see Fig.2) as we translated only the lower annual P and net P responses for the map. For example, at low elevation sites wood density may take on any value between 0.3 g cm^{-3} and 0.9 g cm^{-3} south of 42°N which is about the latitude of New York (Fig. 3A). At the border to Canada, the maximum attainable wood density is predicted to be 0.54 g cm^{-3} and it decreases to values of 0.32 g cm^{-3} at 60°N (northern border of Manitoba). A very similar pattern, slightly shifted northwards, can be observed for seed mass (Fig. S5). For maximum height almost the whole spectrum of values (i.e. up to 100.4 m) is predicted for the north-west coast of North American and the south-east coast including Florida (Fig. 3B). From Florida northwards the maximum attainable max. height values decrease continuously and fall below 50 m north of the Great Lakes. In the arid lowland regions of the Southwest the maximum attainable max. height is reduced to 10 m and below. These results are insensitive to the exclusion of the tall gymnosperm species *Sequoia sempervirens*, the only species with a max. height above 70 m (see Table S3; Fig. S5).

These N-S and E-W gradients are in line with trait assembly rules (Weiher and Keddy 1995) and with trait diversity patterns (Swenson et al. 2011) across large climatic gradients ranging from harsh (boreal and arid) to benign (subtropical and tropical) climate conditions. Under harsh climates, trait ranges are confined to values conveying stress tolerance allowing species to pass strong abiotic filters, while in benign climates biotic filters become more important, which are complex and multifaceted. These are most likely reflected by a multitude of traits and may have less of an equalizing effect on single traits than abiotic stressors. In addition, traits values associated with tolerating harsh conditions (e.g. low wood density) may not be subjected to biotic filtering under benign conditions. This results in a higher functional richness and greater trait variation as has been reported for temperate and subtropical relative to boreal climates (Swenson et al. 2011). If this type of response pattern proves to be consistent across many traits, this would lend support to the climate favorability or physiological tolerance hypothesis of functional richness (Fischer 1960) indicating that towards the tropics a larger number of viable trait configurations become possible and that functional richness therefore increases. The relationship between traits and climatic limits thus provides insights into the processes shaping global scale biodiversity patterns.

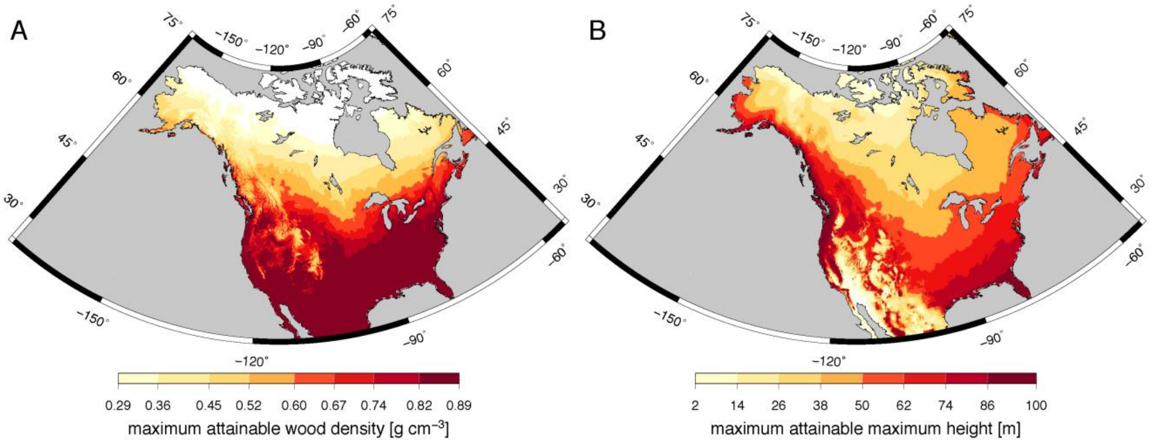

Fig. 3. Maps show maximum attainable trait values for wood density (A) and maximum height (B) given the climate (Fig.2). Dark red depicts regions where trait values are climatically unconstrained whereas the color gradient depicts 'no-go areas' for North American trees as determined by their trait values. White depicts regions outside the considered trait range for which we make predictions. The maximum attainable trait values shown are derived by applying quantile regression equation (Table S2) to gridded climate data and subsequent selection of the minimum trait value predicted per grid cell to visualize the strongest climate constraint on trait variation. Gridded climate data used: mean annual temperature, diurnal temperature range, temperature seasonality, annual precipitation and net precipitation. Maps have a resolution of 5 arc minutes and are projected in Albers equal-area conic projection.

3.4.6 Limitations and the way forward

The ideal trait for a functional climate range prediction in functional biogeography is one 1) whose function directly reflects the physiological or mechanical mechanism compromising vital rates (growth, survival, fecundity) at the range limits (Lavorel and Garnier 2002) and 2) which is available for all species considered in an analysis. One trait satisfying the first condition (but see below) is e.g. 'physiological cold-resistance' which can be quantified experimentally based on conductivity measurements indicating cell membrane leakage (Steponkus 1984). However, this 'hard' trait is not available for all 250 North American tree species. Conversely, our five traits are available for all species, but their functional interpretation is rather indirect albeit plausible. Unlike the above example, the relationship between vital rates and climate are rarely controlled by a single trait. Drought tolerance, for instance, is conveyed by a whole suite of traits (Poorter and Markesteijn 2008), including e.g. deep roots for accessing subsoil water, small vessels for cavitation prevention and high seed mass for rapid penetration of dry top soils. Moreover, often several traits jointly define strategy axes based on fundamental tradeoffs (Reich et al. 2003b). All of our five traits are part of such tradeoffs and have been singled out as *leader traits* representing different bundles of correlated traits, including physiological 'hard' traits (Westoby et al. 2002).

We therefore advocate our pragmatic approach that aims to balance functional precision on the one hand and generality and applicability on the other.

Our approach uses species-specific trait means and thus ignores intra-specific trait variation. It is, however, important to note that our trait-based approach is insensitive to intra-specific variation as long as the mechanisms causing inter- and intra-specific variation are the same. The predictions of our study are valid for trees with particular traits no matter whether these vary within (pheno- or genotypes) or between species. We use linear quantile regression to quantify bivariate trait–climate range relationships. Visual inspection of the *obvious* responses in Fig. 2 shows that quantile relationships indeed tend to be linear when considering at least 75% of the trait range. It is possible that a whole suite of traits and inevitable tradeoffs among these traits can lead to alternative plant designs reaching equal vital rates. This circumstance, in fact, challenges simple bivariate statistical analyses and calls for multivariate approaches, where multi-dimensional quantiles can be fit to one (or several) climatic niche parameters and for more process-based models accounting for this multi-dimensional optimization process (Reu et al. 2010, Pavlick et al. 2013). Nevertheless, our bivariate regression equations have the advantage that they are intuitive, straight forward to implement in models and can easily be used to generate maps visualizing climatic filtering on trait variation (e.g. Fig.3).

3.4.7 Potential for improving global vegetation models

In classic DGVMs functional traits are typically used as variables underlying the definition of plant functional types (e.g. ‘evergreen broad-leaved’ has elements of leaf longevity and SLA) or as model parameters. For example, SLA is often used to convert carbon allocated to the leaf compartment into leaf area available for light capture (models listed in Kattge et al. (2011)). Wood density is used to translate carbon invested into stem growth into size gain (White et al. 1999, Sitch et al. 2003). In modern gap models maximum height is implemented as a site-dependent variable allowing for more pronounced climate-induced changes in productivity (Rasche et al. 2012). Maximum longevity is used to infer mortality rates (LPJ-GUESS, (Smith et al. 2001)). Seed mass is sometimes used as a proxy for dispersal distance in individual based models (Lischke et al. 2006). In short, our five predictor-traits are used as important descriptors of plant functioning in vegetation models. Three of them (seed mass, wood density and maximum height) also turn out to be suitable predictors of range limits and thus may serve a dual purpose in vegetation models. This is precisely mirroring the response-effect framework of trait influence (Lavorel and Garnier 2002), where traits govern vegetation responses to the environment as well as vegetation effects on ecosystem functioning. Future models taking advantage of both facets of traits may become capable of simultaneously predicting shifts in trait spectra and resulting consequences for ecosystem functioning and finally via this link the interactions of climate, functional diversity patterns and vegetation feedbacks.

The trait–climate range relationships reported here may not only be useful to improve existing DGVMs but, more importantly, may serve as benchmark for validating next generation DGVMs (Pavlick et al. 2013). In these, trait–climate range relationships emerge as a consequence of the performance of evolving 'pseudo-species' originating from the implementation of trade-offs in plant functions and functional traits (Reu et al. 2011). This does not only include the responses of these 'pseudo-species' to climatic constraints, but also the interactions among them exerting an additional biotic filter (Bohn et al. 2012). In these approaches, however, 'pseudo-species' differ from real world species, because 1) not all aspects of plant function (trade-offs) can be implemented (Reu et al. 2011, Pavlick et al. 2013), and 2) they may evolve in the model differently as in the real world (Scheiter et al. 2013). Models based on pseudo-species require suitable (meta-) patterns for model evaluation that are decoupled from observed species or PFT geographic distributions. Such an avenue is provided through the reported trait-climate range relationships and the maps showing continental patterns of trait variation. These shall thus be particularly useful for the evaluation of next generation DGVMs, which will most likely be based entirely on traits and trade-offs and not necessarily on species or PFT range limits empirically derived from present-day observations.

3.5 Methods

We derived species-specific climate ranges from intersecting distribution maps of 250 North American tree species (Little 1999) with gridded maps of 8 bioclimatic variables, including mean annual temperature (annual T in °C), diurnal temperature range (diurnal T range in °C), temperature seasonality (T seasonality = standard deviation of monthly mean temperature values), annual precipitation (annual P in mm), precipitation of coldest quarter (P of coldest quart. in mm), and precipitation of warmest quarter (P of warmest quart. in mm) with a resolution of 5 arc minutes (Hijmans et al. 2005). Furthermore, we included growing degree days (GDD) with a base temperature of 5°C (New et al. 1999) and net precipitation (net P in mm) as a measure of humidity calculated as annual P minus potential evapotranspiration (Willmott and Matsuura 2007) both in 0.5 degree resolution. For each bioclimatic variable we derived three species-specific measures: the upper and the lower limit and the median which were obtained from the bioclimatic data covering a species range at the 95th, 5th and 50thquantile, respectively. We used quantiles instead of minimum and maximum values to minimize the effect of outliers caused by potential mismatches intersecting species range maps with climate. We collected the five continuous traits wood density (g cm^{-3}), seed mass (mg), specific leaf area (SLA in cm² g^{-1}), plant maximum height (m) and tree longevity (years) from literature sources (Jenkins et al. 2004, Wirth and Lichstein 2009), databases (USDA 2007, Kew 2008, Zanne et al. 2009) and, in the case of SLA, species-specific estimates corrected for high intra-specific variation (Ogle et al. 2012).We compiled species-specific mean trait values for each of the 250 tree species as described in Stahl et al. (Stahl et al. 2013). To obtain normally distributed trait values, both seed mass and tree longevity were log 10-transformed, whereas wood density and plant maximum height were square-root-transformed. We performed linear quantile regression for each of the three measures against each of the five traits for all 8 bioclimatic variables resulting in a total of 40 trait–climate range relationships. To account for non-linear relationships we did inspect the patterns visually for strong and obvious linear patterns along at least more than 75% of the range in trait values. In such cases (max. height vs. T seasonality in Fig. 2), the data was split and quantile regressions applied for that part of the trait range. We classified response patterns according to Fig. 1 when at least one of the two fitted regression lines of the lower / upper limit had a slope significantly different from zero. We classified patterns as *obvious* when the two lower / upper quantiles (grey shaded in Fig. S1-S3) had significant slopes (see Table S1 for significance levels of slopes). To evaluate the effect of phylogeny on our results, we repeated the analysis for gymnosperms and angiosperms separately (Fig. S2 and S3). In order to compare the slopes of the different trait-climate range relationships we centered and standardized the traits as well as the measures (see Table. S1). To conduct inferences about slopes of quantile regression estimates we computed bootstrapped standard errors (standard xy-pair bootstrap). All analyses were done in R version 2.11.0 (R development Core Team 2010) using package “quantreg” (Koenker 2011). Finally, we mapped the ‘no go areas’ for North American trees as maximum attainable trait values for wood density, seed mass and maximum height from applying quantile regression equations of the outermost significant estimates (Table S2) to gridded mean annual temperature, diurnal temperature range, temperature seasonality, annual precipitation and net precipitation. For each trait we created maps from the bioclimatic variables with a significant relationship and extracted the minimum trait value per grid cell across these maps.

3.6 Acknowledgements

We thank Helge Bruelheide, Carsten Dorman and Erik Welk for sharing their ideas about this work. We thank Kiona Ogle for providing data of specific leaf area and Stefanie Nöllert for assistance in data mining. We thank Jens Kattge and Sophia Ratcliffe for helpful comments on this manuscript as well as three anonymous reviewers. U.S. was supported by the Max-Planck society and the University of Leipzig with a PhD-scholarship.

3.7 Supplementary Material

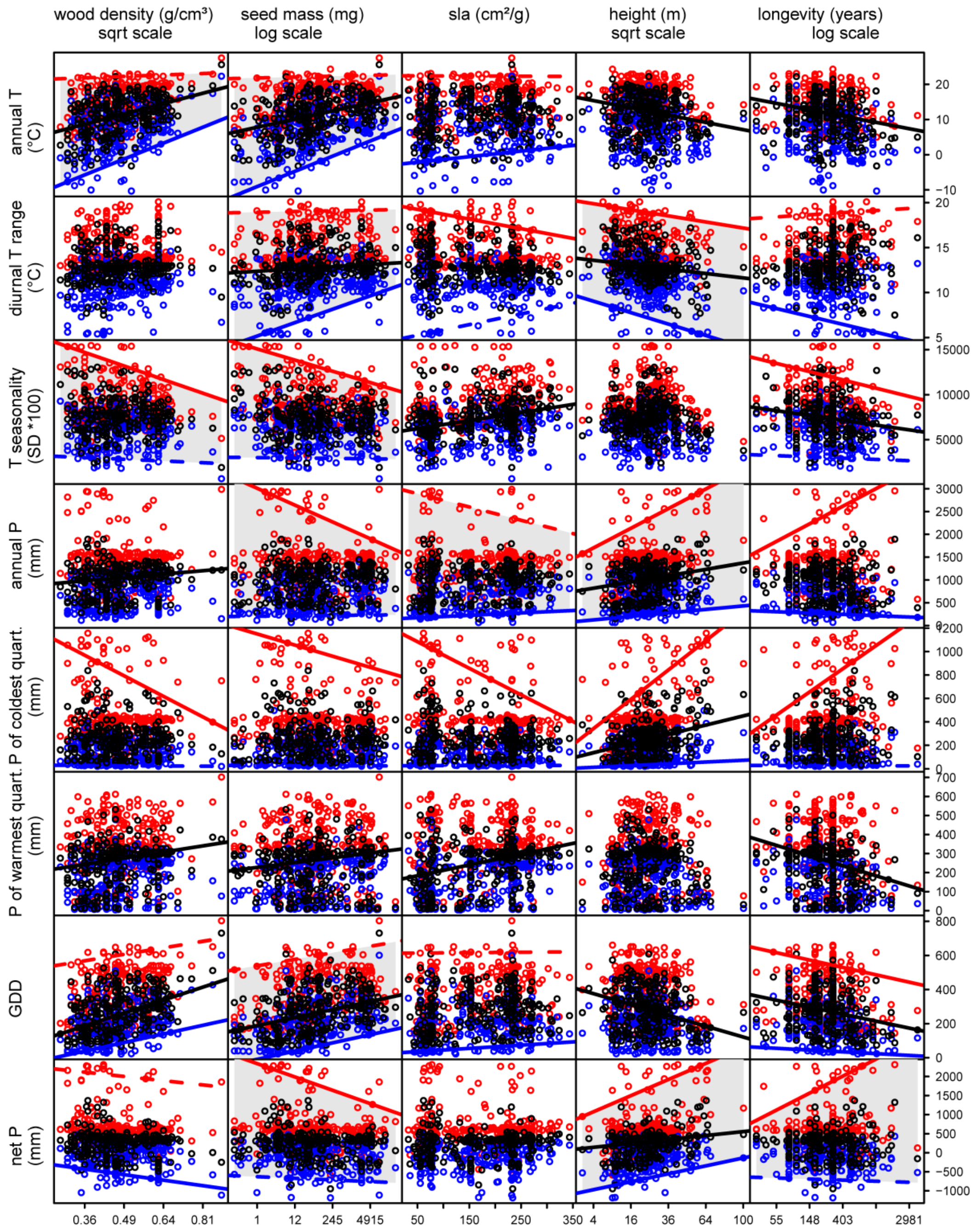

Fig. S1. Trait-climate range relationships based on climate ranges of 250 North American tree species distributed from the boreal to the subtropics for eight bioclimatic variables and five traits. For each trait–climate range relationship the response of the species-specific upper limits (red circles), lower limits (blue circles) and the medians (black circles) to the traits are quantified applying linear quantile regression as follows: for the upper limits the uppermost quantiles (95th and 90th), for the lower limits the lower-most quantiles (10th and 5th) and for the median the 50th quantile were estimated. To evaluate the responses in light of the proposed patterns in Fig.1C (see Methods for rules) we displayed significant slopes (i.e., significant different from zero) as solid lines and non-significant slopes as dashed lines as follows: if the two upper and/or the two lower slopes are both significant the slopes of the 95th and the 5thquantile are shown otherwise the significant slopes are shown, and only if both upper or both lower slopes are non-significant the outermost non-significant slope is shown. Trait-climate range relationships are shaded grey when the two upper quantiles and/or the two lower quantiles have significant slopes, indicating *obvious* significant response patterns. GDD, growing degree day; P, precipitation; sqrt, square root; T, temperature.

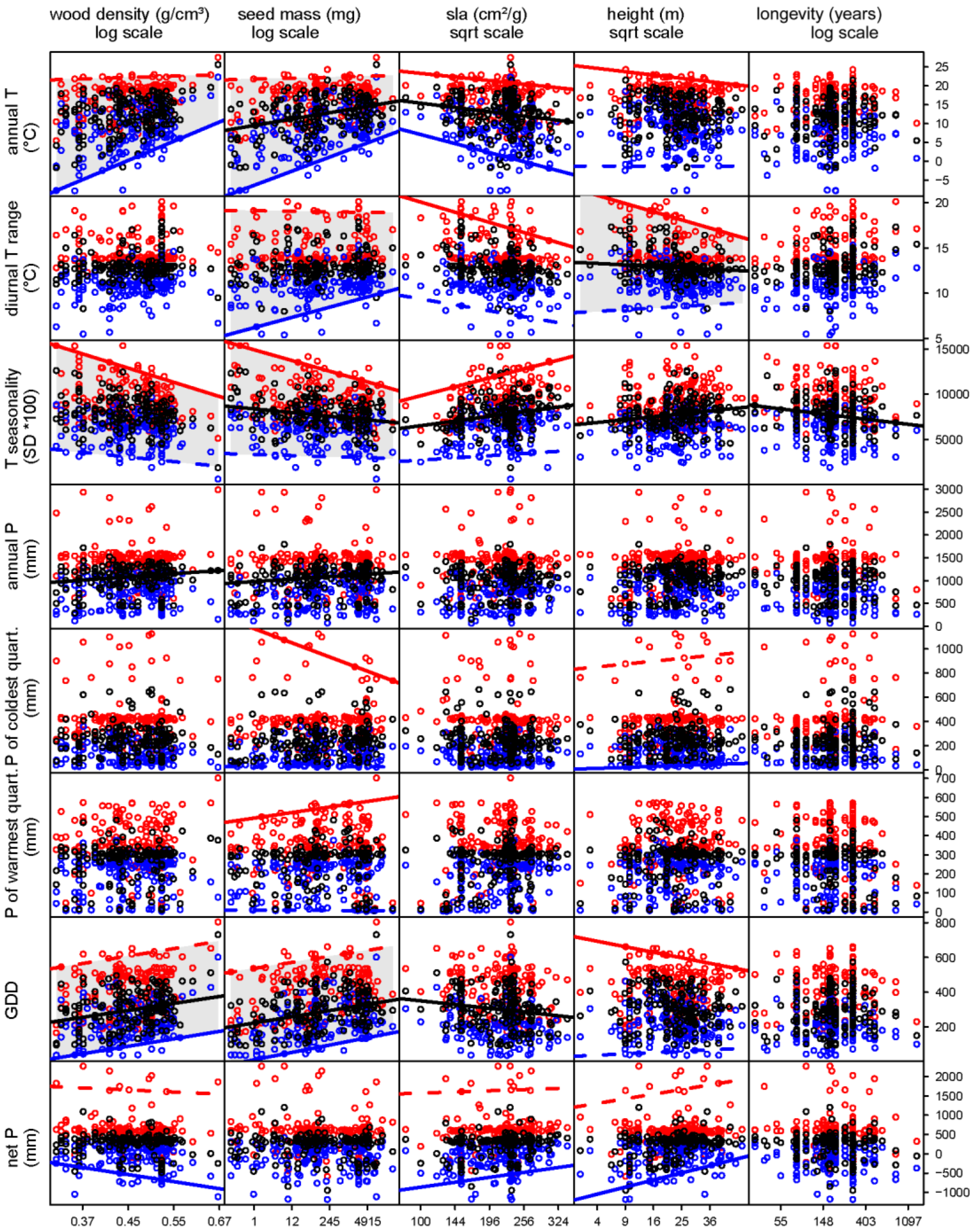

Fig. S2. Trait-climate range relationships based on climate ranges of 166 North American angiosperm tree species distributed from the boreal to the subtropics for 8 bioclimatic variables and 5 traits. For each trait–climate range relationship the response of the species-specific upper limits (red circles), lower limits (blue circles) and the medians (black circles) to the traits are quantified applying linear quantile regression. For details see Fig.S1.

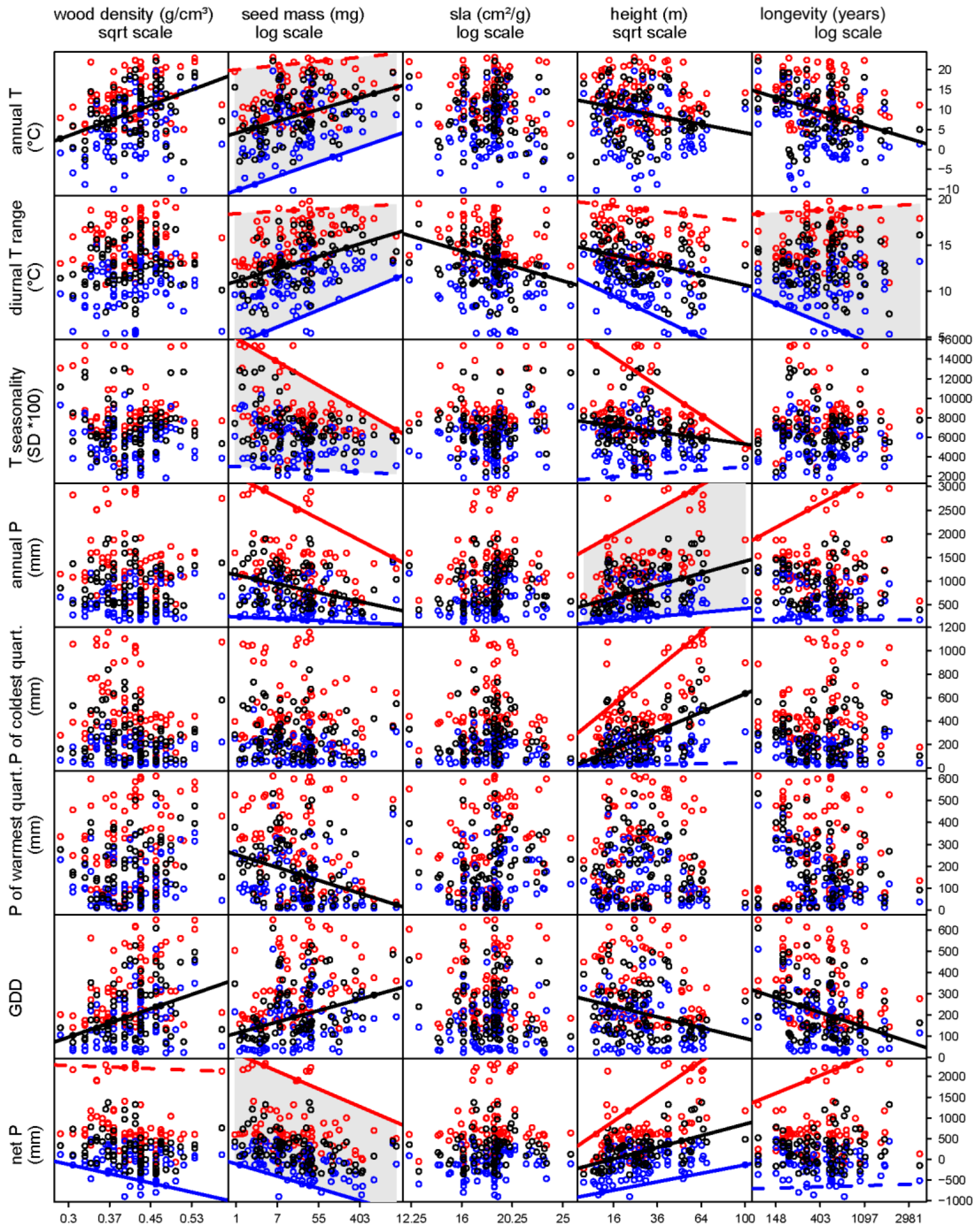

Fig. S3. Trait-climate range relationships based on climate ranges of 84 North American gymnosperm tree species distributed from the boreal to the subtropics for 8 bioclimatic variables and 5 traits. For each trait–climate range relationship the response of the species-specific upper limits (red circles), lower limits (blue circles) and the medians (black circles) to the traits are quantified applying linear quantile regression. For details see Fig. S1.

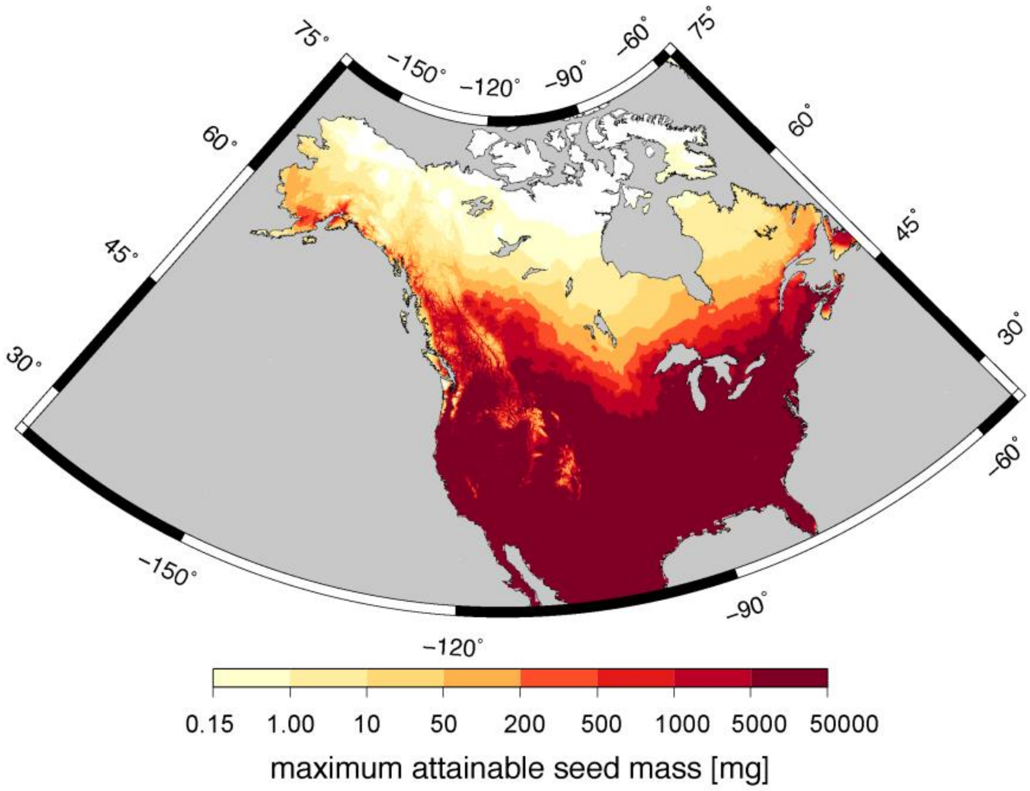

Fig. S4. Map shows maximum attainable seed mass values given the climate. Dark red depicts regions where seed mass values are climatically unconstrained whereas the color gradient depicts ‘no-go areas’ for North American trees depending on seed mass. The maximum attainable seed mass values shown are derived by applying quantile regression equation (Table S2) to gridded climate data and subsequent selection of the minimum seed mass value predicted per grid cell to visualize the strongest climate constraint on seed mass variation. Gridded climate data used: mean annual temperature, diurnal temperature range, temperature seasonality, annual precipitation and net precipitation. The map has a resolution of 5 arc minutes and is projected in Albers equal-area conic projection.

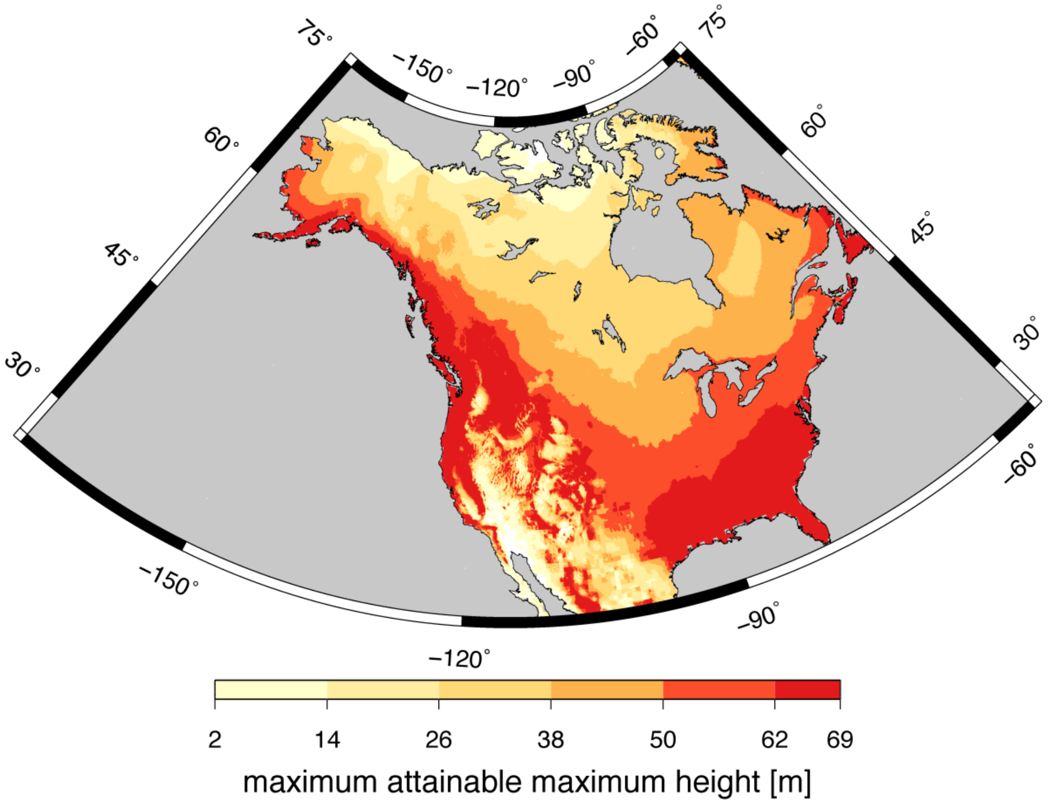

Fig. S5. Map shows maximum attainable maximum height values given the climate for 249 North American tree species (Sequoia sempervirens with 100.4m is excluded). Dark red depicts regions where maximum height values are climatically unconstrained whereas the color gradient depicts ‘no-go areas’ for North American trees depending on maximum height. The maximum attainable maximum height values shown are derived by applying quantile regression equation (Table S2) to gridded climate data and subsequent selection of the minimum max. height value predicted per grid cell to visualize the strongest climate constraint on seed mass variation. Gridded climate data used: temperature seasonality, annual precipitation and net precipitation. The map has a resolution of 5 arc minutes and is projected in Albers equal-area conic projection.

Table S1

Standardized slopes of linear quantile regression lines for the relationships between traits and climate range measures for 250 North American tree species presented in Fig. S1 and Fig. 2.

bioclimatic variable	measure	tau (τ)	wood density		seed mass		sla		height		longevity	
			one-sided		***one-sided***		*one-sided*		*no*		*no*	
annual T	upper	0.95	0.06	n.s.	0.05	n.s.	-0.01	n.s.	-0.05	n.s.	-0.10	n.s.
	upper	0.90	0.14	n.s.	0.07	n.s.	-0.11	n.s.	-0.14	n.s.	-0.15	n.s.
	median	0.50	0.41	***	0.41	***	0.13	n.s.	-0.24	**	-0.25	*
	lower	0.10	0.55	***	0.63	***	0.20	**	0.02	n.s.	-0.11	n.s.
	lower	0.05	0.55	***	0.67	***	0.18	n.s.	0.01	n.s.	0.05	n.s.
			no		***one-sided***		*reverse*		***aligned***		*one-sided*	
diurnal T range	upper	0.95	0.15	n.s.	0.04	n.s.	-0.11	n.s.	-0.21	*	0.09	n.s.
	upper	0.90	0.10	n.s.	0.03	n.s.	-0.42	**	-0.39	***	0.26	n.s.
	median	0.50	0.02	n.s.	0.12	*	-0.11	*	-0.17	*	0.06	n.s.
	lower	0.10	0.25	n.s.	0.62	***	0.11	n.s.	-0.47	*	-0.16	n.s.
	lower	0.05	0.46	n.s.	0.72	***	0.47	*	-0.41	**	-0.33	*
			one-sided		***one-sided***		*no*		***one-sided†***		*one-sided*	
T seasonality	upper	0.95	-0.49	***	-0.51	***	-0.02	n.s.	-0.75	***	-0.14	n.s.
	upper	0.90	-0.45	***	-0.53	***	0.32	n.s.	-0.62	***	-0.29	*
	median	0.50	-0.04	n.s.	-0.11	n.s.	0.36	***	-0.31	***	-0.20	**
	lower	0.10	0.01	n.s.	-0.09	n.s.	0.20	n.s.	-0.06	n.s.	-0.08	n.s.
	lower	0.05	-0.08	n.s.	-0.03	n.s.	0.26	n.s.	0.00	n.s.	-0.06	n.s.
			no		***one-sided***		***one-sided***		***aligned***		*reverse*	
annual P	upper	0.95	-0.40	n.s.	-0.69	***	-0.45	n.s.	0.54	***	0.56	**
	upper	0.90	-0.26	n.s.	-0.75	**	-0.31	n.s.	0.54	**	0.48	*
	median	0.05	0.16	*	0.12	n.s.	0.18	*	0.24	*	-0.18	n.s
	lower	0.10	0.03	n.s.	0.01	n.s.	0.12	***	0.13	**	-0.06	**
	lower	0.05	0.01	n.s.	0.02	n.s.	0.12	***	0.15	**	-0.05	n.s
			one-sided		*one-sided*		*one-sided*		*one-sided*		*one-sided*	
P of coldest quarter	upper	0.95	-0.30	n.s.	-0.40	**	-0.31	n.s.	0.28	n.s.	0.28	n.s.
	upper	0.90	-0.58	*	-0.38	n.s.	-0.77	**	0.69	***	0.64	***
	median	0.50	-0.02	n.s.	0.08	n.s.	-0.06	n.s.	0.33	**	-0.02	n.s.
	lower	0.10	0.00	n.s.	0.00	n.s.	0.01	n.s.	0.10	n.s.	-0.01	n.s.
	lower	0.05	-0.02	n.s.	-0.01	n.s.	0.01	n.s.	0.04	*	-0.01	n.s.
			no		*no*		*no*		*no*		*no*	
P of warmest quarter	upper	0.95	0.05	n.s.	0.12	n.s.	-0.13	n.s.	-0.04	n.s.	-0.02	n.s.
	upper	0.90	0.10	n.s.	0.09	n.s.	-0.11	n.s.	0.03	n.s.	-0.02	n.s.
	median	0.50	0.21	**	0.20	***	0.37	***	-0.01	n.s.	-0.33	***
	lower	0.10	0.03	n.s.	-0.04	n.s.	0.08	n.s.	0.01	n.s.	0.00	n.s.
	lower	0.05	0.00	n.s.	-0.01	n.s.	0.02	n.s.	0.01	n.s.	0.00	n.s.

			one-sided		***one-sided***		*one-sided*		*no*		*aligned*	
GDD	upper	0.95	0.21	n.s.	0.26	n.s.	0.01	n.s.	-0.08	n.s.	-0.16	*
	upper	0.90	0.23	n.s.	0.09	n.s.	-0.05	n.s.	-0.10	n.s.	-0.23	n.s.
	median	0.50	0.47	***	0.37	***	0.19	n.s.	-0.33	**	-0.25	*
	lower	0.10	0.35	***	0.40	***	0.14	*	-0.07	n.s.	-0.10	*
	lower	0.05	0.14	n.s.	0.42	***	0.07	n.s.	-0.01	n.s.	-0.07	*
			one-sided		***one-sided***		*no*		***aligned***		***one-sided***	
net P	upper	0.95	-0.17	n.s.	-0.66	**	-0.42	n.s.	0.53	**	0.65	**
	upper	0.90	-0.44	n.s.	-0.81	**	-0.48	n.s.	0.64	***	0.49	*
	median	0.50	-0.01	n.s.	0.01	n.s.	0.11	n.s.	0.19	***	-0.06	n.s.
	lower	0.10	-0.32	*	-0.24	n.s.	0.10	n.s.	0.36	**	-0.12	n.s.
	lower	0.05	-0.26	n.s.	-0.12	n.s.	0.01	n.s.	0.39	***	-0.06	n.s.

Notes: Slope estimates obtained from linear quantile regression relating the three measures defining the climatic ranges of 250 North American tree species (lower limit, upper limit, median) obtained for 8 bioclimatic variables against the five traits, respectively (see Methods for details). Both the measures and the traits were standardized to mean zero and SD=1 to obtain comparable slope estimates. For the upper limits we estimated the upper regression quantiles (τ=0.95 and τ=0.90), for the lower limits the lower regression quantiles (τ=0.10 and τ=0.05) and for the median the 50thquantile. The type of proposed response patterns matched (see Fig.1C and Methods for rules) is written above each trait-climatic relationship, with bold letters identifying obvious patterns for which both outer quantiles (5th ,10th and/or 90th,95th) show slopes significant different from zero (grey shaded in Fig. S1, see Methods for details). The significance levels of slopes were indicated as follows: not significant (n.s.), P<0.001 (***), P<0.01 (**), P<0.05 (*).†Estimates are based on heights larger than 22.3m which comprises almost 80% of total considered max. height range (146 species), see Fig.2 for presentation.

Table S2

Intercepts and slopes of linear quantile regression lines for the relationships between traits and climate range measures for 250 North American tree species presented in Fig. S1.

		wood density				seed mass				sla				maximum height				longevity			
	τ	β_0	*SE*	β_1	*SE*	β_0	*SE*	β_1	*SE*	β_0	*SE*	β_1	*SE*	β_0	*SE*	β_1	*SE*	β_0	*SE*	β_1	*SE*
annual T	0.95																				
	0.90																				
	0.50	-9.0	4.5	29.4	6.1	8.1	1.0	0.8	0.2					17	1.8	-1.0	0.4	22	4.0	-1.8	0.76
	0.10	-30.8	4.8	45.2	6.9	-4.8	1.6	1.3	0.2	-2.9	1.1	0.02	0.01								
	0.05	-32.8	7.3	45.2	9.9	-8.3	1.0	1.4	0.3												
diurnal T range	0.95													20.6	0.69	-0.34	0.17				
	0.90									19	0.4	-0.01	0.0	21.3	0.74	-0.62	0.13				
	0.50					12	0.2	0.08	0.04	13	0.3	-0.002	0.001	14.1	0.54	-0.24	0.10				
	0.10					6.8	0.7	0.43	0.09					12.3	1.71	-0.73	0.34				
	0.05					5.4	0.7	0.49	0.12	4.64	1.5	0.01	0.006	10.31	1.29	-0.64	0.24	11.7	2.2	-0.88	0.42
T seasonality	0.95	23745	2846	-15083	4053	14876	472	-414	75					25623.	1990	-2078	305				
	0.90	21895	2300	-13876	3125	14325	647	-430	99					22105.	2279	-1727	320	17136	1782	-916	351
	0.50									5779	373	8.97	1.81	11722.	838	-718	135	10364	1011	-534	196
	0.10																				
	0.05																				
annual P	0.95					2949	166	-123	40.7					1270	409	216	61.6	298	801	386	133
	0.90					2720	412	-133	47.8					882	266	218	65.6	137	747	333	161
	0.50	534	212	745	273					905	137	0.82	0.59	682	178	69	31				
	0.10									176	30	0.50	0.17	92	63	35	12	418	70	-29	11
	0.05									145	25	0.53	0.17	48	71	38	14				
P of coldest quarter	0.95					1135	48	-32	11												
	0.90	2022	525	-1756	767					1197	149	-2.3	0.8	91.8	214	125	32	-334	405	198	69
	0.50													58.6	69	39	13				
	0.10																				
	0.05													12.4	8	3.0	1.9				
P of warmest quarter	0.95																				
	0.90																				
	0.50	50	85	323	109	231	19	8.4	2.2	155	21	0.56	0.08					556	71	-53	13
	0.10																				
	0.05																				

GDD	0.95																	761	125	-29	23
	0.90																				
	0.50	-268	120	758	160	196	18	16	3					440	43.5	-32	9	502	87	-41	17
	0.10	-265	71	505	113	18	7.6	15	1.7	26	6.3	0.19	0.07					135	48	-15	7.7
	0.05					-1.5	9.6	16.1	2.5									97	25	-10	4.1
net P	0.95					2281	168	-117	39					649	448	212	65	-674	1008	447	167
	0.90					2111	441	-143	54					57	278	258	71	-527	649	334	142
	0.50													39	92	52	16				
	0.10	438	438	-1148	746									-1023	167	96	32				
	0.05													-1181	116	104	23				

Notes: Intercepts (β_0) and slopes (β_1) of significant (P<0.05) linear quantile regression lines (see Table S1) with their standard error (*SE*) regressing the upper climate ranges limits (τ=0.95 and τ=0.90), the lower climate range limits (τ=0.10 and τ=0.05) and the median climate preference (τ=0.50) of 250 North American tree species (146 species for T seasonality versus maximum height, respectively; see Table S1 for further details) obtained for 8 bioclimatic variables against the five traits, respectively (see Methods for details). Before applying linear quantile regression traits were transformed to obtain normal distribution as follows: wood density was square root transformed, seed mass was log transformed, maximum height was square root transformed, life span was log transformed.

Table S3

Intercepts and slopes of linear quantile regression lines for the relationships between maximum height and climate range measures for all North American tree species without *Sequoia sempervirens* with maximum height of 100.4m.

		maximum height of 249 tree species without *Sequoia sempervirens* = 100.4m			
	τ	β_0	*SE*	β_1	*SE*
annual mean T	0.95				
	0.90				
	0.50	18.5	1.6	-1.2	0.3
	0.10				
	0.05				
diurnal T range	0.95	20.5	0.70	-0.31	0.16
	0.90	21.2	0.86	-0.58	0.16
	0.50	14.2	0.5	-0.27	0.10
	0.10	12.5	1.8	-0.77	0.36
	0.05	10.31	1.30	-0.64	0.24
T seasonality	0.95	26700.55	2280.67	-2294.15	347.50
	0.90	22726.80	2710.90	-1803.77	381.72
	0.50	11633.98	885.80	-702.24	140.13
	0.10				
	0.05				
annual P	0.95	1270	394	215	61.2
	0.90	806	311	228	77
	0.50	677	180	71	31
	0.10	112	59	32	12
	0.05	53	79	37	16
P of coldest quarter	0.95				
	0.90	68	201	131	30
	0.50	62	67	38	13
	0.10				
	0.05	12.4	8	3.0	1.8
P of warmest quarter	0.95				
	0.90				
	0.50				
	0.10				
	0.05				

GDD	0.95				
	0.90				
	0.50	440	47	-32	9
	0.10				
	0.05				
net P (mm)	0.95	649	482	212	75
	0.90	57	267	258	65
	0.50	19	96	56	18
	0.10	-1148	160	128	31
	0.05	-1265	174	124	34

Notes: Intercepts (β_0) and slopes (β_1) of significant linear quantile regression lines (see Table S1) with their standard error (*SE*) regressing the upper envelope limits (τ=0.95, 0.90), the envelope median (τ=0.50) and the lower envelope limits (τ=0.10, 0.05) of 249 North American tree species against maximum height.

Other supporting information files

Dataset (data SI) is provided as txt. file only in the electronic version of this thesis. It contains the maximum attainable trait values of seed mass, wood density and maximum height as presented in the Fig.3 and Fig.S4-S5 and their longitude and latitude coordinates.

CHAPTER 4

4 General Discussion

4.1 Discussion of methods with respect to data type and ecological concepts

In the study represented in Chapter 2 which addresses reseach question one, "*What are fundamental trait spectra and do they reflect general plant strategies corroborating the prevalence of functional tradeoffs?*", we applied a two step approach. In the first step we quantified general trait spectra among 305 North American tree species based on 23 traits applying Principle Coordination Analysis (PCoA). In the second step we quantified how those spectra were correlated with ecological performance measures to determine whether general trait spectra reflect general ecological strategies corroborating the prevalence of fundamental functional tradeoffs (see *Methods* Chapter 2).

PCoA is a distance-based metric ordination method which proceeds by eigenvector decomposition, i.e. the eigenvalues measure the amount of trait variation of the species along the ordination axes similar to a Principle Component analysis (PCA). Compared to PCA, PCoA is free in the choice of the distance measure. This is an advantage in this study because the 23 considered traits have various statistical types (e.g. continuouse, ordinal, nominal, mulit-choice nominal) which are not treatable by Euclidean distance, the measure imposed by PCA. In this study a generalization of Gower's distance (Pavoine et al. 2009) was used, which is able to deal with traits with such various statistical types. The calculated distances among species in the full ordination space are projected onto the space of reduced dimensionality (e.g. the first 3 dimensions) by maximizing the linear correlation between the distances in the distance matrix and the distances in a space of low dimension. That means, PCoA ordination provides a Euclidean representation of distance relationships among species based upon their traits. Thus, obtained PCoA axes reflected major axes of trait variation which are represented by sets of co-varying traits - so called 'trait spectra' reflecting general tradeoffs plants have to deal with. Since PCoA preserves the original distances in the full dimensional space (number of dimension = number of species-1) and is suited if many (or all) ordination axes are sought (Birks et al. 2012), it is generally an appropriate method exploring many tradeoffs (i.e. more than the known 2-3, see Chapter 1 – *Plant functional traits with respect to plant strategy concepts, tradeoffs and species'* *niche differentiation*). In contrast, non-metric multidimensional scaling (NMDS), a non-metric distance-based ordination method, would be preferred when one wants to represent as much as possible of species' distance relationships in few dimensions. But this comes at the cost of preserving only the rank-order of the distances and not the distances themselves (Birks et al. 2012). However, when aiming to quantify many trait spectra and their underlying tradeoffs the araising questions is: What are the number of axes to be considered (how many axes out of 304 when e.g. running PCoA on all species) and which criteria can be used to select the most important axes? Generally, testing obtained axes for significance is seldom used because a strong null-hypothesis is missing. Thus, broken stick models (Frontier 1976) or the bootstrapped eigenvalue method (Jackson 1993) are used to determine how many axes represent important variation with respect to the data set for PCA (Peres-Neto et al. 2003). However, generally methods like PCA or PCoA are more frequently used for explorative analyses which want to formulate hypotheses which can be tested in an experimental setup or in an appropriate statistical design afterwards. The explorative data analysis was one main intention of this study. We explored only the first three axes because explained variance dropped down to values below 6% for the fourth axis upwards. The explained variance of the first three axes together exceeded 45.5% maximally (analyzing the gymnosperms) but single ones did not reach more than 6.1% (analyzing all species). One reason of this small amount of explained variance per axis is the selection criteria of the 23 traits in order to prevent high correlation among traits due to established tradeoffs (e.g. seed mass and seed number would not both be considered) and relations (e.g. seed mass and seed size). Thus, rather many axes, each explaining low variance, than few axes, each explaining high variance, were expected.

In a second step, the general trait spectra (i.e. the obtained PCoA axes) were linearly related to the five species specific ecological performance measures shade, drought and water tolerance and relative growth rate and fire tolerance. This two step approach was chosen because it allows also the detection of general trait spectra, which reflect adaptive strategies not captured by our five selected, namely evolutionary constraints, novel biophysical tradeoffs or specific adaption to other environmental factors (see Fig.3B and discussion in Chapter 2). Applying this two step approach and considering only the first three axes we might not have identified the major trait spectra that explain the five ecological performance measures best. For instance it could be that we missed trait spectra reflecting ecological performances better because they were loaded on higher axes (for instance shade tolerance correlated slightly better with the fifth PCoA axis than with the third axis in 'angiosperm only' analysis). For this reason we compared the results of the PCoA with a distance based Redundancy Analysis (db-RDA) which is the corresponding constrained analysis (not shown in the study of chapter 2 but in the Appendix below). Db-RDA reveals general trait spectra which can be best explained by the ecological performance measures. Thus, if the results of the two-step approach are similar to the results of db-RDA, the quantified trait spectra (i.e. the first three PCoA axes) are indeed reflected by the considered ecological performance measures. The db-RDA results were very similar (if not identical) to the results of the applied two-step approach (see Appendix Fig.A1-A3). This supports that the found fundamental trait spectra among North American woody tree species are mainly driven by species adaption to light and water availability and fast growth strategies. But it also points towards a considerable amount of trait variation which reflects evolutionary constraints and adaptation to other environmental drivers not captured with our five ecological performance measures.

In chapter 3 the predictive power of five functional traits seed mass, wood density, specific leaf area, tree longevity and maxiumum height on species climate range limits is analyzed and the relationships are interpreted with respect to mechanistic processes of plants' adaptation to the environment. In this study we used linear quantile regression instead of ordinary least square regression to predict climate range limits from traits. Linear quantile regression is the preferred approach when one assumes that 'the law of the limiting factor' is a general ecological concept underlying species distribution patterns because it estimates effects of limiting factors on organisms' response (Cade and Noon 2003).

'The law of the limiting factor' (Liebig's law of the minimum) is a basic tenet in ecology and can be generalized as follows: the observed level of a response in a biological process will be governed by the input factor in least supply – the limiting factor. That means, any requisite factor can limit a response of an organism, but only one will be the active constraint at any given time and space (Kaiser et al. 1994). Limiting relationships are manifold in ecology describing for instance animal and plant responses to habitat conditions (Cade et al. 1999, Castedo-Dorado et al. 2012, Kail et al. 2012), predator and prey relationships (Scharf et al. 1998) or algae growth to nutrients (Kaiser et al. 1994). Often these relationships show 'wedge-shaped' response patterns depicting unequal variation through the influence of unmeasured limiting factors. This is, because a biological response cannot change by more than some upper limit set by the measured factor but may change less when other (unmeasured) factors are limiting (Cade and Noon 2003). Thus, exploring the effect of the measured limiting factor one needs to focus rather on changes near the edges (maxima or minima) of the response distribution (i.e. the upper or lower regression quantile) than on changes of the mean (as ordinary least square regression does) where unmeasured factors may be the active limiting constraint (Kaiser et al. 1994, Cade et al. 1999, Huston 2002). Estimating upper (or lower) regression quantiles provides an approximation of the limiting effect of the measured factor by accounting for the unmeasured factors (Cade et al. 1999). Generally, applying quantile regression is appropriate for modeling limiting relationships when one variable is clearly the dependent variable and the other is clearly the independent variable (Cade et al. 1999). In our case we declare the traits as independent variables (predictor) assuming that they limit the species to distribute towards unsuitable environments because they constrain species performance there. This is in line with the trait-based niche approach where traits determine species' niche parameters (Rosenzweig 1987, Violle and Jiang 2009, Chase and Myers 2011) like species minimum tolerable temperature which might be reflected by species range limits (see also Chapter 1 - *The trait-based niche approach and its application*). Thus, in our case, the climate range limits are the dependent variables (response) which are constrained by the traits. Hence, the estimates of the upper or lower quantiles of species' climate range limits for a given trait give an approximation of the limiting effect of the trait on species' climate limits, i.e. the quantiles provide an approximation of the maximum or minimum attainable climate value given a trait value. The major advantage of this approach is that it accounts for unmeasured limiting factors which prevent a species to distribute up to the estimated climate limits. Such unmeasured factors are manifold and could be local habitat factors like soil or mirco-climate requiring certain traits or the species is not in equilibrium with the climate because of historical effects or the observed trait interacts with other traits which do not perform in this climate. The application of the limiting factor theory to the trait-based niche concept (i.e. traits determine species niche and therefore limit species distribution) seems to be a logical consequence because the 'limiting factor theory' also underlies the environmental niche concept (i.e. environmental factors determine species niche and therefore limit species distribution) (Huston 2002, Austin 2007). Both authors state that species presence is determined by multiple environmental factors which can all potentially occur at levels where they limit species survival. Because these factors vary across spatial scale it is very unlikely that the same single factor is always limiting. That means there is likely to be a shift from one limiting factor to another one resulting in 'wedge-shaped' response patterns which consequently requires quantile regression to estimate the limiting effect of the considered factor on species distribution.

4.2 Overall discussion of the results with respect to data and niche concepts

The study presented in chapter 2 showed that wood density, seed mass, maximum height, SLA and life span are important traits of complex trait spectra reflecting shade, drought and water logging tolerance and growth potential. They reflect 'general plant strategy axes' and describe plants adaptation to important environmental drivers and underlying tradeoffs. As seed mass, maximum height and specific leaf area belong to rather different trait spectra which are independent of each other, they can be used as proxy for different plant strategy axes (see e.g. Fig. 3 in Chapter 2). These findings support the conceptual trait-based plant strategy scheme of Westoby (1998). Furthermore, the findings presented confirm the use of these traits for the prediction of species distribution limits because they reflect different ways of plant functioning in dependence of key environmental drivers.

However, analyses quantifying general trait spectra with the aim to detect different general plant strategy axes depend strongly on the selection of traits and on how well the traits reflect the manifold adaptations of plants. Traits are collected from a wide spectrum considering different aspects of plant functioning to capture as many strategy axes as possible (see Chapter 2, Methods). However, the inclusion of additional traits for which data were not available might complete the picture of important trait strategy axes. For example it would be interesting to see whether leaf size, which is thought to be an additional strategy axis beside axes represented by specific leaf area, maximum height ans seed mass (Westoby et al. 2002), would determine an additional independent axis in our study. Furthermore, we did not include traits directly related to temperature (e.g. winter buds, leaf/fruit phenology) despite being aware that temperature is a key driver in North American forest determining species distribution (Morin et al. 2007). At low temperatures water is frozen and thus not available for plants. Thus, adaptations to low temperature might have co-evolved by adaptation mechanisms to drought and traits reflecting high drought tolerance are also related to low temperature. As mentioned in the discussion of Chapter 3 the inclusion of additional traits related to inter-specific competition (e.g. mycorhizza association) have the potential to detect additional trait based strategy axes reflecting recurrent pattern of plant specialization sensu Grime (1979). Generally the inclusion of additional traits could change the importance of the reported trait spectra (e.g. trait spectra reflecting adaptation to drought might explain less of the total variation than quantified in this study) and has the potential to detect further important axes. I expect that the inclusion of additional traits will slightly change the composition of the found trait spectra, which might weaken or strengthen the reported relationships but will not alter or desolve them completely.

Thus, relating wood density, seed mass, maximum height, SLA and life span to species climate range limits has the potential to discover general functional mechanisms controlling species climatic distribution limits. Quantifying the relationships between these five traits and climate range limits we found that some traits control climate range limits and some not (see Chapter 3). Traits related to drought tolerance such as wood density and seed mass affect species' climate range limits like annual mean temperature and annual precipitation (see Fig. 2, Chapter 3), while e.g. specific leaf area which is more related to shade tolerance (see Fig. 3, Chapter 2) does not affect climate range limits clearly (Fig. S1, Chapter 3). However, maximum height which was related to shade tolerance and growth rate (Fig. 1-3, Chapter 2) affects precipitation limits and temperature seasonality (Fig. 3, Chapter 3). The reason for this might be that some traits reflect tradeoffs operating only on local scales while others reflect tradeoffs operating on local and on continental scales. Maximum height might be an example of the second case because it is known to reflect different tradeoffs operating on different scales (Westoby et al. 2002, Falster and Westoby 2005, Moles et al. 2009). Since species climate range limits are derived from species geographical distribution maps, the considered processes operate on scales of 100 to several 1000 km^2, therefore local processes like succession which operate on community scale are not well reflected. This might be the reason why e.g. specific leaf area, which is a proxy for shade tolerance and thus reflects successional processes, does not show a geographical response. Furthermore, specific leaf area reflects species nutrient use efficiency and is therefore related to soil nutrient content which varies largely on local scales. On the investigated scale more abiotic filter processes like physiologically limitation in harsh climates determine species range limits (Wiens 2011) which is supported by climate envelope or habitat models modeling current species distribution of North American woody trees (McKenney et al. 2007). However, since these correlative models are based on the 'environmental niche concept' they do not discover or address the functional mechanism (e.g. physiological limits reflected by traits) operating at these range limits (see Chapter 1 – *The ecological niche concept and its application*) but quantify the abiotic environmental factors determining species distribution instead. Relating climate range limits to traits which reflect species' functional adaptation to biotic and abiotic factors allows the detection of functional mechanisms of species sorting due to climatic constraints along large climatic gradients on continental scales. This approach links the 'trait-based niche concept' (i.e. a species can distribute towards a certain environment when its trait configuration allows it to grow, reproduce and survive there) with the ‘environmental niche concept’ (i.e. a species can distribute towards sites where the environment allows it to grow, reproduce and survive) focusing on the level of the climate niche parameters, which largely determines species distribution on continental scales. Although this approach is still empirical at heart, it provides a novel way to detect whether and how key functional plant traits limit species distribution at this scale. Thus, it deepens our understanding of species sorting processes across large climatic gradients which is important to large scale patterns of functional and species diversity.

4.3 General conclusions and future application

This thesis focused on the investigation of two sets of questions:

1) *What are fundamental trait spectra and do they reflect general plant strategies corroborating the prevalence of functional tradeoffs?*
2) *Can functional traits predict species climate range limits and do the relationships give insights into mechanistic processes of plants’ adaptations to the environment governing finally species distribution patterns on continental scale?*

with the aim to understand plants’ fundamental adaption mechanisms to the environment, plants’ general ecological strategies and functional mechanisms underlying species sorting across large environmental gradients.

Exploring question one we determined fundamental axes of plant trait variation and quantified general trait spectra and we found that they reflect general ecological strategies describing plants’ different responses to the environment and their underlying tradeoffs. However, some general trait spectra might either reflect phylogenetic patterns corroborating the prevalence of evolutionary tradeoffs or adaptation to disturbance causing temporal variation in resource variability. Thus, our results specify the different known constraints of trait variation, namely that traits co-vary because they reflect adaptations to the environment but also because of eco-physiological and/or evolutionary tradeoffs a plant has to deal with (Lavorel et al. 2007). Generally, if well defined trait spectra emerge and these spectra explain a considerable amount of the total trait variation of a large and diverse trait matrix, it supports the notion that only a limited number of traits are necessary to explain a considerable amount of functional diversity and hence a considerable amount of plant strategies (Diaz et al. 2004, Westoby and Wright 2006). The identification of those traits which can together determine the general plant strategies on earth is the ultimate goal of modelers (Cornelissen et al. 2003, Lavorel et al. 2007, Kattge et al. 2011, Weiher et al. 2011); see also Chapter 1 - *On the relevance of the plant trait approach*. Our results show that well known key traits like wood density, seed mass, specific leaf area and maximum height, which represent single trait axes in conceptual plant strategy schemes (Westoby 1998) and/or represent general trait spectra, for instance the leaf economic spectrum (Wright et al. 2004), belong to complex trait spectra reflecting general ecological strategies. This supports the theory, that they are indeed important traits when determining general plant strategies and confirms their use in future DGVMs. Nevertheless, we also found a considerable number of trait spectra explaining low variance which might reflect multiple tradeoff axes. Assuming multiple tradeoff axes could explain the coexistence of many species (i.e. high diversity), which is not possible when only a few tradeoff axes are considered (Clark et al. 2007). Thus, an ultimate future aim should be to repeat the analyses with more traits (ideally traits related to plants competitive behavior) to explore whether there are more important tradeoff axes and/or support found ones. Moreover, a major challenge would be to look for suitable performance measures describing for instance species' competitive performance which enables specification of such tradeoffs. Repeating this kind of analysis for other species with the same set of traits would validate found trait spectra and tradeoffs, which is essential when implementing them in future DGVMs.

Exploring question two we found that most of the key traits which reflect important ecological strategies of North American woody species constrain their climate distribution limits. Thus, our results allow the formulation of hypotheses about functional processes underlying species sorting across large climatic gradients. The functional principles derived can be validated by applying our approach to other species in other environments. Furthermore, the quantified relationships have the potential to be implemented in future DGVMs which go beyond PFT classification replacing there, for example, the fixed bioclimatic limits for PFTs making such models more mechanistic (see Chapter 3, *Discussion*, for more details). The produced trait maps which outline 'no-go' areas (Chapter 3, Fig.3) can be used to derive 'species exclusion maps'. Furthermore, those maps might be useful for evaluation of the predictions made by species distribution models for climate change scenarios. The fact that some key traits did not show a limiting effect on species' climate range limits points to their importance on local scales where biotic processes are assumed to dominate (see Chapter 3, *Results and Discussion*). Thus, considering for example community data (i.e. abundance data on plot level), data on topography (e.g. soil type, elevation, and slope) and measures of disturbance might be a solution to investigate the influence of local-scale processes when predicting species distribution limits. Data on dispersal limitations (e.g. historical legacies) will complete the list of most influencing factors. The implementation of all these data into an integrative framework which links ecological theory, empirical data and statistical models can improve the prediction of species distribution patterns (see Chapter 1- *The ecological niche concept and its application* and (Boulangeat et al. (2012)) and has the potential to shed more light on the processes and rules of how plants are sorted across large gradients and assembled into communities. An enhanced understanding of these mechanisms enables better prediction of ecosystem processes and biodiversity under different climate scenarios what is an ultimate goal in a world subjected to climate change.

4.4 Appendix

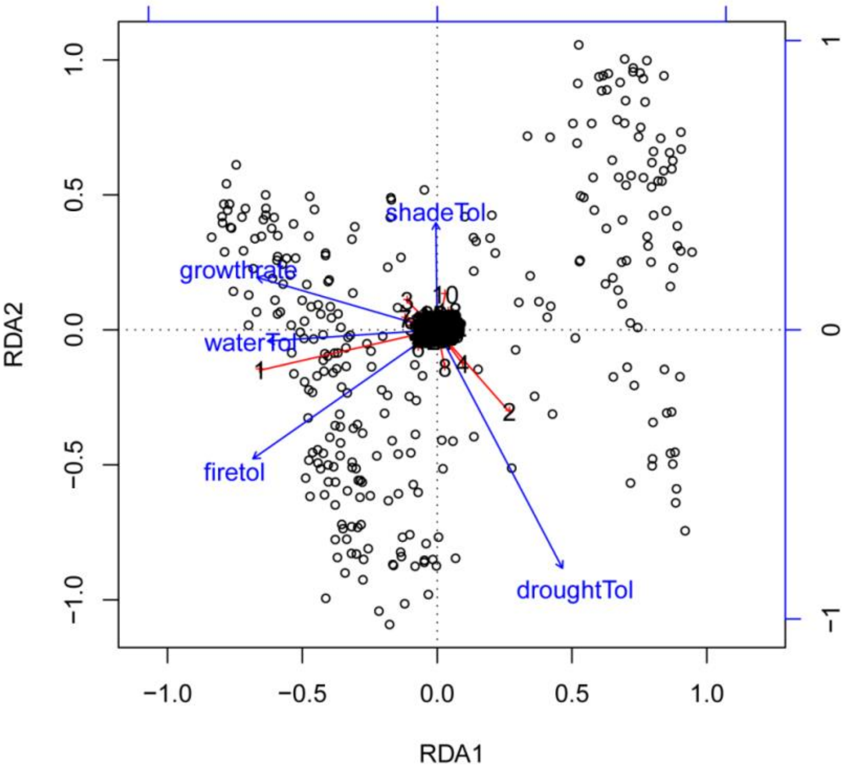

Figure A1.
Triplot result of db-RDA based on 289 species for the first two axes visualizing the species as points (weighted averages), the constraints as blue arrows and the PCoA axes scores as red lines. The arrows point in the direction of most rapid change and the angles among the arrows, lines and RDA axes reflect how strong they are correlated; small angles strong correlation, large angles low correlation, angle of 90 degree no correlation. Growth rate, water-logging tolerance and fire-tolerance determine together the first RDA axis which is reflected by first PCoA axis. This supports that the trait spectra underlying the first PCoA axis is best explained by these performance measures which is in line with the findings applying the two step approach in the study of Chapter 2. Drought tolerance determines the second RDA axis and is reflected by the second PCoA axis. This was also found in the two step approach.

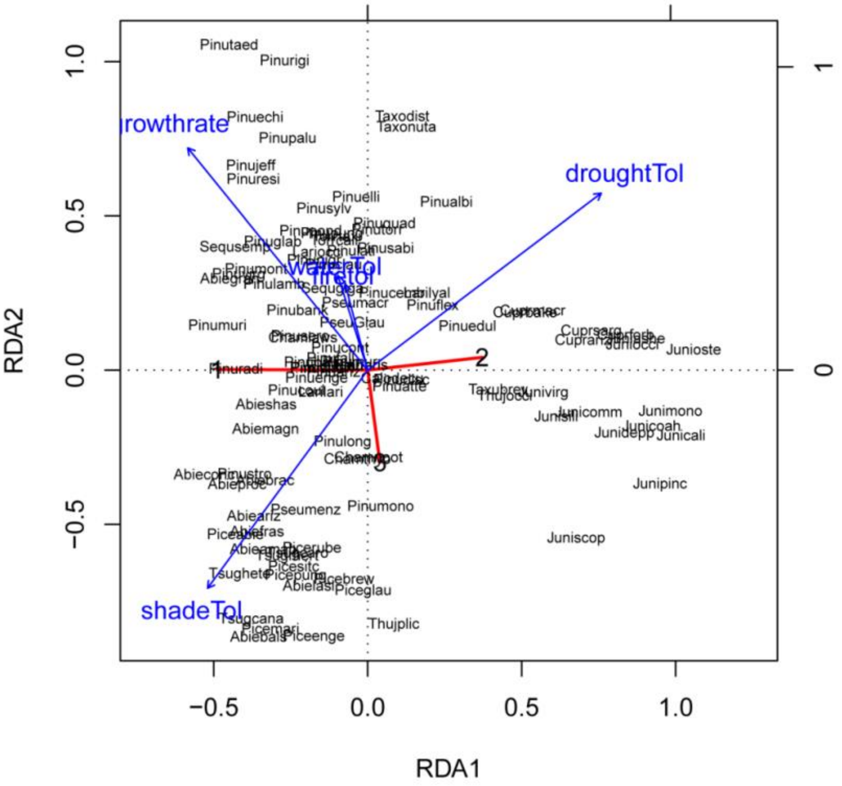

Fig. A2.

Triplot result of db-RDA based on 103 gymnosperm species for the first two axes visualizing the species (weighted averages), the constraints as blue arrows and the three most important PCoA axes scores as red lines. The constraints drought- and shade tolerance are inversely related and determine the first and the second RDA axis while growth rate is rather independent to these two constraints determining the second RDA axis. The PCoA axis 1 and 2 are inversely related and determine RDA axis 1, while PCoA axis 3 is rather independent to these determining RDA axis 3. In the two step approach we quantified also a trait spectrum which reflects the inverse relationship between shade- and drought tolerance which is determined by the first and the second PCoA axes. Independent to this trait spectrum we quantified another one reflecting potential growth rate which is determined by the third PCoA axes.

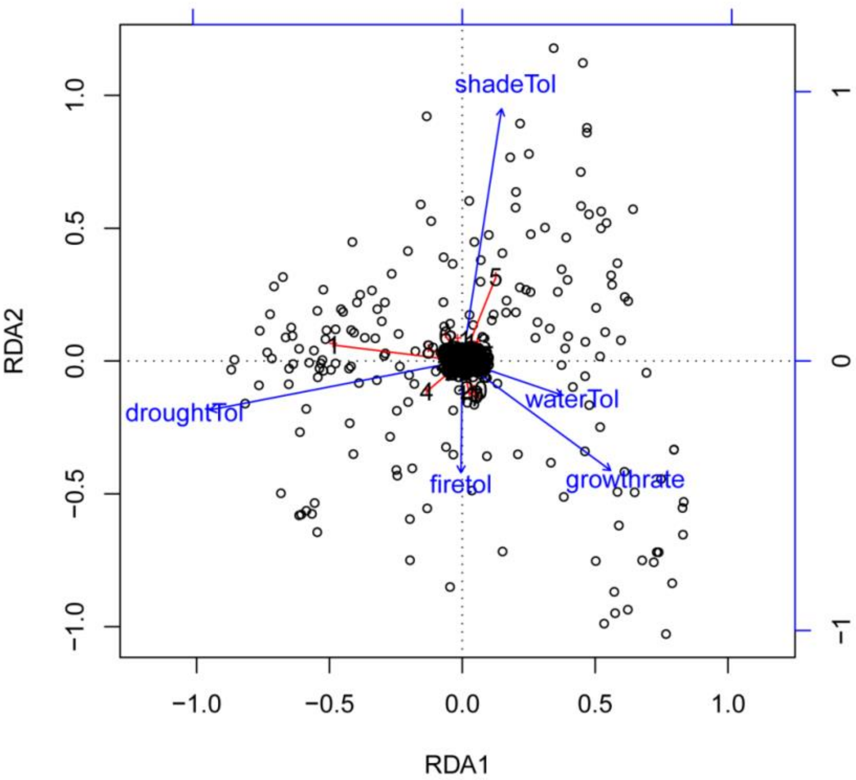

Fig. A3.
Triplot result of db-RDA based on 186 angiosperm species for the first two axes visualizing the species (weighted averages) as points, the constraints as blue arrows and the PCoA axes scores as red lines. Drought tolerance and growth rate are inversely related and determine the first RDA axis which is reflected by the first PCoA axis which is in line with the findings of applying the two step approach. Shade tolerance determines the second RDA axis which is reflected by the fifth PCoA axis which is in line with the two step approach; we found the highest correlation between shade tolerance and the fifth PCoA axis and a weaker correlation with the third axis.

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Eigenständigkeitserklärung

Ich erkläre,

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Jena, den Ulrike Stahl

Curriculum Vitae

Surname: Stahl (born Bartke)
First name: Ulrike
Date of birth: 10.04.1976
Place of birth: Jena

Education

Since 2013	Scientific assistant in the Project - *Plant Trait Semantics - Towards a unifying system of plant trait definition and measurement* funded by iDiv- German Centre for Integrative Biodiversity Research , PI: Stefan Klotz – Helmholz Centre for Environmental Research (UFZ)
Since 2008	PhD student at the MPI for Biogeochemistry, Supervisors: Christian Wirth (MPI), Gottfried Jetschke & Winfried Voigt (FSU-Jena)
2005-2007	Parental leave / tutoring students in natural sciences at the private Institute "Studienkreis Borken" in Borken
2005	Contract for services with the Institute "Evolution and ecology of animals" at the University of Münster, topic - *Analysis and prognosis of the relationships between macrozoobenthos and the structure of streams*
2003-2004	Scientific assistant at the Institute "Evolution and ecology of animals" at the University of Münster, project – *FLUMAGIS*
2003	Diploma in Biology, thesis title - *Recolonisation processes of an experimentally disturbed arctic-subtidal-hard-bottom community*, a joint venture between the Institute of Ecology at the University of Jena (FSU) and The University Courses on Svalbard (UNIS) in Norway
2001	Student assistant at the MPI for Biogeochemistry, project - *Simulation of the carbon cycle in sibirian forests*
1998-2000	Studies at the University of Bergen and at The University Courses on Svalbard (UNIS) in Norway with emphasis on marine ecology and limnology in the context of the student exchange program ERASMUS
1994-1998	Studies at the University of Jena in biology with emphasis on ecology, zoology and physical geography
1994	Abitur, Holzland-Gymnasium Hermsdorf

Publications

Stahl, U., B. Reu, C.Wirth 2014. Predicting species' range limits from functional traits for the tree flora of North America, *PNAS*, *Special Feature Functional Biogeography* accepted 8.1.2014.

Stahl, U., J. Kattge, B. r. Reu, W. Voigt, K. Ogle, J. Dickie, and C. Wirth. 2013. Whole-plant trait spectra of North American woody plant species reflect fundamental ecological strategies. *Ecosphere* **4**:art128.

Talks

Stahl, U., J. Kattge, C. Wirth, B. Reu, W.Voigt, K.Ogle, J. Dickie (2012): Which functional traits reflect fundamental plant strategies and explain differences in species climate niche of 305 North American tree species, internal Seminar at the MPI for Biogeochemie in Jena, Jena

Stahl, U., B. Reu, C. Wirth (2012): Functional traits predict range limits of North American tree species?, Seminar at the University of Leipzig, Group Systematic Botany and Functional Biodiversity, Leipzig

Stahl, U., J. Kattge, C. Wirth, B. Reu, W.Voigt, K.Ogle, J. Dickie (2011): Analyzing large trait-species matrices - what can we learn and use for functional diversity measures, Seminar at Potsdam Institute for climate Impact Research (PIK), Group Earth System Analysis, Potsdam, invited by Kirsten Thonike

Stahl, U., J. Kattge, K. Ogle, C.Wirth (2011): Fundamental trait syndromes of North American forests reflect growth rate and tolerance to shade and drought, TRY workshop hosted by DIVERSITAS and Laboratoire d'Ecologie, Systématique et Evolution (ESE), Paris

Stahl, U., K. Ogle, C. Wirth (2010): What are the main functional axes of trait variation for 305 North American tree species?, Institute of Ecology "Weihnachtssymposium", University Jena, Jena

Stahl, U., K. Ogle, C. Wirth (2010): Functional tradeoffs among 305 North American tree species is there more than shade and drought adaptation?, Seminar at University of Leipzig, Group Systematic Botany and Functional Biodiversity, Leipzig

Stahl, U., C. Wirth (2008): Analysing global patterns of species and functional diversity in forest ecosystem- thesis concept, Institute of Ecology "Weihnachtssymposium", University Jena, Jena

Posters

Stahl, U., C. Wirth, K. Nadrowski, J. Kattge, R.Proulx, K. Ogle. (2009): Unfolding the functional trait space of 188 North American tree species, GFÖ annual meeting, Bayreuth