UNIVERSITÀ DEGLI STUDI DI SASSARI

SCUOLA DI DOTTORATO DI RICERCA

Scienze e Biotecnologie

dei Sistemi Agrari e Forestali

e delle Produzioni Alimentari

Agrometeorologia ed Ecofisiologia dei Sistemi Agrari e Forestali

Ciclo XXVIII

A trait-based approach for forest ecology and management

Tools for theoretical and applied ecology

Dr. José María Costa Saura

Direttore della Scuola: Prof. Antonello Cannas

Referente di Indirizzo: Prof. Donatella Spano

Docente Guida: Prof. Donatella Spano

Tutor: Dr. Simone Mereu

Anno accademico 2014- 2015

UNIVERSITÀ DEGLI STUDI DI SASSARI

SCUOLA DI DOTTORATO DI RICERCA

Scienze e Biotecnologie

dei Sistemi Agrari e Forestali

e delle Produzioni Alimentari

Agrometeorologia ed Ecofisiologia dei Sistemi Agrari e Forestali

Ciclo XXVIII

A trait-based approach for forest ecology and management

Tools for theoretical and applied ecology

Dr. José María Costa Saura

Direttore della Scuola: Prof. Antonello Cannas

Referente di Indirizzo: Prof. Donatella Spano

Docente Guida: Prof. Donatella Spano

Tutor: Dr. Simone Mereu

Anno accademico 2014- 2015

Table of contents

Abstract

Global change threats affecting forests require better understanding of mechanisms driving species environmental responses, but also species effects on ecosystems, to identify optimal management strategies for safeguarding the services they provide. Thus, this thesis serves on trait ecology and tools as Species Distribution Modelling, Remote Sensing, and Climate Change Modelling to explore ecological concepts that prove useful for determining specific management actions. Specifically we hypothesised about three main aspects: 1) the capacity of several traits to explain the characteristics of species niche in the Mediterranean; 2) the influence of trait diversity on the temporal stability of forest productivity in Temperate and Boreal zones; and 3) current and future effects of climate on the mean traits of Mediterranean forest communities. Forest inventories from Spain and Quebec (eastern Canada) were used to obtain species distribution and community composition whereas species traits values were retrieved from the literature. Main results showed that: 1) Specific Leaf Area (SLA) can be used to accurately represent species aridity limits in the Mediterranean; 2) trait diversity provides stability in Temperate forests; and 3) climate change may reduce SLA values of forest communities suggesting notable impacts on ecosystem functioning in the Mediterranean. The thesis suggests that management strategies should be based on trait ecology in order to best adapt to global change.

Riassunto

Le minacce del cambiamento globale sulle foreste richiedono una migliore comprensione dei meccanismi attraverso i quali le specie rispondono ai cambiamenti ambientali e influiscono sulle funzione ecosistemiche, permettendo di mettere in pratica delle strategie di gestione migliori per salvaguardare i servizi che loro forniscono. In questa tesi vengono utilizzati la trait ecology (cioè una ecologia basata sugli attributi funzionale delle piante) e tools come Species Distribution Modelling (Modelli di Distribuzione di Specie), Remote Sensing (Telerilevamento), e Climate Change Modelling (Modelli di Cambiamento Climatico) per esplorare dei concetti ecologici che servono per determinare le azioni specifiche di gestione forestale. Tre sono gli aspetti principali presi in esame: 1) la capacità di diversi tratti funzionali per spiegare le caratteristiche della nicchia in specie del Mediterraneo; 2) l'influenza della diversità di tratti funzionali sulla stabilità temporale nella produttività delle foreste Temperate e Boreali; e 3) gli effetti attuali e futuri del clima sui tratti funzionali medi delle comunità forestali nel Mediterraneo. Gli inventari forestali della Spagna e del Quebec (est del Canada) sono stati utilizzati per ricavare la distribuzione geografica delle specie e la composizione delle comunità, mentre i valori dei tratti funzionali per ogni specie sono stati ricavati dalla letteratura scientifica. I risultati principali della tesi mostrarono che: 1) l'area specifica fogliare (Specific Leaf Area, SLA) potrebbe essere utilizzata per rappresentare accuratamente i limiti massimi di aridità che le specie del Mediterraneo possono tollerare; 2) la diversità funzionale procura stabilità nella produttività delle foreste Temperate; e 3) il cambiamento climatico può ridurre i valori medi di SLA nelle comunità forestali del Mediterraneo, influenzando notevolmente le funzioni ecosistemiche. I risultati di questa tesi suggeriscono che, per un migliore adattamento al cambiamento globale, le strategie di gestione forestale devono essere basate su la trait ecology.

Resumen

Las amenazas del cambio global sobre los bosques requieren una mejor compresión de los mecanismos a través de los cuales las especies responden a cambios ambientales, y que a su vez influyen sobre los ecosistemas, con el objetivo de aplicar estrategias de gestión óptimas que permitan salvaguardar los servicios que estos proveen. El presente trabajo se sirve de la "trait ecology" (es decir una ecología basada sobre los rasgos funcionales de las plantas) y de herramientas como Species distribution Modelling (Modelos de Distribución de Especie), Remote Sensing (Teledetección), y Climate Change Modelling (Modelos de Cambio Climático) para explorar conceptos ecológicos que son útilies para determinar acciones concretas de gestión forestal. En esta tesis se ha hipotizado sobre tres aspectos principales: 1) sobre la capacidad de ciertos rasgos funcionales para explicar las características de nicho en especies forestales del Mediterráneo; 2) la influencia de la diversidad funcional sobre la estabilidad temporal de la productividad en comunidades forestales, tanto en zonas Templadas como Boreales; y 3) los efectos actuales y futuros del clima sobre los valores medios de los atributos funcionales en las comunidades forestales del Mediterráneo. Los datos del Invenatário Forestal Español y del Quebec (Este de Canada) fueron utilizados para obtener la distribución geográfica de las especies de estudio así como para determinar la composición de especies de las comunidades forestales. En cambio los valores de los rasgos funcionales de las especies fueron adquiridos a través de la literatura científica. Los resultados principales de la tesis han mostrado que: 1) El área específica foliar (Specific Leaf Area, SLA) puede ser utilizada para representar la máxima aridez que las especies en el Mediterráneo pueden tolerar; 2) la diversidad funcional proporciona estabilidad temporal en la productividad de los bosques Templados; y que 3) el cambio climático podría reducir los valores medio de SLA en las comunidad forestales del Mediterráneo sugiriendo notables impactos en el funcionamiento de los ecosistemas de esta región. Los resultados de la tesis muestran que para una mejor adaptación al cambio global las estrategias de gestión forestal pueden basarse en la "trait ecology".

Key Abbreviations

AMT	Annual Mean Temperature
AP	Annual Precipitation
CV	Coefficient Variation
CWM	Community Weighted Mean
EVI	Enhanced Vegetation Index
FD	Functional Diversity
FT	Functional Traits
N_{mass}	Nitrogen leaf content per unit of mass
PLC_{50}	The water potential at which 50% of hydraulic conductivity is lost
RCP	Representative Concentration Pathways
SDM	Species Distribution Models
SLA	Specific Leaf Area
SM	Safety Margin
WD	Wood Density

Chapter 1. Introduction

A General Overview

Forests benefits on humans are numerous and range from direct, tangible and traded products to indirect, less palpable and not marketed services (Bartczak et al., 2014). For instance, wood, cork, mushrooms, and resin are some examples of direct goods provided by forest, instead carbon store and sequestration, hydrological regulation, biodiversity conservation, soil protection, recreational services and cultural heritage represent those "less quantifiable" forest externalities from which humans also benefit (Bartczak et al., 2014). In addition, forests also provide work to 54 million people across the world, contribute to the shelter of 1.3 billion people, accounts for the 27% of the primary energy supply in Africa and about 90 million people in Europe and North America use energy coming from forests for domestic heating (FAO, 2014).

However, despite all those benefits, consequences of human activities as land use change, air pollution, and climate change are predicted to cause losses in biodiversity, and losses or deterioration of a number of services provided by forests (Liang et al., 2015). Indeed, deforestation is found to cause habitat alterations in terms of quality, amount and spatial configuration, which directly influence population vital rates (Hansen et al., 2001). Even so, forest area has decreased approximately 66 million ha during the period 1990-2005 (Lindquist et al., 2012) and the rate of loss has increased from 9.5 million ha year^{-1} in the decade 1990-2000 to 13.5 million ha year^{-1} in the period 2000-2005 (Fig.1.1).

At the same time, because of human activities pre-industrial era greenhouse gas emissions have increased and reached the highest known atmospheric concentrations at least in the past 800,000 years (IPCC, 2014). Their consequences haven been already observed, and the period from 1993 to 2012 was warmest in the last 1,400 years (IPCC, 2014). In addition, nine of the ten warmest years have occurred since year 2000 (Hansen et al., 2010). Thus, models projected under different climatic scenarios predict an increase of global surface temperature (Fig.1.2) at the end of the 21st century from 0.3º to 4.8ºC for 2.6 and 8.5 RCP scenarios, respectively (IPCC, 2014). Extreme events, (droughts, heat waves, storms) are also projected to increase in frequency while their magnitude has already increased in some areas by three to five standard deviations beyond historical averages (Hansen et al., 2013). Both extreme events and changes in climatic means have the potential to modify species distribution, forest age structure and species composition (Bakkenes et al., 2002; Thuiller et al., 2005), increase fire risk (Piñol et al., 1998) and pest attacks (Volney and Fleming, 2000), and consequently impact on ecosystem functioning (Chapin et al., 2000; Grimm et al., 2013).

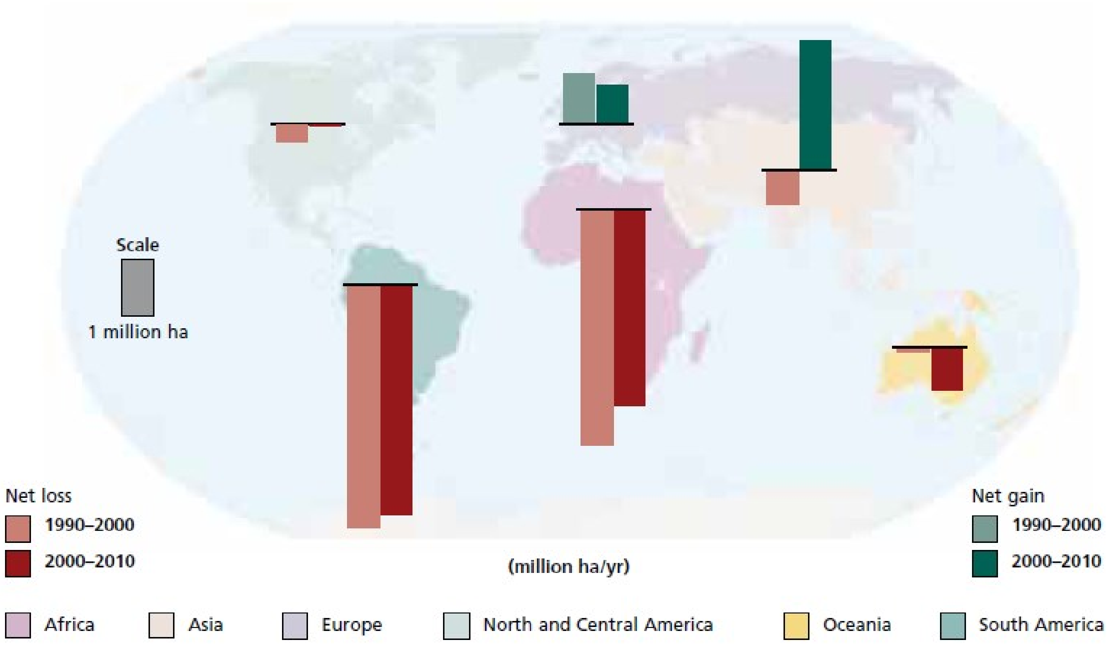


Figure 1.1: Annual change in forest area by region (from FAO 2010)

Species mechanisms to respond to climatic changes involve acclimatization and phenotypic plasticity, adaptation, and migration (Bussotti et al., 2014): failure in these mechanism likely implies extinction (Thomas et al., 2004). Phenotypic plasticity (i.e. the diversity of phenotypes expressed by single genotype) allows fast and plastic response to environmental changes which is basic to plant acclimatization (Nicotra et al., 2010). However, plasticity is not equal for all traits and it “saturates” at specific limits (Chevin et al., 2010). Adaptation instead, reflects new genotype selection according to the new environmental conditions but it is also constrained by genetic variability and genetic correlation among traits (i.e. two traits can be adaptive but negative genetically related, Etterson and Shaw, 2001). Migration, which refers to species geographical displacements, depends both on species dispersal ability and biotic interactions (Aitken et al., 2008). Thus, is not clear which mechanism will prevail under the great amount of different situations. Numerous studies analyzed the possible impacts of climate change on species distribution. For instance, Benito Garzón et al., (2009) studying Iberian tree species observed higher risks on Mountainous and Temperate species which are genetically different from central Europe populations, which suggest potential losses on genetic diversity. Thuiller et al., (2005) studying 1350 plant species from Europe also observed high threatens for Mountainous regions and predicted greatest changes in the transition between the Mediterranean and Euro-Siberian regions. Accordingly to projected changes in species distributions, species composition it is also expected to change (Walther, 2010). Bakkenes et al., (2002) predicted for large areas of Europe that more than 50% of the species composition will be formed by new species, and Frenette-Dussault et al., (2013) for Morocco steppes predicted changes from ruderal to stress-tolerant sub-shrubs species. Changes in species composition will likely lead to changes in ecosystem processes since species via their attributes mediate the energy and element fluxes on ecosystems (Chapin et al., 2000). Indeed, studies based on dynamic global vegetation models (DGVM) project reductions in net ecosystem production because of changes on vegetation types (Cramer et al., 2001). Despite the importance of DGVM for assess climate change impacts on ecosystem functioning, drawbacks due to functional simplifications of communities and coarse resolutions limit their use. Indeed, different studies suggest a trait-based approach for scaling up from community composition to ecosystem functions in order to best predict the consequences of global change (Chapin, 2003; Díaz and Lavorel, 2007; Suding et al., 2008).

Thus, these frameworks rely on trait based ecology which is promoting an exciting new research approach to classical questions in ecology and a promising tool to study the effect of climate change on forests and the services that they provide (Lavorel, 2013). Trait ecology is based on functional traits (FT), which are species-specific characteristics (morphological, structural, physiological) that reflect the eco-physiology of the species and its ecological strategy (Violle et al., 2007). The great advantage of traits based ecology is that it unleashes the analysis from the species level and sets the ecological distance among species along a continuous axis represented by the value of one trait or a multidimensional space represented by multiple traits. Additionally, all the emerging links between one or multiple traits with specific eco-physiological process are giving a great contribution to the current trend towards a predictive ecology (Enquist et al., 2015) allowing to reduce uncertainties around the effects of global change on ecosystems. For instance, a trait-based approach proves useful to identify which plant attributes determine species environmental limits, that allow to predict changes in species composition and consequently their effects on ecosystem functioning. Indeed, trait ecology is required for forest management in order to deal with the challenges posed by climate change (Bussotti et al., 2014). For instance in restoration plans, the selection of appropriate species genotypes and provenances are suggested to be done according to the identification and quantification of those traits providing adaptation to future climatic conditions (Bussotti et al., 2014). Silvicultural strategies are also suggested to be oriented to improve competition of species with future suitable traits in order to accommodate changes adaptively (Millar et al., 2007). In addition to those adaptation actions, mitigation efforts can be improved with “trait-based silvicultural treatments” (i.e. managing species abundances to promote trait diversity and specific traits values) in order to increase carbon store and sequestration (Diaz et al., 2009; Ruiz-Benito et al., 2014).

Finally, it is noted that social awareness demands that scientists and public authorities unify efforts to halt the loss of biodiversity and to develop forest management policies oriented towards an optimization of ecosystem services while safeguarding from the effects of climate change. Indeed, a number of European policies and directives promote better understanding of ecological process for determining proper adaptation actions. For instance, i) The European Commission's White Paper ‘Adapting to climate change – Towards a European framework for action’ (2009) recommends member states to include the development of methods, models and data sets to increase the predictive capacity to assess the cost and benefits of adaptation options; and ii) The EU Green

Paper on "Forest Protection and Information in the EU: Preparing forests for climate change" (EFI, 2010) states that "Safeguarding forest multi-functionality requires balanced management approaches based on adequate forest information". Thus, this thesis explores the potentialities of trait-based ecology for understanding different ecological process that prove useful for forest management under this changing world.

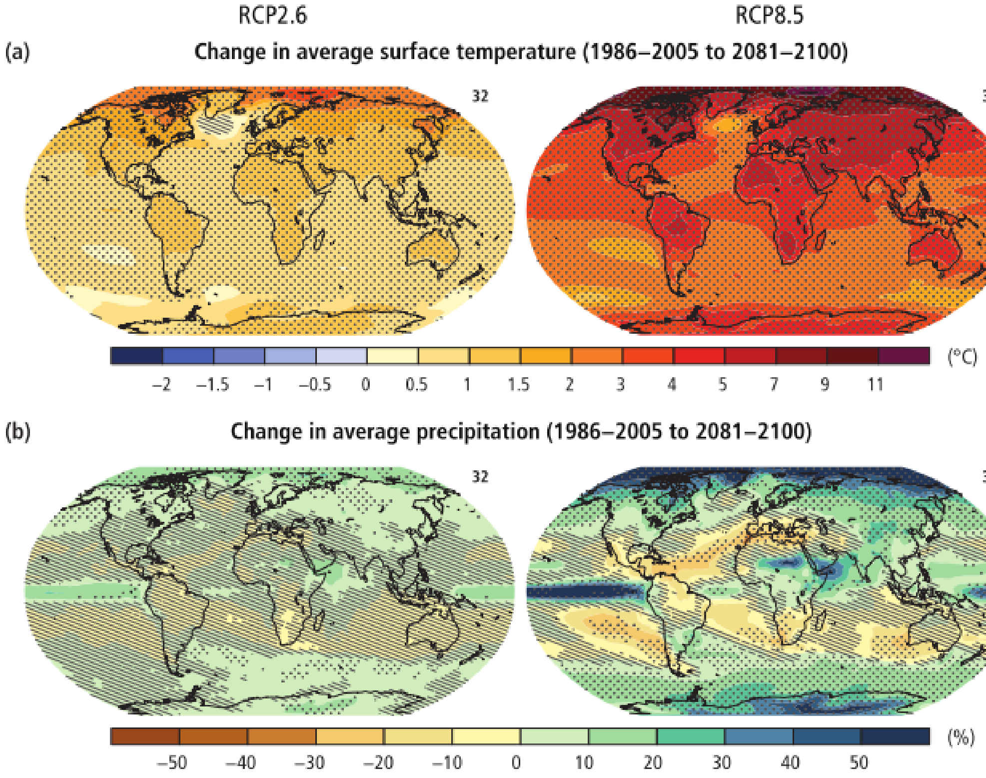


Figure 1.2: Change in average surface temperature (a) and in average precipitation (b) based on multi-model mean projections for 2081–2100 relative to 1986–2005 under the RCP2.6 (left) and RCP8.5 (right) scenarios (from IPCC 2014).

Objectives and Thesis Structure

The main objective of this thesis is to integrate trait based ecology with well stabilised tools (i.e. Species Distribution Modelling, Remote Sensing, and Climate Change Modelling, see chapter 2 for a general overview of these tools) in order to investigate the role of plant functional traits on different ecological aspects that closely link with the environmental response and functioning of forests. Thus, this thesis through its three research works, explores different ecological theories to provide forest managers new instruments and background information for dealing with the challenges posed by global change.

The first research work, addressed in chapter 3, serves on Species Distribution Models (SDM) to determine how specific functional traits (FT) shape species niche in the Mediterranean. Despite the great number of literature addressing general patterns of trait variability across environmental gradients (Cornwell and Ackerly, 2009; Reich et al., 2003; Wright et al., 2005), little is known about how FT determine the different characteristics of species niche, e.g. species climatic limits or climatic optimums (but see Stahl et al., 2014). Thus based on environmental filtering theory (Keddy, 1992), we explore if traits associated with drought adaptation can explain those niche characteristics related with aridity (i.e. the arid limits of species and their optimal values). In addition, it was studied if those niche predictions can be improved combining different traits. The study allow forest managers to identify which traits determine species arid limits providing useful information for species selection in restoration plans and climate change adaptation actions.

The second research work, addressed in chapter 4, uses remote sensing data to assess if communities with a higher diversity in traits are more temporal stable in terms of productivity (i.e. stable against climate fluctuations). Despite accumulated evidence on biodiversity positive effects on forest productivity (Paquette and Messier, 2011; Ruiz-Benito et al., 2014), much less evidence exists regarding its effect on forest stability. Indeed, studies have been focalized on grass communities (Cardinale et al., 2013; Hector et al., 2010; Tilman, 1996) and only Jucker et al., (2014) explored those effects on forests. In addition, the diversity effect has been traditionally tested using species richness or broad functional characterization of communities (i.e. into categorical plant functional types) which not account for the potential effect of species differences in trait values (i.e. a continuous axis of functioning). Thus, for Temperate and Boreal forests we assess the biodiversity-stability effect (i.e. the insurance hypothesis, Yachi and Loreau, 1999) controlling simultaneously the influence of potential confounding factors such as dominant trait values within communities and climatic effects. The approach used in this study is easily applicable on other regions and provides foresters an approach to orient silvicultural strategies for dealing with climatic fluctuations induced by global change.

Finally, the third research work which is addressed in chapter 5, presents a novel approach based on environmental filtering theory (Keddy, 1992; Weiher and Keddy, 1995) for assessing climate change impacts on the functional structure of woody plant communities in the Mediterranean. The study stress the hypothesis that dominant trait values of communities (i.e. community weighted mean trait, CWM) will change in future because of new environmental conditions (i.e. climate change) suggesting important changes in ecosystem functioning. The approach overcomes drawbacks of others approaches as functional simplifications (Scheiter et al., 2013) or assumptions on variations in species pools (Frenette-Dussault et al., 2013). Thus, this study provides forest managers an approach to identify major risk zones predicting the magnitude of change in CWM values which proves useful to orient forest management practices in order to adapt to climate change.

Bibliography

Aitken, S.N., Yeaman, S., Holliday, J. a., Wang, T., & Curtis-McLane, S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1: 95–111.

Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R., & Latour, J.B. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology* 8: 390–407.

Bartczak, A., Giergiczny, M., Jacobsen, Jette Bredahl Mavsar, R., Mäntymaa, E., Ovaskainen, V., Varela, E., Pettenella, D., Thorsen, B.J., Tyrväinen, L., Vedel, S.E., & Wunder, S. 2014. *The Provision of Forest Ecosystem Services: Quantifying and valuing non-marketed ecosystem services* (B. J. Thorsen, R. Mavsar, L. Tyrvainen, I. Prokofieva, & A. Stenger, Eds.). EFI, Joensuu, FI.

Benito Garzón, M., Sánchez de Dios, R., & Sainz Ollero, H. 2009. Effects of climate change on the distribution of Iberian tree species. *Applied Vegetation Science* 11: 169–178.

Bussotti, F., Pollastrini, M., Holland, V., & Bruggemann, W. 2014. Functional traits and adaptive capacity of European forests to climate change. *Environmental and Experimental Botany* 111: 91–113.

Cardinale, B.J., Gross, K., Fritschie, K., Flombaum, P., Fox, J.W., Rixen, C., Van Ruijven, J., Reich, P.B., Scherer-Lorenzen, M., & Wilsey, B.J. 2013. Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. *Ecology* 94: 1697–1707.

Chapin, F.S. 2003. Effects of plant traits on ecosystem and regional processes: A conceptual framework for predicting the consequences of global change. *Annals of Botany* 91: 455–463.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., & Díaz, S. 2000. Consequences of changing biodiversity. *Nature* 405: 234–42.

Chevin, L.M., Lande, R., & Mace, G.M. 2010. Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *Plos Biology* 8: 1–8.

Commission of the European Communites. 2009. *White Paper. Adapting to climate change: Towards a European framework action*. Brussels,BE.

Cornwell, W.K., & Ackerly, D.D. 2009. Community Assembly and Shifts in Plant Trait Distributions across an Environmental Gradient in Coastal California. *Ecological Monographs* 79: 109–126.

Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R. a., Brovkin, V., Cox, P.M., Fisher, V., Foley, J. a., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S., Smith, B., White, A., & Young-Molling, C. 2001. Global response of terrestrial ecosystem structure and function to CO2 and climate change: Results from six dynamic global vegetation models. *Global Change Biology* 7: 357–373.

Diaz, S., Hector, A., & Wardle, D. a. 2009. Biodiversity in forest carbon sequestration initiatives : not just a side benefit. *Environmental Sustainability* 1: 55–60.

Díaz, S., & Lavorel, S. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences* 104: 20684–20689.

EFI. 2010. *Green Paper Forest Protection and Information in the EU : Preparing forests for climate change*. Joensuu, FI.

Enquist, B.J., Norberg, J., Bonser, S.P., Violle, C., Webb, C.T., Henderson, A., Sloat, L.L., & Savage, V.M. 2015. Scaling from Traits to Ecosystems: Developing a General Trait Driver Theory via Integrating Trait-Based and Metabolic Scaling Theories. In Pawar, Woodward, & Dell (eds.), *Advances in Ecological Research. Trait-Based Ecology - From Structure to Function*, pp. 249–317. Elsevier Ltd.

Etterson, J.R., & Shaw, R.G. 2001. Constraint to adaptive evolution in response to global warming. *Science* 294: 151–154.

FAO. 2014. *State of the World's Forests. Enhancing the socioeconomics benefts from* *forest*. Rome, IT.

Frenette-Dussault, C., Shipley, B., Meziane, D., & Hingrat, Y. 2013. Trait-based climate change predictions of plant community structure in arid steppes. *Journal of Ecology* 101: 484–492.

Grimm, N.B., Chapin, F.S., Bierwagen, B., Gonzalez, P., Groffman, P.M., Luo, Y., Melton, F., Nadelhoffer, K., Pairis, A., Raymond, P. a., Schimel, J., & Williamson, C.E. 2013. The impacts of climate change on ecosystem structure and function. *Frontiers in Ecology and the Environment* 11: 474–482.

Hansen, A.J., Neilson, R.P., Dale, V.H., Flather, C.H., Iverson, L.R., Currie, D.J., Shafer, S., Cook, R., & Bartlein, P.J. 2001. Global Change in Forests: Responses of Species, Communities, and Biomes. *BioScience* 51: 765–779.

Hansen, M.C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S. a, Tyukavina, A., Thau, D., Stehman, S. V, Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., & Townshend, J.R.G. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342: 850–853.

Hansen, J., Ruedy, R., Sato, M., & Lo, K. 2010. Global surface temperature change. *Reviews of Geophysics* 48: 1–29.

Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Scherer-Lorenzen, M., Sphen, E.M., Bazeley-White, E., Weilenmann, M., Caldeira, M.C., Dimitrakopoulus, P.G., Finn, J.A., Huss-Danell, K., Jumpponen, A., Mulder, C.P.H., Palmborg, C., Pereira, J., Siamantziouras, A.S.D., Terry, A.C., Troumbis, A.Y., Schmid, B., & Loreau, M. 2010. General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology* 91: 2213–2220.

IPCC. 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Team Core Writing, R. K. Pachauri, & L. A. Meyer, Eds.). Geneva, CH.

Jucker, T., Bouriaud, O., Avacaritei, D., & Coomes, D. a. 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. *Ecology Letters* 17: 1560–1569.

Keddy, P. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3: 157–164.

Lavorel, S. 2013. Plant functional effects on ecosystem services. *Journal of Ecology* 101: 4–8.

Liang, J., Watson, J. V., Zhou, M., & Lei, X. 2015. Effects of productivity on biodiversity in forest ecosystems across the United States and China. *Conservation Biology*. doi: 10.1111/cobi.12636

Lindquist, E.J., D'Annunzio, R., Gerrand, A., MacDicken, K., Achard, F., Beuchle, R., Brink, A., Eva, H.D., Mayaux, P., San-Miguel-Ayanz, J., & Stibig, H.-J. 2012. *Global forest land-use change 1990-2005*. Rome, IT.

Millar, C.I., Stephenson, N.L., & Stephens, S.L. 2007. Climate change and forest of the future: Managing in the face of uncertanity. *Ecological Applications* 17: 2145–2151.

Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, a. M., Finnegan, E.J., Mathesius, U., Poot, P., Purugganan, M.D., Richards, C.L., Valladares, F., & van Kleunen, M. 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* 15: 684–692.

Paquette, A., & Messier, C. 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography* 20: 170–180.

Piñol, J., Terradas, J., & Lloret, F. 1998. Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. *Climatic Change* 38: 345–357.

Reich, P., Wright, I., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M., & Walters, M. 2003. The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences* 164: 143–164.

Ruiz-Benito, P., Gómez-Aparicio, L., Paquette, A., Messier, C., Kattge, J., & Zavala, M.A. 2014. Diversity increases carbon storage and tree productivity in Spanish forests. *Global Ecology and Biogeography* 23: 311–322.

Scheiter, S., Langan, L., & Higgins, S. 2013. Next generation dynamic global vegetation models: learning from community ecology. *New Phytologist* 198: 957–969.

Stahl, U., Reu, B., & Wirth, C. 2014. Predicting species ' range limits from functional traits for the tree flora of North America. *Proceedings of the National Academy of Sciences of the United States of America* 111: 13739–13744.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., & Navas, M.L. 2008. Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology* 14: 1125–1140.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., & Williams, S.E. 2004. Extinction risk from climate change. *Nature* 427: 145–148.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., & Prentice, I.C. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* 102: 8245–8250.

Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77: 350–363.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.

Volney, W.J. a, & Fleming, R. a. 2000. Climate change and impacts of boreal forest insects. *Agriculture, Ecosystems & Environment* 82: 283–294.

Walther, G.R. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2019–2024.

Weiher, E., & Keddy, P. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos* 74: 159–164.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Warton, D.I., & Westoby, M. 2005. Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography* 14: 411–421.

Yachi, S., & Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America* 96: 1463–1468.

Chapter 2. Background theory and methods

Trait-Based Ecology

Functional traits (FT) are species-specific characteristics (morphological, physiological and phenological) that reflect the ecological strategy of species but also its effects on ecosystems (Violle et al. 2007). The great advantage of traits based ecology is that it unleashes the analysis from the species level and sets the ecological distance among species along a continuous axis represented by the value of one trait (or in a multidimensional space when multiple traits are used). Additionally, since FT are proxies of eco-physiological processes, there use allows to identify the underlying biological mechanisms reducing the hidden uncertainty of empirical models and favouring the current trends towards a more predictive ecology (Enquist et al. 2015).

FT represent plant "decisions" on where to allocate resources with consequences in terms of growth and survival (Fig. 2.1 and Table 2.1, Reich, 2014). For instance, species with low Specific Leaf Area (i.e. low leaf area per unit of mass, SLA) are common in harsh environments (e.g. dry or cold, Niinemets, 2001; Reich et al., 2003; Wright et al., 2005). Low SLA values (i.e. expensive leaves, Villar and Merino, 2001) are associated with tissue reinforcement which prevents cell damages during dry events enhancing plant performances in arid environments (Poorter et al. 2009; Micco & Aronne 2012). PLC50 (i.e. the water potential at which 50% of hydraulic conductivity is lost) is also a trait usually correlated with precipitations (Maherali et al. 2004; Choat et al. 2012), indeed, species with low PLC50 have great xylem cavitation resistance which is an advantage in arid environments.

However, plant investment in one trait is often not independent from investment in other traits resulting in trade-offs among traits and their functions (Fig. 2.1). For instance, species with low SLA (i.e. species investing in expensive stress adapted leaves) are also found to have low relative growth rates suggesting a trade-off between fast growth and stress resistance (Poorter 1989). Instead, greater cavitation resistance (i.e. low PLC50) is associated with low hydraulic conductance suggesting a trade-off among hydraulic dysfunction resistance and efficiency (Hacke & Sperry 2001; Nardini et al. 2012). In addition, multiple traits can also vary simultaneously evidencing single axis of traits co-variation. For instance, the best know example is the “worldwide leaf economic spectrum” (Wright et al. 2004) which shows the co-variation at global scale of SLA, leaf nitrogen content (N_{mass}), leaf photosynthetic capacity (A_{mass}), and leaf life-span (LLS), which represents a trade-off among the “construction and maintenance costs of leaves, and duration of photosynthetic returns from those investments” (Westoby et al. 2013). The existence of a “worldwide wood economic spectrum” has been also suggested, which relates traits as wood density, PLC50, conduit diameter and size, hydraulic conductivity and the modulus of elasticity and rupture of wood (Chave et al. 2009). However the same authors suggested that more empirical support is needed to evidence trade-offs among hydraulic efficiency, cavitation resistance and mechanical resistance.

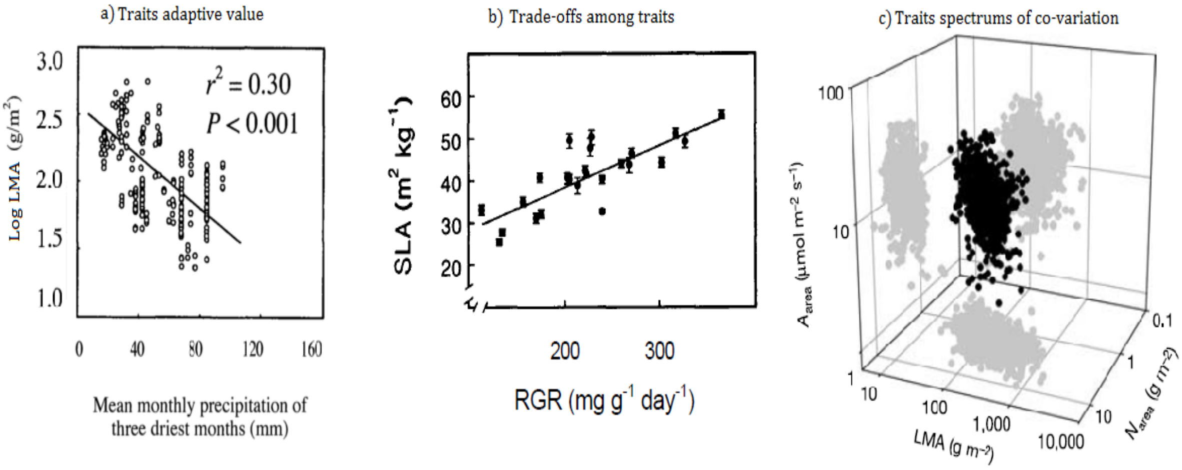


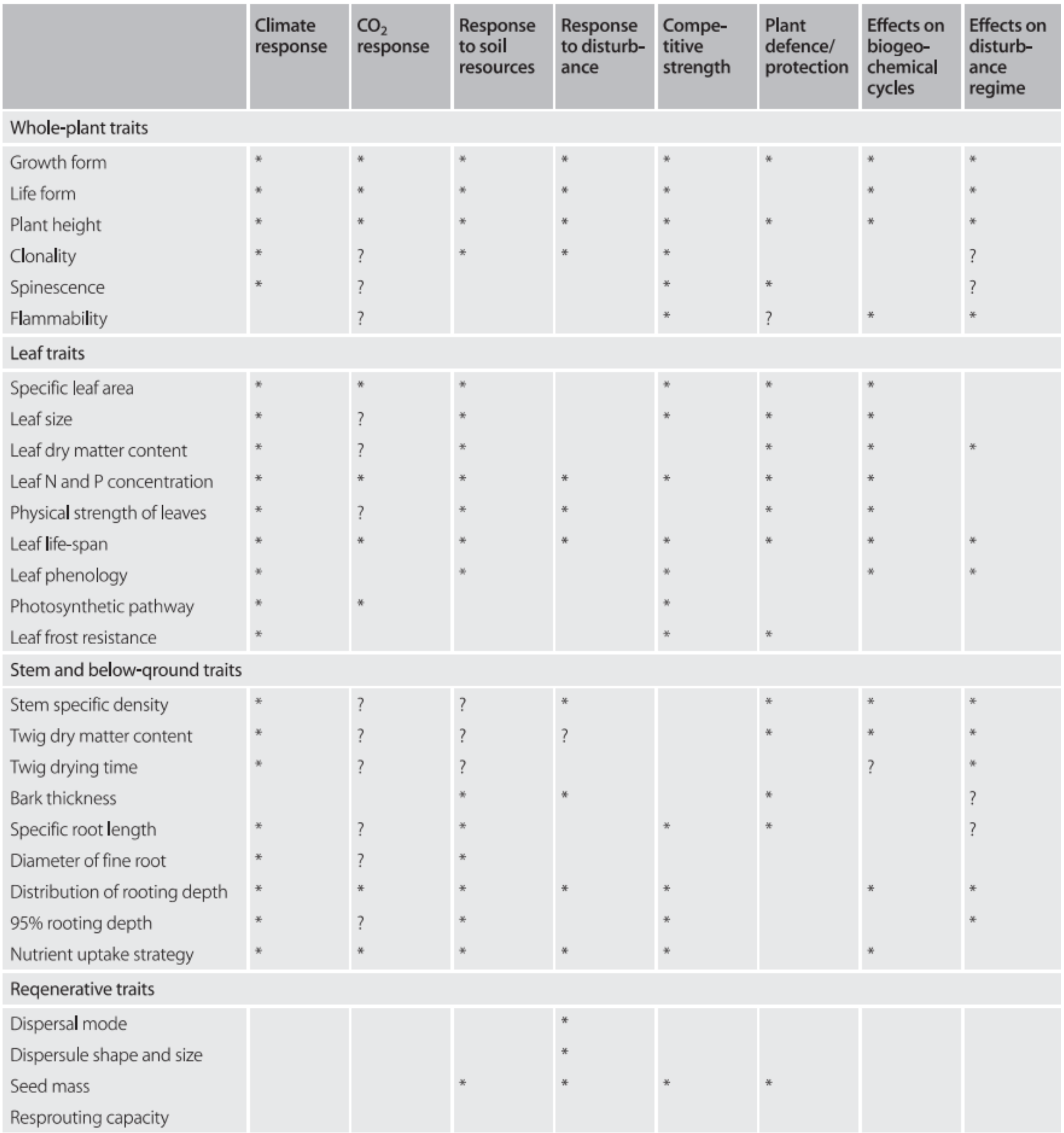
Figure 2.1: Correlations within traits and environment. a) Leaf Mass Area (LMA, i.e. 1/SLA) increased with site aridity (from Niinemets, 2001), b) trade-offs among SLA and species relative growth rate (RGR, from Poorter and Remkes, 1990), and c) the worldwide correlations among leafs traits (from Wright et al., 2004).

The co-variation among traits may be due to causal links. For instance, A_{mass} co-varies with N_{mass} since photosynthesis (A_{mass}) largely depends on the concentration of photosynthetic enzymes on leaves (i.e. N_{mass}, Reich et al., 1999). Instead, PLC50 co-varies with conduit wall strength since cavitation resistance depends (among other factors) on conduit implosion resistance (Hacke et al. 2001). Nevertheless, co-variation may be observed even if traits are mechanistically and/or physiological independent because different combinations of traits may be adopted by species to maximize their performance in a given environmental condition (Maire et al. 2013). Thus, despite leaf and hydraulic traits can represent independent trait dimensions (Brodribb et al. 2003; Li et al. 2015), their coordination under drought conditions might improve fitness (Manzoni 2014). Indeed, Markesteijn et al., (2011) in tropical dry forest observed that species with greatest xylem cavitation resistance had also lowest leaf turgor loss point and great modulus of elasticity (i.e. great leaf wilting resistance).

FT are also seen as species mechanisms through which they influence ecosystems (Table 2.1). Since specific traits directly represent resource processing at plant level (e.g. light, carbon and nitrogen) they directly mediate energy and material fluxes on ecosystems (Chapin et al. 2000; Garnier et al. 2004). Indeed, Garnier et al., (2004) showed how leaf traits (i.e. SLA, N_{mass} and leaf dry matter content) correlated with net primary productivity, litter decomposition rate, and soil carbon and nitrogen content in grass communities. Lavorel et al., (2011) also observed that several traits influenced different ecosystem properties in the French Alps. Thus, a trait-based approach proves useful for scaling up from species organs to ecosystems functions (Chapin 2003; Díaz & Lavorel 2007; Suding et al. 2008).

Indeed, functional characterization of communities (i.e. how traits are distributed within communities) has been used to assess trait effects on ecosystems. The most common index for functional characterization of plant communities is the community weighted mean (CWM, Lepš et al., 2011). CWM is the averaged trait value weighted by species relative abundances within a community. CWM is closely related with the mass ratio hypothesis which states that dominant traits in a community are the main contributors of different ecosystem functions (Grime 1998). Grime, (1998) suggested that since dominants account for the highest proportion of biomass in the community, they also determine in an "overwhelming extent" some ecosystem functions as primary production. Indeed, the study of Garnier et al., (2004) showed how strongly dominant traits influence ecosystem functioning and Mokany et al., (2008) and Májeková et al., (2014) also evidenced this “identity effect” on functions as productivity and stability, respectively.

Table 2.1: Association of plant traits with plant responses, competition, protection and effects on ecosystem process (from Lavorel et al., 2007)

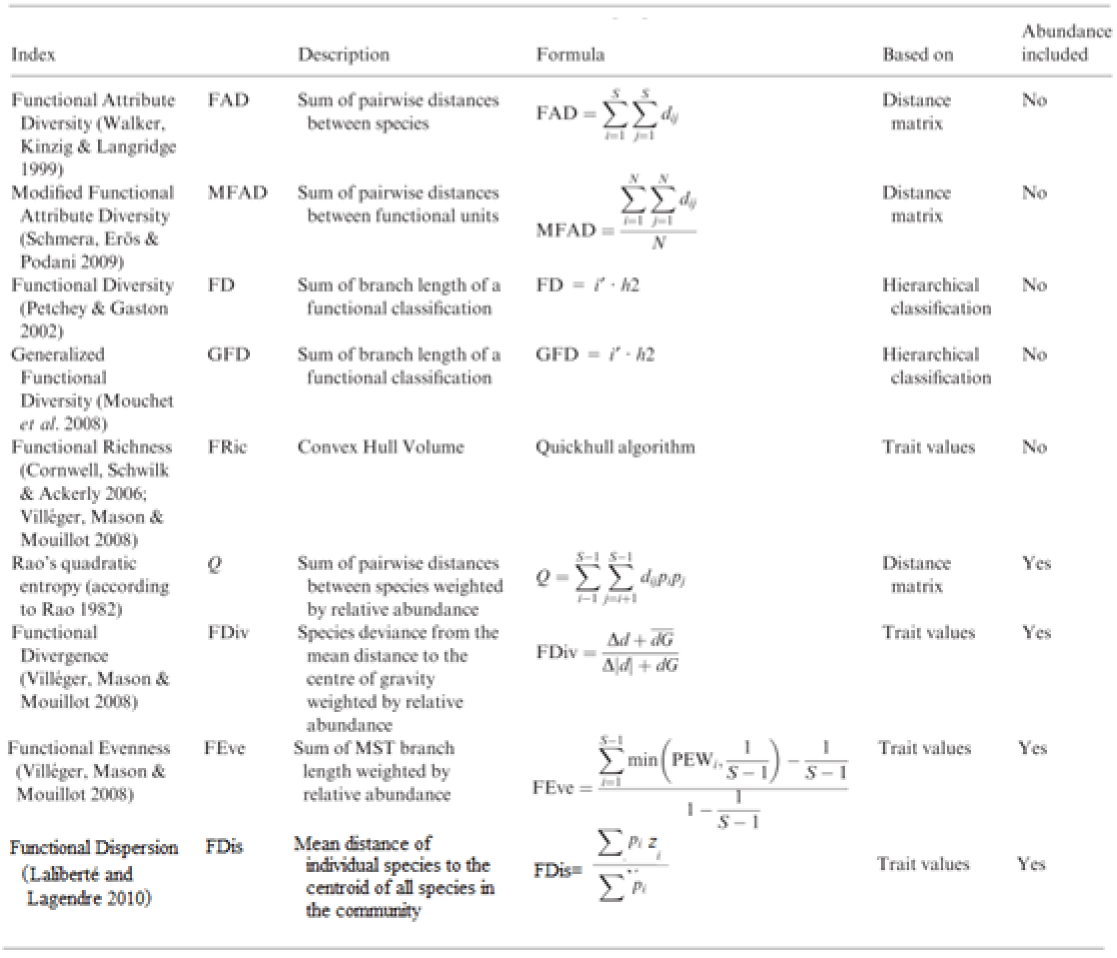


	Climate response	CO_2 response	Response to soil resources	Response to disturbance	Competitive strength	Plant defence/ protection	Effects on biogeochemical cycles	Effects on disturbance regime
Whole-plant traits								
Growth form	*	*	*	*	*	*	*	*
Life form	*	*	*	*	*		*	*
Plant height	*	*	*	*	*	*	*	*
Clonality	*	?	*	*	*			?
Spinescence	*	?			*	*		?
Flammability		?			*	?	*	*
Leaf traits								
Specific leaf area	*	*	*		*	*	*	
Leaf size	*	?	*		*	*	*	
Leaf dry matter content	*	?	*			*	*	*
Leaf N and P concentration	*	*	*	*	*	*	*	
Physical strength of leaves	*	?	*	*		*	*	
Leaf life-span	*	*	*	*	*	*	*	*
Leaf phenology	*		*		*		*	*
Photosynthetic pathway	*	*			*			
Leaf frost resistance	*				*	*		
Stem and below-ground traits								
Stem specific density	*	?	?	*		*	*	*
Twig dry matter content	*	?	?	?		*	*	*
Twig drying time	*	?	?				?	*
Bark thickness			*	*		*		?
Specific root length	*	?	*		*	*		?
Diameter of fine root	*	?	*					
Distribution of rooting depth	*	*	*	*	*		*	*
95% rooting depth	*	?	*		*			*
Nutrient uptake strategy	*	*	*	*	*		*	
Regenerative traits								
Dispersal mode				*				
Dispersule shape and size				*				
Seed mass			*	*	*	*		
Resprouting capacity								

However, diversity it is also pointed to play an important role in ecosystem functioning (Hooper et al. 2005). Two key mechanism, complementarity (Tilman 1997) and selection effects (Loreau & Hector 2001), are invoked for explaining the positive effects of diversity on ecosystem functions. Complementarity influences ecosystem processes in two ways: by favorably shaping species interactions and by increasing resource use efficiency as a result of niche partitioning. Indeed, mixing tree species with contrasting ecological strategies can therefore increase annual wood production by alleviating competitive inhibition among neighboring trees (Potvin & Gotelli 2008; Pretzsch & Schu 2009; Gómez-Aparicio et al. 2011), and by allowing diverse forest patches to use a greater portion of available resources and growing space (Morin et al. 2011; Brassard et al. 2013; Vilà et al. 2013; Tobner et al. 2014). However, at higher diversity levels there is also a higher chance of including highly productive species, thus the positive effect of diversity may be confounded by the inclusion of a highly productive species that drives the ecosystem function (i.e. the selection effect).

Thus, functional diversity indexes instead of species richness “per se” are recently used for testing the long-standing hypothesis of a positive relationship between Biodiversity and Ecosystem Functions (since it accounts for differences on species attributes that may mediate ecosystem functioning). Functional diversity refers to the kind, range, and relative abundance of functional traits present in a given community. Metrics to capture aspects of functional diversity are numerous (Table 2.2) including: functional richness, evenness, divergence, Rao’s quadratic entropy, and dispersion (Laliberté & Legendre 2010; Mouchet et al. 2010). Functional richness represents the range of trait values inside a community (the minimum convex hull in a multi-trait space) but its drawback relies on not providing information about how trait space is filled. Instead, functional evenness and divergence account for this aspect, and represent the regularity (i.e. evenness) and the spread (i.e. divergence) of abundances along this space, respectively (Villéger et al. 2008). However, since those indexes have limitations as dealing with both quantitative and qualitative data, and with missing values, Laliberté and Legendre (2010) proposed a new index called functional dispersion (FDis). FDis, which is closely related with Rao’s quadratic entropy, represents species mean distance from the multi-trait space centroid. Indeed, FDis is currently one of the most common used as diversity metric in BEF. For instance, Paquette and Messier, (2011) and Ruiz-Benito et al.,(2014) used FDis to detect the positive effects of functional diversity on forest productivity.

Table 2.2: d_{ij}: is the dissimilarity between species i and j. S: species richness. N: the number of functional units. p_i the relative abundance of species i. x: trait values. dG: mean distance to the center of gravity. Δd: sum of abundance-weighted deviances. PEW: partial weighted evenness. i': branch presence/absence row vector. h_2: branch length vector. z_i: the distance of species i from the weighted centroid (adapted from Mouchet et al., 2010).



Index		Description	Formula	Based on	Abundance included
Functional Attribute Diversity (Walker, Kinzig & Langridge 1999)	FAD	Sum of pairwise distances between species	$\mathrm{FAD} = \sum_{i=1}^{S}\sum_{j=1}^{S} d_{ij}$	Distance matrix	No
Modified Functional Attribute Diversity (Schmera, Erős & Podani 2009)	MFAD	Sum of pairwise distances between functional units	$\mathrm{MFAD} = \frac{\sum_{i=1}^{N}\sum_{j=1}^{N} d_{ij}}{N}$	Distance matrix	No
Functional Diversity (Petchey & Gaston 2002)	FD	Sum of branch length of a functional classification	$\mathrm{FD} = i' \cdot h2$	Hierarchical classification	No
Generalized Functional Diversity (Mouchet *et al.* 2008)	GFD	Sum of branch length of a functional classification	$\mathrm{GFD} = i' \cdot h2$	Hierarchical classification	No
Functional Richness (Cornwell, Schwilk & Ackerly 2006; Villéger, Mason & Mouillot 2008)	FRic	Convex Hull Volume	Quickhull algorithm	Trait values	No
Rao's quadratic entropy (according to Rao 1982)	Q	Sum of pairwise distances between species weighted by relative abundance	$Q = \sum_{i=1}^{S-1}\sum_{j=i+1}^{S-1} d_{ij}p_ip_j$	Distance matrix	Yes
Functional Divergence (Villéger, Mason & Mouillot 2008)	FDiv	Species deviance from the mean distance to the centre of gravity weighted by relative abundance	$\mathrm{FDiv} = \frac{\Delta d + \overline{dG}}{\Delta\lvert d\rvert + dG}$	Trait values	Yes
Functional Evenness (Villéger, Mason & Mouillot 2008)	FEve	Sum of MST branch length weighted by relative abundance	$\mathrm{FEve} = \frac{\sum_{i=1}^{S-1}\min\left(\mathrm{PEW}_i, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$	Trait values	Yes
Functional Dispersion (Laliberté and Lagendre 2010)	FDis	Mean distance of individual species to the centroid of all species in the community	$\mathrm{FDis} = \frac{\sum p_i\, z_i}{\sum p_i}$	Trait values	Yes

Species Distribution Models

Species Distribution Models (SDM) are numerical models "that relate species distribution data (occurrence or abundance at known locations) with information on the environmental and/or spatial characteristics of those locations" (Elith & Leathwick 2009). Thus, SDM allow to analyze theoretical and practical issues relating species and environment (Higgins et al. 2012). For instance, SDM has been used to test the effect of extreme events on species distributions (Zimmermann et al. 2009), assess facilitative mechanisms among species (Pellissier et al. 2010), or evaluate potential impacts of climate change on species distribution, vegetation types, and diversity (Thuiller et al. 2005; Thuiller et al. 2006; Thuiller et al. 2011). The First study relating species distribution and environment dates back to 1924, when Johnston studied the invasive spread capacity of cactus species in Australia (reference in Guisan and Thuiller, 2005). However, was during the 80's when this "discipline" started to growth mainly due to developments on computational and statistical sciences. Latterly, in the turn of century, greatest improvements were carried out on theoretical and technical related issues as clarifications over the niche concept or implementation of new statistical methods (see reviews from Guisan & Zimmerman 2000; Guisan & Thuiller 2005; Elith & Leathwick 2009; Zimmermann et al. 2010).

SDM have been also referred as "ecological niche models", "habitat suitability models", or "predictive distribution models", mainly due to different interpretations of what is being modeled and what they are predicting, i.e. if SDM represent species niche or simply species potential distributions (Franklin, 2009). However, it is recognized that SDM are strongly linked with Hutchinson definition of species niche (Araujo & Guisan 2006). Hutchinson, (1957) defined the fundamental niche of species as a hypervolume representing the '*n*' environmental dimensions in which species can exist (accordingly to Grinnell 1917). Nevertheless, Hutchinson also distinguished the realized niche, i.e. the restricted part of the fundamental niche because of distributional constrains imposed by biotic interactions (Fig. 2.2). Thus, since SDM are based on the realized distribution of species (i.e. after overcoming biotic and abiotic filters), SDM are commonly interpreted as a representation of species realized niche (Franklin, 2009; Guisan and Zimmerman, 2000).

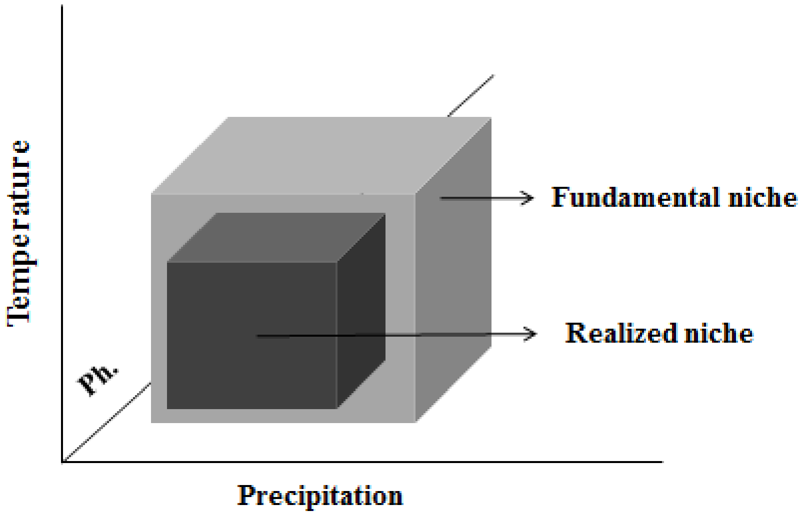


Figure 2.2: The niche concept. Hutchinson defined the fundamental niche as a hypervolume representing the '*n*' environmental dimensions in which species can exist (in these example it is represented over three dimensions). He also distinguished the realized niche, i.e. the restricted part of the fundamental niche because of distributional constrains imposed by biotic interactions.

The modeling procedure can be dived into different steps (see Guisan and Zimmerman, 2000 for further details). Conceptual formulation is the first step and sets the underlying theories, assumptions and factors controlling species distribution. Their consideration is necessary for an appropriate model design and proper interpretation of results. For instance, assumptions on species pseudo-equilibrium with the environment (Araújo et al. 2005) and theories regarding general patterns constraining species range limits (Brown et al. 1996) should be considerate for an appropriate geographical and physiological interpretation of SDM.

Following steps are data collection and algorithm selection which also should be in agreement with the purpose of the model (Austin 2007). Data used should cover an appropriate area extent (at least the whole species environmental range) and the resolution or work scale should be adequate enough to detect the underlying ecological process (Franklin 2009). For instance, coarse resolutions and "un-sampled" environmental gradients might not allow detecting species environmental responses. Instead, the selection of statistical model is important since it conditions the kind of relationship among species and environment (e.g. if it is linear, quadratic, or asymmetric). Traditionally, it was considerate that species response to a resource gradient was bell shaped (it was assumed that competition constrained the range but not the optima), however, theoretical and applied studies had showed that species responses may take numerous forms (e.g. skewed or even bimodal, Fig. 2.3, Austin & Smith 1990). Thus, it is suggested that statistical algorithms used in SDM should not constrain species environmental responses to specific shape (specially without explicit theoretical justification, Austin 2007).

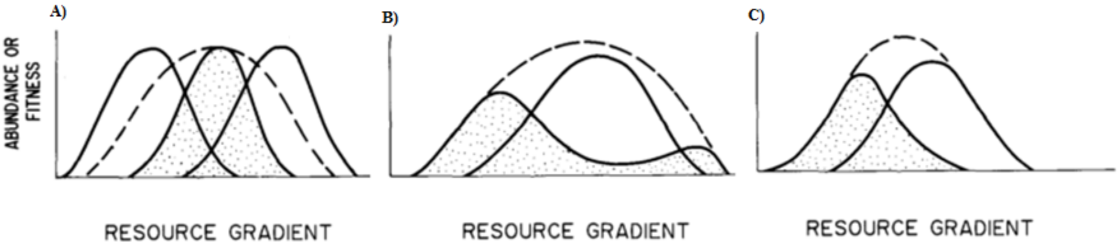


Figure 2.3: Species environmental responses modulated by biotic interactions. Species fundamental responses (dotted line) could have different realized shapes depending on how other species affect it. A) Traditional assumption suggesting that the optimum is not affected by biotic interactions; B) and C) bimodal and unimodal realized responses with alterations on species physiological optimum (adapted from Austin and smith 1990).

Different algorithms are used to fit SDM, for instance regression based models (e.g. Generalized Linear and Additive Models), classification techniques (e.g. Classification and Regression Trees), environmental envelopes (e.g. BIOCLIM) or machine learning approaches (e.g. MAXENT, Artificial Neural Networks, Boosted Regression Trees and Random Forests). These techniques differ in several aspects (see Franklin 2009 for more deep insights) but the main difference relies on how the relationships among species and environment is "structured" (Fig. 2.4). Indeed, the complexity of the algorithms has conditioned their use in ecology. For instance, despite machine learning techniques might outperform traditional methods (Elith et al. 2006), their “black box” nature has promote more comprehensive techniques as regression methods since they easily allow to understand how species relates with environment (Elith & Leathwick 2009).

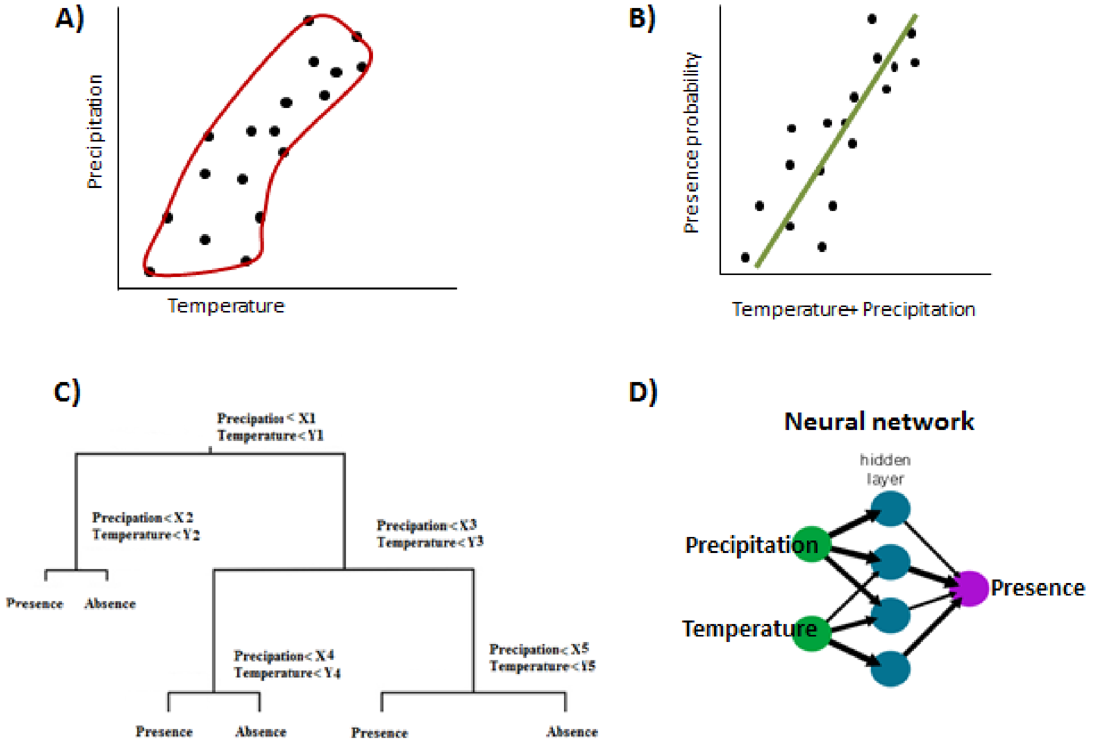


Figure 2.4: Representation of how different algorithms structure the relationships among species and environment. A) Envelope models create a “bioclimatic surface” which envelopes the conditions over which species can be found; B) regression models fit an equation relating the probability to find a species based on environmental data; C) classification techniques create “conditional trees” which classify locations as a presence or absence according to their environmental values; D) Machine learning techniques (e.g. neuronal networks), create hidden cause-effect relationships among variables as consequence of a learning process.

The last steps for building SDM are model calibration (i.e. parameters estimation) and evaluation. Since is not common to have independent datasets to use for each step (despite it will be the most optimal practice, Fielding & Bell 1997), usually data are split into calibration and evaluation datasets to avoid the overestimations problems caused when using the same dataset for both tasks. However if the dataset is not large enough, other techniques like Jack-Knife, cross-validation, or bootstrapping, which are based on the stability of the model, are considered more approapirate (for further details see Guisan and Zimmerman, 2000). The most common parameters used for evaluate the accuracy of SDM are the Area Under the Curve (AUC) and Kappa statistic (Elith & Leathwick 2009). Both methods depend on the confusion matrix, i.e. a contingency table with the correct predicted and wrong predicted presence, and correct predicted and wrong predicted absence. However, Kappa is a threshold dependent method and thus it explicitly needs to set a probability threshold to transform occurrence probability into presence and absence (see Valverde-Jimenez & Lobo 2007 for different methods) . Instead, AUC is a method which provides a single measure of overall accuracy without depending upon a particular threshold (Fielding & Bell 1997). Both methods have their own drawbacks since their performance depend on data characteristics. For instance, since Kappa is influenced by species prevalence (i.e. the ratio among presence and absences), its performance might depend on the method used to set the threshold (Valverde-Jimenez & Lobo 2007). Instead, AUC largely depends on the extent of analysis (i.e. higher AUC scores are obtained increasing the geographical extent outside species environmental domain, Lobo et al. 2008). Thus, it is usually recommended to jointly use different evaluation parameters to assess the accuracy of SDM (see suggestions in Fielding and Bell, 1997).

Remote Sensing

Remote sensing is referred to the acquisition of electromagnetic signals from satellite or airborne sensors, which allows inferring information about land properties (Turner et al. 2003). Remote sensing is based on “objects” spectral properties to absorb, transmit and reflect different wavelengths of the electromagnetic spectrum. Thus, since “objects” like vegetation, water and soil differ on their spectral response (Fig. 2.5), remote sensing proves useful for study different aspects of natural earth systems. The use of remote sensing for vegetation analysis dates back to 2nd World War when color infrared films were used to detected vegetation health (Ustin and Gamon, 2010). However, was in the 70’s when the global digital imagery begun thanks to the first land observing satellite, the Earth Resources Technology Satellite (ERTS 1, later renamed LANDSAT, Ustin & Gamon 2010). Since that moment, developments on sensors characteristics, advances in informatics, launching of new satellites, and a better understanding of objects spectral behaviors have allowed to globally and routinely monitor ecosystems.

The main characteristics of satellite sensors that condition analysis are spatial, temporal and spectral resolutions. Spatial resolutions of sensors characterize the landscape levels of analysis, with the highest resolution (< 1 m) able to identify individual tree plants and lowest resolution (e.g. 1km) to infer information at ecosystem level. Temporal resolution identifies vegetation under different aspects, wherein with monthly image detections is possible to observe seasonal changes in phenology, while image detection over the years reveal longer term changes associated with anthropic activities (land use changes) or climate trends. Instead, spectral resolution refers to the number of bands discriminated by the sensor which allow to detect, in the case of hyperspectral sensors, subtle difference among objects proving useful information for assessing species composition (Wang et al. 2010).

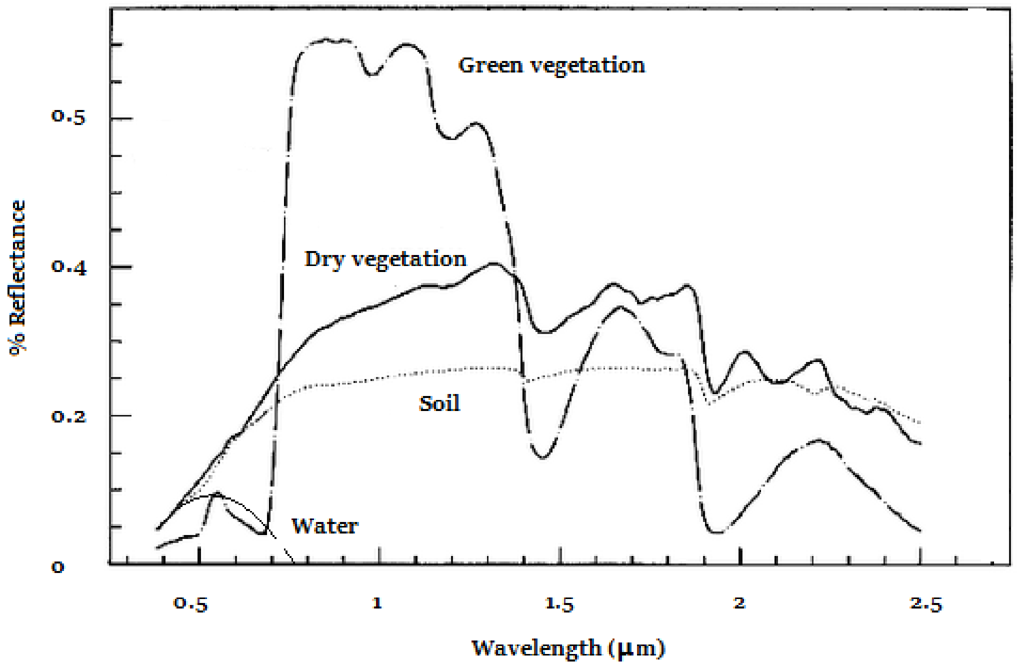


Figure 2.5: Typical spectral reflectance curves for vegetation, soil and water.

Plants spectral response is characterized by the absorption at the visible region of the light spectrum (mostly on blue and red, and less on the green portion of spectrum) while reflecting most of the light in the near infrared (750-1400 nm, Fig. 2.5). The absorption in the visible is due to chlorophylls and carotenoids located in the palisaded parenchyma whereas reflection is consequence of spongy parenchyma structure (cell wall air interfaces), which allows reflecting the excess of energy that arrives via the near infrared region (Jensen 2000). However, stress conditions (e.g. drought, cold, or pathogens) might lead to reductions on chlorophyll content and changes on spongy parenchyma structure resulting on changes in plant spectral responses. Thus, these changes allow the identification of stress effects on plant performance.

$$NDVI = \frac{NIR\ band - RED\ band}{NIR\ band + RED\ band}$$

$$EVI = G * \frac{NIR\ band - RED\ band}{NIR\ band + C_1 * RED\ band - C_2 * BLUE\ band + L}$$

Equations note: L is the background adjustment coefficient for near infrared (NIR) and red radiant transfer through the canopy; C_1 and C_2 are the aerosol correction coefficients for red and blue bands, respectively; and G is a gain scaling factor. The coefficients adopted by MODIS are L=1, C_1=6, C_2=7.5, and G=2.5.

A great number of vegetation indexes have been developed using combinations of reflectance values at different wavelengths allowing stress effects to be monitored. Among these indexes, the most widely used is the Normalized Difference Vegetation Index (NDVI). NDVI is the normalized difference between near infrared and the visible reflectance (equation 1). However, some limitations have been observed in the NDVI (i.e. saturates at well vegetated areas and it does not consider background effects on reflectance, Gao et al., 2000). Thus, new indexes, like the Enhanced Vegetation Index (EVI) or Soil-Adjusted Vegetation Index (SAVI), have been suggested for monitoring vegetation as they overcome some of the limitations of NDVI. EVI, which also uses information on the blue band to remove atmospheric and soil influences (equation 2), has been proved to be more sensitive to canopy variations than NVDI or SAVI (Huete et al. 2002; Jiang et al. 2008).

Vegetation indexes are provided by different sensors having different characteristics (i.e. in spatial and spectral resolution, temporal series and to be or not free of charge; see Table 2.3 for a summary of some characteristics of different sensors and Xie et al., 2008 for further details). Thus, the scope and availability of economic resources determines which sensor to use. For instance, MODIS provides data at a resolution of 250-500 m but from the year 2000, however AVHRR, can provide data from 1980 but at coarse resolution (1000 m). Instead LANDAST can supply data at great resolution (30 m), but data availability may be limited by weather conditions especially on tropical/subtropical areas where cloud conditions may be persistent over long periods and rare satellite passes (once every 16 days) limits acquisition of cloud-free data. On the other hand, options like SPOT or IKONOS had very fine resolution but also the disadvantage of being relatively expensive.

Different studies have demonstrated the scientific utility of these products comparing data retrieved by sensors with both field biophysical and top-of-canopy reflectance measures (Huete et al. 2002; Dong et al. 2003; Fensholt et al. 2009). For instance, NDVI and EVI from MODIS showed great correspondence with top-of canopy reflectance in different biomes (Huete et al. 2002). In addition, Dong et al., (2003) in Boreal and Temperate forest observed that NDVI accurately represented forest biomass across different spatial and temporal scales. Thus, vegetation index retrieved from remote sensing has been proved useful to study different vegetation aspects as phenology, diversity, productivity and for monitoring trends (Pettorelli et al. 2014). For instance, Gaitán et al., (2014) used inter-annual differences on the yearly cumulated NVDI to assess species richness effect on ecosystem functioning. Instead Huesca et al., (2015) using also MODIS data, assessed the functional behavior of different forest types.

Table 2.3: Main features of image products from the different sensors products (from Xie et al. 2008).

Products (sensors)	Features	Vegetation mapping applications[a]
Landsat TM	Medium to coarse spatial resolution with multispectral data (120 m for thermal infrared band and 30 m for multispectral bands) from Landsat 4 and 5 (1982 to present). Each scene covers an area of 185 × 185 km. Temporal resolution is 16 days.	Regional scale mapping, usually capable of mapping vegetation at community level.
Landsat ETM+ (Landsat 7)	Medium to coarse spatial resolution with multispectral data (15 m for panchromatic band, 60 m for thermal infrared and 30 m for multispectral bands) (1999 to present). Each scene covers an area of 185 km × 185 km. Temporal resolution is 16 days.	Regional scale mapping, usually capable of mapping vegetation at community level or some dominant species can be possibly discriminated.
SPOT	A full range of medium spatial resolutions from 20 m down to 2.5 m, and SPOT VGT with coarse spatial resolution of 1 km. Each scene covers 60 × 60 km for HRV/HRVIR/HRG and 1000 × 1000 km (or 2000 × 2000 km) for VGT. SPOT 1, 2, 3, 4 and 5 were launched in the year of 1986, 1990, 1993, 1998 and 2002, respectively. SPOT 1 and 3 are not providing data now.	Regional scale usually capable of mapping vegetation at community level or species level or global/national/regional scale (from VGT) mapping land cover types (i.e. urban area, classes of vegetation, water area, etc.).
MODIS	Low spatial resolution (250–1000 m) and multispectral data from the Terra Satellite (2000 to present) and Aqua Satellite (2002 to present). Revisit interval is around 1–2 days. Suitable for vegetation mapping at a large scale. The swath is 2330 km (cross track) by 10 km (along track at nadir).	Mapping at global, continental or national scale. Suitable for mapping land cover types (i.e. urban area, classes of vegetation, water area, etc.).
AVHRR	1-km GSD with multispectral data from the NOAA satellite series (1980 to present). The approximate scene size is 2400 × 6400 km	Global, continental or national scale mapping. Suitable for mapping land cover types (i.e. urban area, classes of vegetation, water area, etc.).
IKONOS	It collects high-resolution imagery at 1 m (panchromatic) and 4 m (multispectral bands, including red, green, blue and near infrared) resolution. The revisit rate is 3–5 days (off-nadir). The single scene is 11 × 11 km.	Local to regional scale vegetation mapping at species or community level or can be used to validate other classification result.
QuickBird	High resolution (2.4–0.6 m) and panchromatic and multispectral imagery from a constellation of spacecraft. Single scene area is 16.5 × 16.5 km. Revisit frequency is around 1–3.5 days depending on latitude.	Local to regional scale vegetation mapping at species or community level or used to validate vegetation cover extracted from other images.
ASTER	Medium spatial resolution (15–90 m) image with 14 spectral bands from the Terra Satellite (2000 to present). Visible to near-infrared bands have a spatial resolution of 15 m, 30 m for short wave infrared bands and 90 m for thermal infrared bands.	Regional to national scale vegetation mapping at species or community level.
AVIRIS	Airborne sensor collecting images with 224 spectral bands from visible, near infrared to short wave infrared. Depending on the satellite platforms and latitude of data collected, the spatial resolution ranges from meters to dozens of meters and the swath ranges from several kilometers to dozens of kilometers.	At local to regional scale usually capable of mapping vegetation at community level or species level. As images are carried out as one-time operations, data are not readily available as it is obtained on an 'as needs' basis.
Hyperion	It collects hyperspectral image with 220 bands ranging from visible to short wave infrared. The spatial resolution is 30 m. Data available since 2003.	At regional scale capable of mapping vegetation at community level or species level.

[a] Many sensors provide imagery for producing VI (e.g. NDVI) that is calculated from the bands in the visible and near-infrared regions.

Climate Change Modeling

Climate change modeling refers to the projection of Global Circulation Models (GCM) into different future scenarios (i.e. into different human development paths), which allows to predict how socio-economic human activities will affect climate (IPCC 2014) and the different process with which it closely links (Cramer et al. 2001). Despite greenhouse gasses (GHG) effects on climate was early notice by Svante Arrhenius in 1896, the implementation of warming predictions started only during 70's (Bodansky 1992). However, from that moment and thanks to great developments on computer science, models have increased their complexity (i.e. including more process affecting energy transfer) and feasibility at high spatial and temporal resolutions improving the confidence of their results (Treut et al. 2007).

GCM are based on mathematical equations, regulating climate, hydrology and bio-geochemical cycles, and representing physical laws that govern the state (i.e. conservation of the mass, energy and momentum, and gases kinetics) of atmosphere, landforms and oceans. GCM use a three dimensional grid over the globe with several vertical layers in the atmosphere and oceans to calculate vertical and horizontal mass and energy exchanges based on those equations (Fig. 2.6; Edwards 2011). Climatic models are typically classified as Atmosphere-Ocean General Circulation Models (AOGCM) or Earth System Models (ESM), which differ in complexity and computational cost. ESM expand AOGCM, since they can include biogeochemical cycles. Both AOGCM and ESM provide hourly, daily and monthly climate data at a spatial resolution varying between 100 and 600 km. In order to provide more information at a finer scale for climate impact assessment, these models are usually downscaled using three main methods: Dynamic downscaling (Regional Circulation Models, RCM), Statistical downscaling and simple methods (e.g. Delta method). RCM typically "re-model" general circulation models for a regional extent at higher resolution, whereas statistical methods derive from empirical relations the regional spatial trends of climate as function of key climate variables at global level. Instead, simple methods like the Delta method, create a smoothed surface of change on climate based on anomalies and then applies to high-resolution baseline climates (i.e. WorldClim).

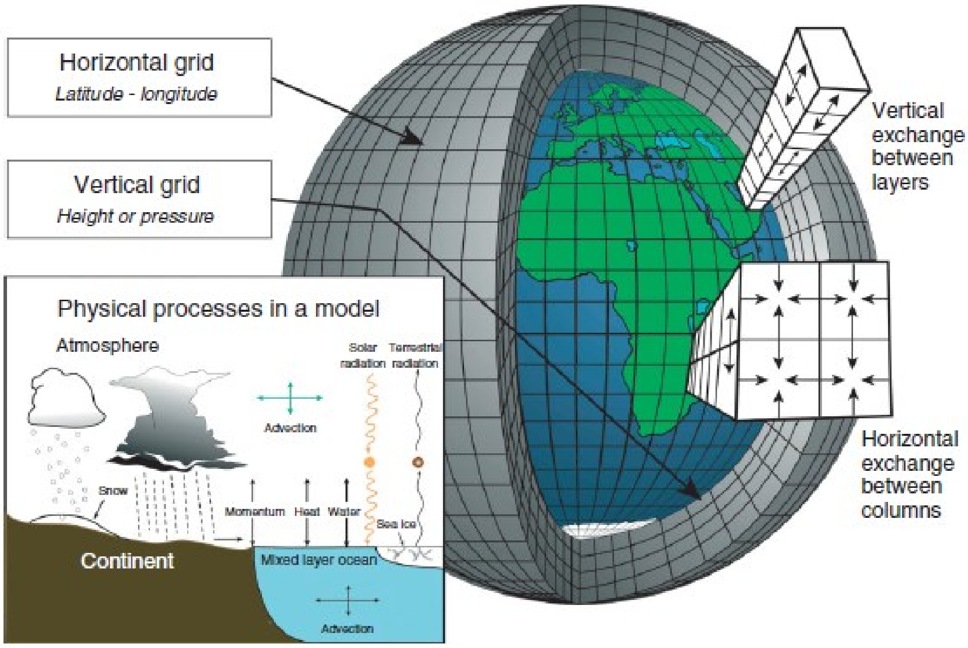


Figure 2.6: Schematic representation of a Global Circulation Model (From Edwards 2011)

In order to assess how socio-economic human activities will affect climate, GCM are projected into different future scenarios (i.e. as input data). Scenarios refer to different future trends on socio-economic development (e.g. population growth, economic activity, or technology) that will affect climate trough GHG emissions and atmospheric concentrations, air pollutant emissions and land use (IPCC 2014). From SA90 (used in the 1st IPCC report), passing through IS92 and SRES (used in the 2nd and 3rd-4th IPCC reports, respectively), different scenarios have been specified in order to adapt to the new specificities of climatic models and for exploring different approaches on how to reach specific climate change targets. Thus, the advantage of the current RCP scenarios (i.e. the Representative Concentration Pathways) is that allow to assess how different combinations on social, economic and technological circumstances are compatible with a specific pathway or temperature target but at the same time allow climatic modelers to continue to assess the effect of radiative forces on climate and ecosystems (van Vuuren et al. 2011). The new four RCP cover a wide range of GHG concentration (and radiative forcing) trajectories noticed in the scientific literature (Fig 2.7). For instance, RCP 2.6 represents a future scenario where efforts have been done to reduce emissions and content temperature increase below preindustrial era. Instead, RCP 4.5 (associated to SRES B1) and 6.0 (associated to SRES B2) represent intermediate scenario whereas RCP 8.5 (associated to SRES A1F1) represents continuity on high GHG emissions.

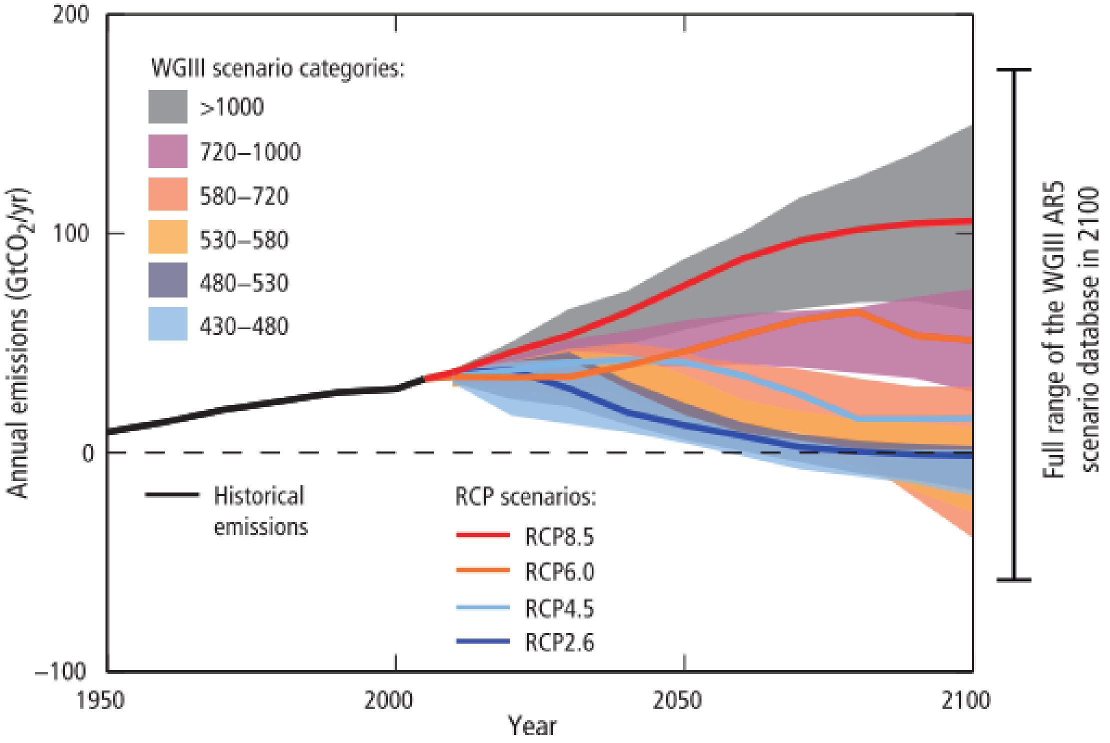


Figure 2.7: Emissions of carbon dioxide (CO_2)for the different Representative Concentration Pathways (RCP) and the associated categories from the Working Group III (WGIII, i.e. cumulative anthropogenic CO_2 emissions predicted; from IPCC 2014).

Since different climate models have been used to predict climatic changes contradictory results were caused as model uncertainties, by the reliability different assumptions taken by models (e.g. clouds, Cess et al., 1989). Thus, in order to intercompare model predictions the Coupled Model Intercomparison Project (CMIP) was established (Taylor et al. 2012). CMIP, which it is at its 5th phase, set a standardized protocol for explaining the mechanism responsible for model differences on climatic projections (i.e. why different models give different output in response to the same input data). Models projections from different GCM used in the CMIP5 and downscaled with the Delta method at 1 km resolution are freely available at WorldClim website (http://www.worldclim.org/), specifying monthly average over 2045-2065 period of precipitation, minimum and maximum temperature. Thus, climatic data from CMIP allow to assess uncertainties on climate change impacts in vegetation and ecosystem dynamics, e.g. Yu et al., (2014) evaluated vegetation responses joining dynamic vegetation models and CMIP climatic predictions.

Bibliography

Araujo, M.B., & Guisan, A. 2006. Five (or so) challenges for species distribution modelling. *Journal of Biogeography* 33: 1677–1688.

Araújo, M., Pearson, R., & Rahbek, C. 2005. Equilibrium of species' distribution with climate. *Ecography* 28: 693–695.

Austin, M. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling* 200: 1–19.

Austin, M., & Smith, T. 1989. A new model for the continuum concept. *Vegetatio* 83: 35–47.

Bodansky, D. 1992. History of the global change regime. In Luterbacher, U. & Sprinz, D.F. (eds.), *International Relations and Global Climate Change*, pp. 23–39. The MIT Press, Massachusetts, USA.

Brassard, B.W., Chen, H.Y.H., Cavard, X., Laganiere, J., Reich, P.B., Bergeron, Y., Pare, D., & Yuan, Z. 2013. Tree species diversity increases fine root productivity through increased soil volume filling. *Journal of Ecology* 101: 210–219.

Brodribb, T.J., Holbrook, N.M., Edwards, E.J., & Gutiérrez, M. V. 2003. Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant, Cell and Environment* 26: 443–450.

Brown, J.H., Stevens, G.C., & Kaufman, D.M. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* 27: 597–623.

Cess, R.D., Potter, G.L., Blanchet, J.P., Boer, G.J., Ghan, S.J., Kiehl, J.T., LE Treut, H., Li, Z.X., Liang, X.Z., Mitchell, J.F., Morcrette, J.J., Randall, D. a, Riches, M.R., Roeckner, E., Schlese, U., Slingo, A., Taylor, K.E., Washington, W.M., Wetherald, R.T., & Yagai, I. 1989. Interpretation of cloud-climate feedback as produced by 14 atmospheric general circulation models. *Science* 245: 513–516.

Chapin, F.S. 2003. Effects of plant traits on ecosystem and regional processes: A conceptual framework for predicting the consequences of global change. *Annals of Botany* 91: 455–463.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., & Díaz, S. 2000. Consequences of changing biodiversity. *Nature* 405: 234–42.

Chave, J., Coomes, D., & Jansen, S. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–66.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., & Zanne, A.E. 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491: 752–5.

Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R. a., Brovkin, V., Cox, P.M., Fisher, V., Foley, J. a., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S., Smith, B., White, A., & Young-Molling, C. 2001. Global response of terrestrial ecosystem structure and function to CO2 and climate change: Results from six dynamic global vegetation models. *Global Change Biology* 7: 357–373.

Díaz, S., & Lavorel, S. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences* 104: 20684–20689.

Dong, J., Kaufmann, R.K., Myneni, R.B., Tucker, C.J., Kauppi, P.E., Liski, J., Buermann, W., Alexeyev, V., & Hughes, M.K. 2003. Remote sensing estimates of boreal and temperate forest woody biomass: Carbon pools, sources, and sinks. *Remote Sensing of Environment* 84: 393–410.

Edwards, P.N. 2011. History of climate modeling. *Wiley Interdisciplinary Reviews: Climate Change* 2: 128–139.

Elith, J., Graham, C.H., Anderson, R.P., Dudık, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.C.J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S., & Zimmermann, N.E. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129– 151.

Elith, J., & Leathwick, J.R. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics* 40: 677–697.

Enquist, B.J., Norberg, J., Bonser, S.P., Violle, C., Webb, C.T., Henderson, A., Sloat, L.L., & Savage, V.M. 2015. Scaling from Traits to Ecosystems: Developing a General Trait Driver Theory via Integrating Trait-Based and Metabolic Scaling Theories. In Pawar, Woodward, & Dell (eds.), *Advances in Ecological Research. Trait-Based Ecology - From Structure to Function*, pp. 249–317. Elsevier Ltd.

Fensholt, R., Rasmussen, K., Nielsen, T.T., & Mbow, C. 2009. Evaluation of earth observation based long term vegetation trends - Intercomparing NDVI time series trend analysis consistency of Sahel from AVHRR GIMMS, Terra MODIS and SPOT VGT data. *Remote Sensing of Environment* 113: 1886–1898.

Fielding, A., & Bell, J. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24:

38–49.

Franklin, J. 2009. *Mapping species distributions: spatial inference and prediction*. Cambridge University Press, Cambridge,UK.

Gaitán, J., Bran, D., & Oliva, G. 2014. Plant species richness and shrub cover attenuate drought effects on ecosystem functioning across Patagonian rangelands. *Biology Letters* 10: 1–4.

Gao, X., Huete, A.R., Ni, W., & Miura, T. 2000. Optical-biophysical relationships of vegetation spectra without background contamination. *Remote Sensing of Environment* 74: 609–620.

Garnier, E., Cortez, J., Billès, G., & Navas, M. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630–2637.

Gómez-Aparicio, L., García-Valdés, R., Ruíz-Benito, P., & Zavala, M.A. 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: Implications for forest management under global change. *Global Change Biology* 17: 2400–2414.

Grime, J. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.

Grinnell, J. 1917. The niche-relationships of the California trasher. *Auk* 34: 427–433.

Guisan, A., & Thuiller, W. 2005. Predicting species distribution: Offering more than simple habitat models. *Ecology Letters* 8: 993–1009.

Guisan, A., & Zimmerman, N.E. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186.

Hacke, U.G., & Sperry, J.S. 2001. Functional and ecological xylem anatomy. *Perspectives in Plant Ecology Evolution and Systematics* 4: 97–115.

Hacke, U., Sperry, J., & Pockman, W. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126: 457–461.

Higgins, S.I., O'Hara, R.B., & Romermann, C. 2012. A niche for biology in species distribution models. *Journal of Biogeography* 39: 2091–2095.

Hooper, D.U., Chapin, F.S., Ewel, J.J., & Hector, A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75: 3–35.

Huesca, M., Merino-de-Miguel, S., Eklundh, L., Litago, J., Cicuéndez, V., Rodríguez-Rastrero, M., Ustin, S.L., & Palacios-Orueta, A. 2015. Ecosystem functional assessment based on the "optical type" concept and self-similarity patterns: An application using MODIS-NDVI time series autocorrelation. *International Journal of Applied Earth Observation and Geoinformation* 43: 132–148.

Huete, a., Didan, K., Miura, T., Rodriguez, E.P., Gao, X., & Ferreira, L.G. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment* 83: 195–213.

Hutchinson. 1957. Concluding remarks. *Cold spring Harbor symp* 22: 415–427.

IPCC. 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Team Core Writing, R. K. Pachauri, & L. A. Meyer, Eds.). Geneva, CH.

Jensen, J.R. 2000. *Remote sensing of the environment: an earth resource perspective*. Prentice-Hall, Inc., Upper Saddle River, USA.

Jiang, Z., Huete, a, Didan, K., & Miura, T. 2008. Development of a two-band enhanced vegetation index without a blue band. *Remote Sensing of Environment* 112: 3833–3845.

Laliberté, E., & Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305.

Lavorel, S., Díaz, S., Cornelissen, J.H.C., Garnier, E., Harrison, S.P., Mcintyre, S., Pausas, J.G., Catherine, N.P., Carlos, R., Roumet, C., Natalia Pérez-harguindeguy, & Urcelay, C. 2007. Plant functional types: are we getting any closer to the Holy

Grail? In Canadell, J.G., Pataki, D.E., & Pitelka, L.F. (eds.), *Terrestrial Ecosystems in a Changing World*, pp. 149–160. Springer-Verlag, Berlin, Heidelberg,DE.

Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.-P., Garden, D., Girel, J., Pellet, G., & Douzet, R. 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology* 99: 135–147.

Lepš, J., de Bello, F., Šmilauer, P., & Doležal, J. 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography* 34: 856–863.

Li, L., McCormack, M.L., Ma, C., Kong, D., Zhang, Q., Chen, X., Zeng, H., Niinemets, Ü., & Guo, D. 2015. Leaf economics and hydraulic traits are decoupled in five species-rich tropical-subtropical forests. *Ecology Letters* 18: 899–906.

Lobo, J.M., Jiménez-valverde, A., & Real, R. 2008. AUC: A misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17: 145–151.

Loreau, M., & Hector, a. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412: 72–76.

Maherali, H., Pockman, W., & Jackson, R. 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* 85: 2184–2199.

Maire, V., Gross, N., Hill, D., Martin, R., Wirth, C., Wright, I.J., & Soussana, J.F. 2013. Disentangling Coordination among Functional Traits Using an Individual-Centred Model: Impact on Plant Performance at Intra- and Inter-Specific Levels. *Plos One* 8: 1–16.

Májeková, M., de Bello, F., Doležal, J., & Lepš, J. 2014. Plant functional traits as determinants of population stability. *Ecology* 95: 2369–2374.

Manzoni, S. 2014. Integrating plant hydraulics and gas exchange along the drought-response trait spectrum. *Tree Physiology* 34: 1031–1034.

Markesteijn, L., Poorter, L., Paz, H., Sack, L., & Bongers, F. 2011. Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell and Environment* 34: 137–48.

Micco, V. De, & Aronne, G. 2012. Morpho-anatomical traits for plant adaptation to drought. In Aroca, R. (ed.), *Plant Responses to Drought Stress*, pp. 37–61. Springer Berlin Heidelberg, Berlin, Heidelberg, DE.

Mokany, K., Ash, J., & Roxburgh, S. 2008. Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology* 96: 884–893.

Morin, X., Fahse, L., Scherer-Lorenzen, M., & Bugmann, H. 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters* 14: 1211–1219.

Mouchet, M. a., Villéger, S., Mason, N.W.H., & Mouillot, D. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* 24: 867–876.

Nardini, A., Pedà, G., & Rocca, N. 2012. Trade-offs between leaf hydraulic capacity and drought vulnerability: morpho-anatomical bases, carbon costs and ecological consequences. *New Phytologist* 196: 788–798.

Niinemets, Ü. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* 82: 453–469.

Paquette, A., & Messier, C. 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography* 20: 170–180.

Pellissier, L., Anne Bråthen, K., Pottier, J., Randin, C.F., Vittoz, P., Dubuis, A., Yoccoz, N.G., Alm, T., Zimmermann, N.E., & Guisan, A. 2010. Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. *Ecography* 33: 1004–1014.

Pettorelli, N., Laurance, W.F., O'Brien, T.G., Wegmann, M., Nagendra, H., & Turner, W. 2014. Satellite remote sensing for applied ecologists: Opportunities and challenges. *Journal of Applied Ecology* 51: 839–848.

Poorter, H. 1989. Interspecific variation in relative growth rate : on ecological causes and physiological consequences. In Lambers, H., Cambridge, M.L., Konings, H., & Pons, T.L. (eds.), *Causes and consequences of variation in growth rate and productivity of higher plants*, pp. 45–68. SPB Academic Publishing, The Hague, NL.

Poorter, H., Niinemets, U., Poorter, L., Wright, I.J., & Villar, R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *The New Phytologist* 182: 565–88.

Poorter, H., & Remkes, C. 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* 83: 553–559.

Potvin, C., & Gotelli, N.J. 2008. Biodiversity enhances individual performance but does not affect survivorship in tropical trees. *Ecology Letters* 11: 217–223.

Pretzsch, H., & Schu, G. 2009. Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe : evidence on stand level and explanation on individual tree level. *European Journal of Forest Research* 128: 183–204.

Reich, P. 2014. The world-wide “fast–slow”plant economics spectrum: a traits manifesto. *Journal of Ecology* 102: 275–301.

Reich, P., Ellsworth, D., & Walters, M. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955–1969.

Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M., & Walters, M.B. 2003. The evolution of plant functional variation: traits, specctra, and strategies. *International Journal of Plant Sciences* 164: 143–164.

Ruiz-Benito, P., Gómez-Aparicio, L., Paquette, A., Messier, C., Kattge, J., & Zavala, M.A. 2014. Diversity increases carbon storage and tree productivity in Spanish forests. *Global Ecology and Biogeography* 23: 311–322.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., & Navas, M.L. 2008. Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology* 14: 1125–1140.

Taylor, K.E., Stouffer, R.J., & Meehl, G. a. 2012. An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society* 93: 485–498.

Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B., & Araujo, M.B. 2011. Consequences of climate change on the tree of life in Europe. *Nature* 470: 531–534.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., & Prentice, I.C. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* 102: 8245–8250.

Thuiller, W., Lavorel, S., Sykes, M.T., & Araújo, M.B. 2006. Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions* 12: 49–60.

Tilman, D. 1997. The Influence of Functional Diversity and Composition on Ecosystem Processes. *Science* 277: 1300–1302.

Tobner, C.M., Paquette, A., Reich, P.B., Gravel, D., & Messier, C. 2014. Advancing biodiversity-ecosystem functioning science using high-density tree-based experiments over functional diversity gradients. *Oecologia* 174: 609–621.

Treut, H. Le, Cubasch, U., Ding, Y., Mauritzen, C., Mokssit, A., Peterson, T., & Prather, M. 2007. Historical Overview of Climate Change Science. In Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M.T. and H.L.M. (ed.), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, UK and New York, USA.

Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E., & Steininger, M. 2003. Remote sensing for biodiversity science and conservation. *Trends in Ecology and Evolution* 18: 306–314.

Ustin, S.L., & Gamon, J.A. 2010. Remote sensing of plant functional types. *The New Phytologist* 186: 795–816.

Valverde-Jimenez, A., & Lobo, J.M. 2007. Threshold criteria for conversion of probability of species presence to either – or presence – absence. *Acta Oecologica* 31: 361–369.

Vilà, M., Carrillo-Gavilán, A., Vayreda, J., Bugmann, H., Fridman, J., Grodzki, W., Haase, J., Kunstler, G., Schelhaas, M.J., & Trasobares, A. 2013. Disentangling Biodiversity and Climatic Determinants of Wood Production. *Plos One* 8: 1–9.

Villar, R., & Merino, J. 2001. Comparison of leaf construction costs in woody species with differing leaf life-spans in contrasting ecosystems. *New Phytologist* 151: 213–226.

Villéger, S., Mason, N., & Mouillot, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89: 2290–2301.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.

van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., & Rose, S.K. 2011. The representative concentration pathways: An overview. *Climatic Change* 109: 5–31.

Wang, K., Franklin, S.E., Guo, X., & Cattet, M. 2010. Remote sensing of ecology, biodiversity and conservation: A review from the perspective of remote sensing specialists. *Sensors* 10: 9647–9667.

Westoby, M., Reich, P., & Wright, I. 2013. Understanding ecological variation across species: area-based vs mass-based expression of leaf traits. *New Phytologist* 199: 322–323.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Warton, D.I., & Westoby, M. 2005. Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography* 14: 411–421.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., & Villar, R. 2004. The worldwide leaf economics spectrum. *Nature* 12: 821–827.

Xie, Y., Sha, Z., & Yu, M. 2008. Remote sensing imagery in vegetation mapping: a review. *Journal of Plant Ecology* 1: 9–23.

Yu, M., Wang, G., Parr, D., & Ahmed, K.F. 2014. Future changes of the terrestrial ecosystem based on a dynamic vegetation model driven with RCP8.5 climate projections from 19 GCMs. *Climatic Change* 127: 257–271.

Zimmermann, N.E., Edwards, T.C., Graham, C.H., Pearman, P.B., & Svenning, J. 2010. New trends in species distribution modelling. *Ecography* 33: 985–989.

Zimmermann, N.E., Yoccoz, N.G., Edwards, T.C., Meier, E.S., Thuiller, W., Guisan, A., Schmatz, D.R., & Pearman, P.B. 2009. Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences of the United States of America* 106: 19723–19728.

.

Chapter 3. Specific leaf area and hydraulic traits explain niche segregation along an aridity gradient in Mediterranean woody species

Abstract

Despite the great interest shown by the scientific community on the role of plant functional traits in plant strategies, community ecology and ecosystem functioning, the way in which they determine species environmental niches remains little understood. Given the potential of niche-traits relationships to contribute developing basic ecology, as well as forest management and climate change adaptation policies, the following questions were addressed: Are traits related with drought resistance adequate to predict species environmental niche in Mediterranean environments? Can the predictor power be increased using combinations of different traits? Are functional traits better related with the limits of the species environmental niche? The environmental niches of 21 Mediterranean species were characterised using Species Distribution Models and regressed against species traits values retrieved from literature. Species leaf traits, mostly Specific Leaf Area (SLA), were highly correlated with species niche characteristics regarding aridity (especially with the more arid limit). Instead hydraulic traits, i.e. the water potential at which a species loses 50% of xylem hydraulic conductivity due to cavitation (PLC_{50}), and species hydraulic safety margins (SM) were better correlated with species arid optimums. Niche predictions improved when SLA was combined with PLC_{50} or SM. The study shows how in the Mediterranean region traits commonly associated with drought responses strongly affect species distribution and consequentlly their environmental niches evidencing the close link between some FT and species niches. By setting the environmental limits of the species distribution range, the proposed approach relies on the physiological limit of a species and, to a certain extent, on the mechanisms behind it, adding robustness and accuracy to predict species distribution and mortality under climate change scenarios. We also introduced new elements for the study of the interplay between the fundamental and the realized niche.

Introduction

Functional Traits (FT) may be defined as the "morpho-physio-phenological" plant attributes that drive species success on the environment (Violle et al. 2007). Despite the great interest on the role of plant FT in plant strategies, community ecology, and ecosystem functioning (Keddy 1992; Westoby et al. 2002; Lavorel et al. 2007), the way in which they determine species environmental niches remains less understood (but see Thuiller et al. 2004; Violle & Jiang 2009; Pollock et al. 2012; Stahl et al. 2014). Whereas species' physiological responses to abiotic factors determine their fundamental niche (Austin et al. 1984; McGill et al. 2006) and consequently their distribution (Woodward & Williams 1987), it is reasonable to hypothesise that a relationship between specific FT and species environmental niche should exist, which may provide insights on the mechanisms governing plant communities assemblage and species distribution (McGill et al. 2006; Westoby & Wright 2006).

The role of FT in determining species establishment in a given ecological space was early underlined by Keddy's (1992) assembly rules, who suggested that environmental filtering eliminates species with unsuitable traits. Many studies have shown that species living in different environments display different trait values. For instance, Specific Leaf Area (SLA) usually decreases with site aridity and nutrient scarcity (Fonseca et al. 2000;Wright et al. 2001; Niinemets 2001) because low SLA are associated with drought resistance and also increase nutrient residence time (Poorter et al. 2009). Similarly, the water potential at which a species loses 50% of xylem hydraulic conductivity due to cavitation (PLC_{50}) tends to be lower in species from arid areas (Maherali et al. 2004; Choat et al. 2012). Besides the observed patterns among species, traits values within species (i.e. intraspecific trait variability) also tend to vary across environments (Jung et al. 2010; Laforest-Lapointe et al. 2014), with specific relationships depending on the traits and species under consideration (Albert et al. 2010). For instance, SLA and wood density (WD) vary in *Nothofagus pumilio* according to temperature and moisture gradients, respectively (Fajardo & Piper 2011).

Some functional traits have been shown to co-vary, giving origin to global spectrums of traits (Wright et al. 2004; Chave et al. 2009; Reich 2014). Indeed, the FT value of a species reflects adaptive “decisions” on where to allocate resources, with consequences in terms of growth and survival, but also represents trade-offs between plant strategies (Wright et al. 2004; Reich 2014). Correlations among FT may reflect causality or coordination between FT (Reich et al. 2003). An example of causal link is that species photosynthetic rate largely depends on photosynthetic enzymes concentration in leaves, i.e. their leaf nitrogen content. Instead, coordination reflects an improvement of species response when two or more specific traits that appear to be mechanistically independent co-vary (Reich et al., 2003). For instance, in tropical dry forests, xylem cavitation resistance in evergreen species coordinate with leaf turgor loss point and modulus of elasticity (Markesteijn et al. 2011). Coordination among FT may imply that different combinations of traits may be adopted by species to maximize their performance in a given environment (Maire et al. 2013; Manzoni 2014).

Since FT determine the success of a species in a given environment they should affect as well the species’ environmental niche. However, it is not clear what specific characteristics of the niche will be better reflected by species traits and, in particular, whether FT will reflect mostly the optimal conditions or the environmental limits over which a species can strive. Indeed, several studies suggested that along a gradient, competition mostly affect species performance on the high-resource end part of the gradient, whereas their low-resource boundary would be mostly influenced by species physiological tolerance (Brown et al. 1996; Normand et al. 2009). Cornwell & Ackerly (2010) observed that SLA scaled with species abundance across different plant communities in coastal California, suggesting that SLA accurately represented species optimal conditions in those environments. However, species are not always abundant at their physiological optimal because biotic interactions affect species realized niche (McGill et al. 2006). For instance, *Pinus sylvestris* is commonly displaced from its optimal temperature location due to competition processes (Rehfeldt et al. 2002). Thus, the accuracy and reliability of studies in land-plant ecology (Westoby & Wright 2006), community ecology (McGill et al. 2006), or climate change impacts (Guisan & Thuiller 2005) would benefit from a deeper understanding of how FT, or combinations of FT, relate with their niche characteristics e.g. the optimal value or the upper and lower limits.

Species Distribution Models (SDM) is a well-established method in ecology to establish species niche and to address theoretical and applied issues (Higgins et al. 2012). SDM are based on species occurrences data and the environmental values at those locations allowing to predict species distribution across the territory (Guisan & Zimmerman 2000). Caution must be put in interpreting the results as their interpretation requires knowledge of underlying ecological processes (Guisan & Thuiller 2005; Elith & Leathwick 2009), nevertheless they have been used to answer a number of hypothesis including e.g. niche stability and evolution (Pearman et al. 2010).

The objective of this study was to determine the relationship between several FT and the environmental niche of 21 woody species in the Mediterranean region, where water availability is the main limiting factor for plants. We hypothesize that: i) the environmental niche of Mediterranean species is better predicted by traits related to drought resistance rather than by traits related to other functions; ii) since coordination among traits implies that traits may contribute to the performance of a species independently, or at least partially independently, from other traits we expect that predictions of species environmental niches will improve when a combination of traits is used rather than a single trait; iii) finally, since niche characteristics are not equally set by competition and species physiological tolerance, we also expect that drought resistance traits would be better correlated with the arid limit of species rather than with other niche characteristics as the optimum or the high-resource limits (i.e. the humid limit).

Materials and Methods

Study area and datasets

The study area covered the Spanish continental territory, located between 36º N and 44ºN of latitude, and between 10º W and 3 º E longitudes. The main Koppen climatic domains are Dry and Temperate, with annual mean temperatures ranging from ~3 to ~17ºC and precipitations from ~300 to ~2200 mm/year (Chazarra 2011). Biogeographically more than three quarters of the territory belong to the Mediterranean region being conifers, and sclerophyllous shrubs and forest the main vegetation types (Rivas-Martínez 1987).

Species distribution data (i.e. presence and absence) were obtained from the Third Spanish National Forest Inventory (IFN3) (http://www.magrama.gob.es/; Direccion General de Conservacion de la Naturaleza 2006). IFN3 includes periodical surveys (every ~10 years) of the whole forested area of Spain for reporting exhaustive information about stand composition, structure, and productivity. IFN3 has a regular sampling design with one sample plot every ~1km^2 accounting for more than 90 000 plots in total. We selected 21 of the most abundant Mediterranean woody species from ten different families and six functional groups (Table 3.1). For all selected species the Spanish environmental range represents a substantial portion of the variation across the overall environmental (climate) species' range (i.e., species such as *Quercus robur* and *Fagus sylvatica* were excluded).

WorldClim data were downloaded for the area of interest (http://www.worldclim.org/). The dataset includes 19 bioclimatic variables at a resolution of 30 arc-seconds (Hijmans et al. 2005). A soil pH dataset at a resolution of 5 km^2 was downloaded from the European Soil Portal (http://eusoils.jrc.ec.europa.eu/, Panagos et al. 2012). The number of potential explanatory variables was reduced to limit collinearity and obtain more parsimonious models (Bolker 2008). Variables were selected based on their known ecological relevance and pairwise correlations (Dormann et al. 2013). At the end of the process, the variables selected were Annual Precipitation (AP), Mean Annual Temperature (MAT), Precipitation of the Driest Quarter (PDQ), and pH.

Niche models

SDM were generated for each species using the presence and absence dataset and the selected environmental variables. Absences were randomly selected until reaching three times the number of presences because some methods to evaluate SDM usually outperforms at low prevalence (e.g. Kappa coefficient, Valverde-Jimenez & Lobo 2007). The algorithm used to build SDM were Generalized Additive Models (GAM) since it is known not to constrain species response curves to a predetermined shape (Austin 2007).

Goodness of fit of the models was evaluated by the deviance explained (D^2), while their accuracy was assessed after a 5 k-fold cross validation by the Area Under the Curve (AUC) and Kappa coefficient. To convert predicted probabilities into presences and absences the threshold selected was that which minimized the difference between specificity and sensibility (Valverde-Jimenez & Lobo 2007).

Niche characteristics

Niche characteristics were calculated after projecting SDM over continental Spain and associating each predicted location with its occurrence probability and its environmental value (see Fig. 3.1 for details). Thus, for each species and environmental variable a set of niche characteristics were obtained: a) the value at which the probability to find the species was highest (i.e. the optimum), b) the lowest and highest values at which the species can be found (i.e. the minimum and maximum, respectively), c) and the difference among those limits (i.e. the range). In addition, in order to integrate in the analysis the joint effect of the variables used in the SDM, niche characteristics were also calculated for a latent variable (hereafter called aridity) obtained from the first axis of a Principal Component Analysis of the four selected environmental variables (first axis explained 60 % of variance, and loadings for each variable were 0.49, -0.56, -0.59, 0.32 for AMT, AP, PDQ, and pH, respectively).

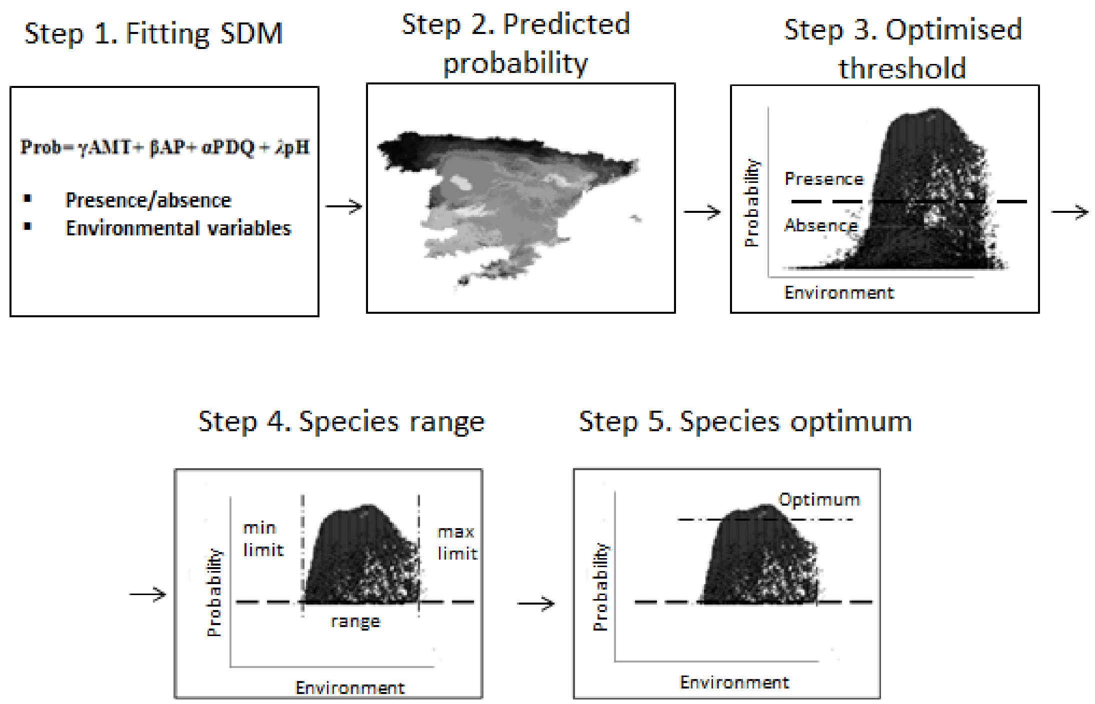


Figure 3.1: Work flow to obtain niche characteristics. Step 1. For each species a SDM was fitted using the selected environmental variables in order to obtain the most accurate models. Step 2 and 3. The SDM was later projected into the Spanish territory and a threshold was set to remove locations where species probability was so low that it was predicted to not occur (i.e. predicted absences). Step 3. For each remaining location both presence probability and environmental variables were associated (i.e. each environmental variables used in the SDM and the latent variable, i.e. aridity). Step 4. Minimum and maximum limits were obtained selecting the 1st and 99th percentiles of environmental values, respectively. The range was calculated as the difference between both limits. Step 5. The optimum was calculated as the mean environmental value of the locations with the highest probability (i.e. locations with probability of occurrence over the 97th percentile).

Species functional traits

A set of 14 morphological and physiological FT for the 21 study species were extracted from the literature (see Appendix 3.1 for sources used). Leaf level traits included maximum photosynthetic rate per unit mass (A_{mass}) and per unit area (A_{area}), maximum stomatal conductance (G_{max}), intrinsic water use efficiency (WUE), leaf area (LA), specific leaf area (SLA), and nitrogen content per unit of mass (N_{mass}). Traits related with plant hydraulics and cavitation resistance included Minimum Leaf Water Potential (MLWP, leaf water potential measured at midday during the driest period of the year), the water potential at which 50% of hydraulic conductivity is lost (PLC_{50}), and hydraulic safety margin (SM, the difference between MLWP and PLC_{50}). Maximum height (MH), seed dry weight (SDW), and wood density (WD), which are usually related with competition and life history strategies, were also included. When more than one value was found for a FT of a species, the average of the value was used for further analysis.

Data analysis

Trait data normality was checked using Shapiro-Wilk normality tests, and we transformed data when it ensured normality (i.e. log transformation for A_{mass}, MH, SDW, SM, and SLA, and root square transformation for LA). The independency among traits was assessed by pairwise correlations and a PCA of FT.

We tested single correlations between FT values and niche characteristics among species by linear regressions using *P* values and Pearson correlation coefficient to test the statistical significance and strength of the relationships, respectively (Warton et al. 2006). The combined effects of multiple traits on niche characteristics were tested using multiple linear regressions. Because gymnosperms and angiosperms greatly differ in their wood anatomy and other relevant attributes (Brodribb et al. 2012; Carnicer et al. 2013), multiple regressions were performed including a dichotomic variable to assess the phyla effect. Traits were standardized to assess their weights on regressions, and the Akaike Information Criterion (AIC) was used as a measure of model performance in multi-model selection (Burnham & Anderson 1998). All analyses were conducted using R software (version 3.2.0., R Development Core Team 2015, www.R-project.org).

Results

Species Distribution Models

The accuracy of the SDM were satisfactory (Fielding & Bell 1997) being *Quercus pubescens* the species in which SDM performed best and *Erica arborea* the one in which they performed worst (Table 3.1). Considering all species, mean D^2 was 39% (min 20%, and max 66%), mean AUC was 0.88 (ranging from 0.79 to 0.96) and mean Kappa was 0.56 (ranging from 0.37 to 0.8).

Table 3.1: Species Distribution Models performance. Calibration and accuracy parameters for each species, including Deviance explained (D^2), Kappa, and the Area Under the Curve (AUC).

Species	Number of presence	D^2	Kappa	AUC
Acer monspessulanum	1445	0.31	0.47	0.85
Arbutus unedo	8192	0.29	0.46	0.85
Erica arborea	9168	0.2	0.37	0.79
Erica multiflora	3171	0.46	0.67	0.92
Juniperus oxycedrus	20 694	0.41	0.57	0.9
Juniperus phoenica	9226	0.4	0.57	0.9
Olea europaea	7369	0.48	0.63	0.93
Pinus halepensis	16 386	0.62	0.76	0.96
Pistacia lentiscus	9172	0.51	0.66	0.93
Prunus spinosa	7443	0.25	0.42	0.83
Pistacia terebinthus	2565	0.27	0.47	0.84
Quercus faginea	14 885	0.23	0.42	0.82
Quercus pubescens	5040	0.66	0.8	0.96
Quercus pyrenaica	9829	0.4	0.59	0.9
Quercues suber	5694	0.49	0.66	0.93
Rosmarinus officinalis	17 851	0.44	0.62	0.92
Quercus coccifera.	12 311	0.44	0.62	0.91
Rhamnus alaternus	9703	0.35	0.52	0.88
Phyllerea latifolia	3245	0.39	0.55	0.9
Pinus pinea	5276	0.41	0.6	0.9
Quercus ilex	42 689	0.25	0.45	0.81

Functional Traits

Pairwise comparisons between traits showed that leaf traits were correlated among each other, whereas significant correlations among hydraulic traits were not always present (see Appendix 3.2). There were no significant correlations between leaf and hydraulic traits, but some of them were related with life history traits (i.e. WD, was correlated with A_{area}, G_{max}, and N_{mass};, and MH was correlated with LA, MLWP and PLC_{50}). PCA performed on species FT showed similar results. Leaf traits were the largest contributors to the first axis (40% of variance explained), whereas the second axis was mainly determined by hydraulic traits and maximum height (20% of variance explained, Fig. 3.2).

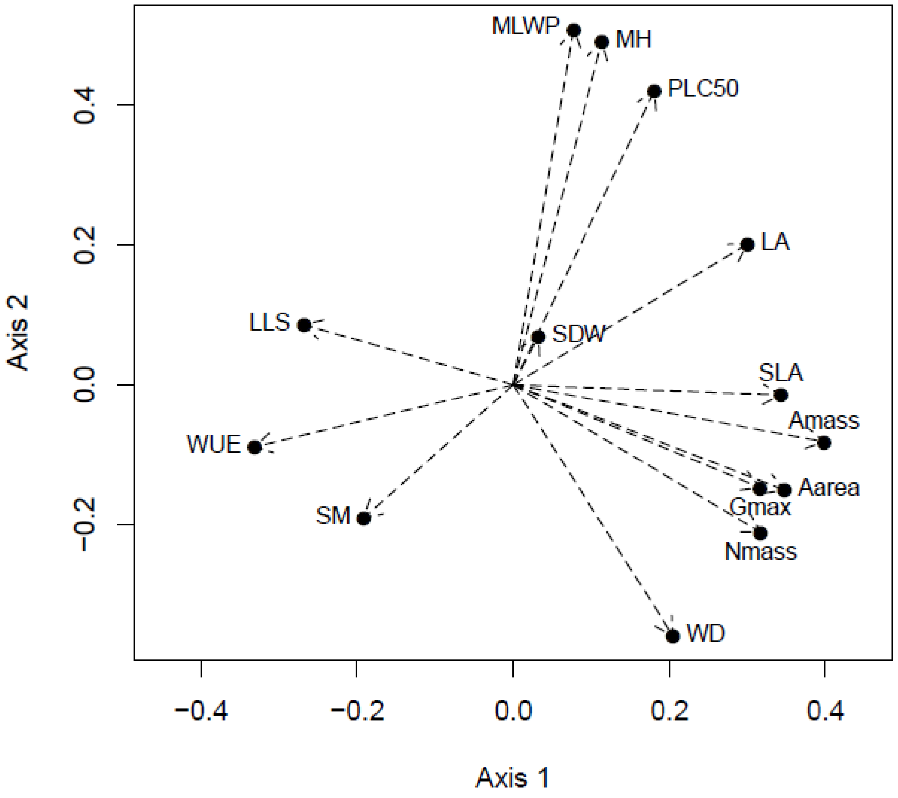


Figure 3.2: Principal Component Analysis of plant functional traits, including: maximum photosynthetic rate per unit of mass (A_{mass}), and per unit of area (A_{area}), maximum stomata conductance (G_{max}), intrinsic Water Use Efficiency (WUE), Leaf Area (LA), Specific Leaf Area (SLA), Leaf LifeSpan, (LLS), nitrogen content per unit of mass (N_{mass}), Minimum Leaf Water Potential (MLWP), Maximum Height (MH), Seed Dry Weight (SDW), water potential at which 50% of hydraulic conductivity is lost (PLC_{50}), hydraulic safety margin (SM), and wood density

(WD). The perpendicularity of hydraulic and leaf traits shows their relative independence. The first axis was mostly determined by leaf traits and explained 40 % of the total variance; the second axis explained 20% of the variance%, and was mostly explained by hydraulic traits.

Functional traits and niche characteristics

Single traits

FT showed correlations with the niche characteristics computed for each environmental variable considered (focus is given on aridity, i.e. the latent variable obtained from the PCA, since it integrates the effects of precipitation and temperature). However, not all of the fourteen FT were equally correlated with the niche characteristics of species being SLA almost always the traits most strongly related (Table 3.2). All leaf traits, except A_{area}, significantly scaled with niche aridity values. Thus, species with more arid distribution had lower SLA, N_{mass}, A_{mass}, G_{max}, and LA, and greater LLS and WUE (Fig. 3.3). The hydraulic traits that displayed the best correlations with the aridity niche were PLC_{50} and SM (Table 3.2), while MLWP was not correlated. SDW, MH, and WD did not show significant correlations with the aridity niche of species, and only MH and WD appeared to be related with the aridity niche when the phyla effect was considered. Overall, similar patterns were observed when analysing traits correlations with the niche characteristics of the other environmental variables, such as AP, PDQ, and AMT (i.e. traits values that decreased with aridity, also decreased with precipitations and increased with temperatures, see Appendix 3.2 for the complete correlation matrix).

Leaf traits were most strongly correlated with species maximum aridity (i.e. the most arid conditions that species reach), whereas hydraulic traits were best correlated with species optimum (i.e. the aridity conditions that species are more likely to occupy). None of the considered FT showed a correlation with species aridity range, but some traits were correlated with the niche ranges of other environmental variables e.g. WUE was inversely correlated with the annual precipitation range or SLA with the annual mean temperature range (see Appendix 3.3).

Trait combinations

Multiple regression analysis showed that SLA combined with traits perpendicular to it (Fig. 3.2) performed better than SLA alone in explaining species niche characteristics (Table 3.3). Best-fitting models for the optimum and minimum aridity niche characteristics were obtained when combining SLA with SM, while the best model for the maximum of aridity was a combination of SLA with PLC_{50}. SLA weights on regressions were almost always greater than the other traits, except for species optimum. Combinations with WD or MLWP did not increase the goodness of fit of the models. In addition, separating gymnosperms from angiosperms did not enhance model performance (data not shown).

Table 3.2: Pearson correlation coefficient between functional traits and aridity niche characteristics.* significant relationships (P values < 0.05). Values between brackets report significant correlation coefficients when only angiosperms were considered. Abbreviations as in Fig. 2.

Aridity niche	Leaf traits								Hydraulic traits			Life history traits		
	Log(SLA)	LLS	sqrt(LA)	N_{mass}	Log(A_{mass})	A_{area}	G_{max}	WUE	PLC_{50}	MLWP	Log(SM)	WD	Log(MH)	Log(SDW)
Opitimum	-0.73*	0.39	-0.5*	-0.36	-0.66*	-0.38	-0.52*	0.52*	-0.59*	-0.18	0.74*	-0.14	-0.31	-0.19
Minimum	-0.65*	0.62*	-0.37	-0.37	-0.56*	-0.29	-0.54*	0.64*	-0.48	-0.19	0.57*	-0.17 [0.38*]	-0.14	0.08
Maximum	-0.8*	0.59*	-0.61*	-0.5*	-0.73*	-0.44	-0.62*	0.67*	-0.52*	-0.4	0.59*	-0.17	-0.31 [-0.47*]	-0.24
Range	-0.26	0.42	0.01	-0.1	-0.17	-0.02	-0.27	0.38	-0.3	0.04	0.44	-0.1	0.1	0.38

Table 3.3: Δ AIC for models of niche characteristics as a function of functional traits (model with smaller values are preferable). Models including only SLA as the explanatory variable (first column) are compared with models combining SLA with PLC_{50}, WD, SLA SM, and MLWP (columns 2 to 5, respectively). Traits are standardized. D^2 is the deviance explained. Abbreviations as in Fig. 2.

Aridity niche	SLA	Traits combined with SLA			
		+ PLC_{50}	+ WD	+ SM	+ MLWP
Optimum	7.4	2.7	9.4	0	9.3
Minimum	1.5	0.2	2.1	0	2.3
Maximum	6.1	0	7.2	4	3.2

Note: equations of the best models

Optimum= -0.44*SLA + 0.55* SM; $D^2 = 69\%$

Minimum = -0.71 *SLA +0.28*SM; $D^2 = 74\%$

Maximum = -0.67*SLA -0.41* PLC_{50}; $D^2 = 78\%$

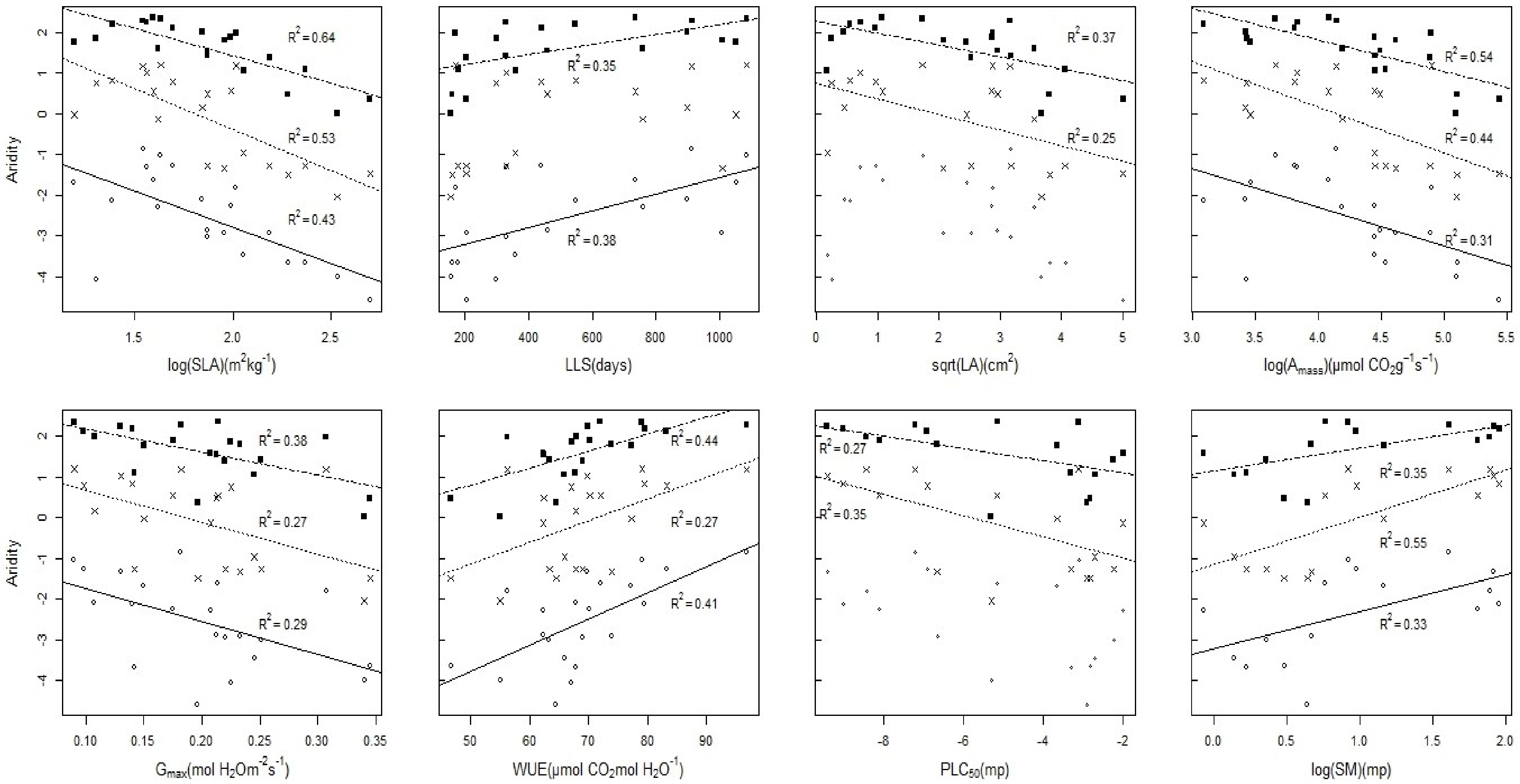


Figure 3.3: Scatterplot and regression lines of different characteristics of the species' aridity niche as a function of species functional traits. Only the significant regression lines are shown (*P* values < 0.05). Crosses represent species optimum, and filled squares and open circles the species maximum (more arid) and minimum (less arid) limits, respectively. The variance explained is also given for each regression line. Abbreviations as in Fig. 2.

Discussion

The results of the present study highlight the close link between FT and species niches, confirming our first hypothesis and demonstrating how in the Mediterranean region traits commonly associated with drought responses (i.e. SLA, PLC_{50}, and SM, Micco & Aronne 2012; Nardini et al. 2014) strongly affect species distribution and consequentlly their environmental niches. Such finding was possible thanks to the use of an appraoch that combined trait based ecology with niche modelling, highlighting the potential of functional traits to predict species environmental niches and suggesting that an approach based on niche-trait relationships could improve our understanding of how traits govern species niche (McGill et al. 2006; Westoby & Wright 2006; Violle & Jiang 2009). Furthermore, by setting the environmental limits of the species distribution range, the approach used relies on the physiological limit of a species and, to a certain extent, on the mechanisms behind it, adding robustness and accuracy to predict species distribution and mortality under climate change scenarios (Williams et al. 2008).

Relatively few previous studies have analysed the relationships between species environmental niches and FT, but their results were generally promising. For instance, Maharjan et al. (2011) observed that the optimum of rainforest species along a rainfall gradient scaled with wood density of the different species. Thuiller et al. (2004) observed that in the Cape Florist Region species from Leucadendron taxa that occupy more arid niches had lower leaf areas than those with more humid niches. Stahl et al. (2014), observed that WD, SDW, and MH of North American flora were related with species distribution limits regarding temperature and humidity.

Of all traits considered, SLA proved to be the one with the strongest ability to explain the distribution of species along the aridity gradient. It is perhaps not surprising for SLA to have a key role in setting species niche in arid environments since SLA has been associated with several important aspects of plant drought resistance. Low SLA values are mainly consequence of high leaf density, which is acquired by increasing concentration of lignin and structural carbohydrates in leaves (Poorter et al. 2009). Thus, SLA is considered a good index for leaf sclerophylly (Groom & Lamont 1999): a tissue reinforcement that prevents mechanical cell damages during dry events and thus enhances leaf wilting resistance, which extends leaf photosynthesis under drought stress (Micco & Aronne 2012). This result is consistent with global patterns showing that species from dry and hot environments (low water availability) tend to have low SLA values (Niinemets 2001; Wright et al. 2005).

SLA is known to be causally linked with other leaf traits and to reflect trade–offs between construction and maintenance costs of leaves, and duration of photosynthetic returns from those investments (Reich et al. 1997; Niinemets 2001; Wright et al. 2004). It is thus not simple to separate the individual contributions of single traits to trait-environment relationships, and rather than observing these traits separately they should be viewed as a constellation of traits, most of which are known to be involved in drought resistance mechanisms (Markesteijn et al. 2011; Nardini et al. 2014). Low SLA leaves are known to also have longer leaf life span, higher N_{mass} and lower A_{mass} and stomatal conductance (Wright et al. 2004). It is thus not surprising that also these leaf traits were correlated with the environmental niche in our study. The observed increment of WUE with aridity is consistent with species from drier sites having greater photosynthetic rates for a given stomatal conductance (Dudley 1996), which is part of a water saving strategy that involves N use efficiency (Wright et al. 2001). LA also decreased with aridity, most likely because it facilitates energy exchange and prevents excessive leaf temperature (Givnish 1987; Thuiller et al. 2004).

Although SLA was the FT that showed the highest degree of correlation with the aridity niche (and in general with the overall environmental niche; see Appendix 3), other functional traits, which did not co-vary with SLA, explained part of the variability in species aridity niche. Results were in agreement with studies that report how species from arid places tend to have a greater resistance to cavitation (i.e. low PLC_{50}, Maherali et al. 2004; Choat et al. 2012): low PLC_{50} allows species to maintain hydraulic functionality in dry conditions and thus to sustain leaf gas exchange, potentially improving their performances and survival (note however that drought-induced mortality mechanisms are complex stressors McDowell 2011; Klein 2015). In addition, our results showed that species occupying more arid niches also maintain wider hydraulic safety margins, which is common in plants living in water limited environments, including the Mediterranean (Vilagrosa et al. 2012). This finding would suggest a higher resilience of drought adapted species to climate change. However, species with a higher WUE and a lower SLA were found to strive over a narrower range of annual precipitations and annual mean temperatures respectively, suggesting a lower intrinsic adaptation potential to climate change by those species that are mostly specialized for warm and dry environments.

As initially hypothesized, our results also showed that trait combinations (in our case SLA with PLC_{50} or SM) improved the ability to explain the different characteristics of species aridity niche and highlight the complementarity among mechanisms to deal with drought in the Mediterranean. In addition, despite the known coordination between leaf transpiration and xylem water transport (Martinez-Vilalta et al. 2014), our results showed that both kind of traits were poorly correlated, in agreement with (Li et al. 2015). All these results suggest that leaf and hydraulic mechanisms may act somewhat independently. Brodribb et al. (2003) already observed that leaf wilting point and PLC_{50} are not necessarily related. Thus, not only increasing leaf wilting resistance (i.e. low SLA) but also hydraulic adjustments during drought periods would enhance species probability to reach more arid locations. In fact, species ability to avoid or resist embolism, and to compensate or repair embolized conduits, have been suggested as complementary strategies driving species performance in the Mediterranean (Nardini et al. 2014). Therefore, specific combinations of traits may be adopted by species to maximize their performance under a given environment (Maire et al. 2013; Manzoni 2014). Although they were not considered in this study, rooting habits are likely to be an important component to understanding niche segregation over aridity gradients. E.g. rooting depth gives access to water stored in deeper soil layers richer in water, while superficial roots give access to sporadic and light rain events that may occur during summer (Mereu et al. 2009). Other roots traits as specific root length also seem to play a role in plant water relations (Burgess 2006; Nardini et al. 2014).

Finally, leaf traits were better correlated with the arid limit of species niche rather than with the niche optimum. Similarly to our results, Stahl et al. (2014) also observed that some traits of North America flora are related with species' niche limits but not with their optimums. As also other authors suggested, we add evidence to the idea that leaf traits and possibly physiology set the environmental limit over which species can strive, while other traits are influencing species performance at their niches optimums. Some studies have indeed suggested that competition plays a major role at the high-resource end of species distributions, whereas physiological tolerance sets the limits at the low-resource end (Brown et al. 1996; Normand et al. 2009). Interestingly, and despite their known role in drought resistance, hydraulic traits were best correlated with optimal niche conditions, again suggesting that drought resistance is multifaceted and that hydraulic traits per se are not enough to describe the species tolerance limits to drought, in agreement with previous results in Mediterranean ecosystems (Miranda et al. 2010). Our results also showed that species' ranges do not seem to be constrained by any of the traits considered in this study, likely evidencing that species environmental ranges are more related to trait variability or plasticity within species (not considered here) than with trait averages (Sultan 2000).

Conclusions

Environmental filtering in the Mediterranean mostly affects leaf-level traits (mainly SLA) and, secondarily, hydraulic traits such as SM or PLC_{50}, whereas traits as MH or WD appeared to be less important. The relevant FT show a greater influence on setting the low resource limit of species' environmental niche (rather than its optimum), reinforcing the idea that such limit is mostly determined by physiological process, while interaction among species have a greater role in the rest of the niche. However, environmental niches are better predicted by combinations of different FTs, rather than any FT alone.

Future studies including traits more commonly associated with interspecific competition are likely to increase our understanding on species distribution with practical consequences for forest management and climate change adaptation policies. Growth of trait databases both in terms of species accounted for and number of traits together with accessibility to forest inventories would further expand the potential of combining species distribution models with trait-based ecology. In addition, since different aspects can affect the observed distribution of species also at scales different than the one used in this study, including sink-source process (Pearman et al. 2008), species non-equilibrium with the environment (Araújo & Pearson 2005) and extreme events (Zimmermann et al. 2009), a multi-level characterization of the relationships between niche attributes and FT at different spatial scales may help to better understand these processes.

Bibliography

Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S., & Lavorel, S. 2010. A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Functional Ecology* 24: 1192–1201.

Araújo, M., & Pearson, R. 2005. Equilibrium of species' distributions with climate. *Ecography* 28: 693–695.

Austin, M. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling* 200: 1–19.

Austin, M.P., R.B.Cunningham, & P.M.Fleming. 1984. New approaches to direct gradient analysis using environmental scales statistical curve-fitting procedure. *Vegetation* 55: 11–27.

Bolker, B. 2008. *Ecological models and data in R*. Princeton University Press, New Jersey, USA.

Brodribb, T.J., Holbrook, N.M., Edwards, E.J., & Gutiérrez, M. V. 2003. Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant, Cell and Environment* 26: 443–450.

Brodribb, T.J., Pittermann, J., & Coomes, D. a. 2012. Elegance versus Speed: Examining the Competition between Conifer and Angiosperm Trees. *International Journal of Plant Sciences* 173: 673–694.

Brown, J.H., Stevens, G.C., & Kaufman, D.M. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* 27: 597–623.

Burgess, S.S.O. 2006. Measuring transpiration responses to summer precipitation in a Mediterranean climate: A simple screening tool for identifying plant water-use strategies. *Physiologia Plantarum* 127: 404–412.

Burnham, K.P., & Anderson, D.R. 1998. *Model Selection and Multimodel Inference*. Springer-Verlag, New York,USA.

Carnicer, J., Barbeta, A., Sperlich, D., Coll, M., & Peñuelas, J. 2013. Contrasting trait syndromes in angiosperms and conifers are associated with different responses of tree growth to temperature on a large scale. *Frontiers in Plant Science* 4: 1–19.

Chave, J., Coomes, D., & Jansen, S. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–66.

Chazarra, A. 2011. *Atlas Climático Ibérico*. Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid,SP.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., & Zanne, A.E. 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491: 752–5.

Cornwell, W.K., & Ackerly, D.D. 2010. A link between plant traits and abundance: evidence from coastal California woody plants. *Journal of Ecology* 98: 814–821.

Direccion General de Conservacion de la Naturaleza. 2006. *Tercer Inventario Forestal Nacional 1997-2006*. Ministerio de Medio Ambiente, Madrid, SP.

Dormann, C.F.C., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., Mcclean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., & Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 27–46.

Dudley, S. 1996. Differing selection on plant physiological traits in response to environmental water availability: a test of adaptive hypotheses. *Evolution* 50: 92–102.

Elith, J., & Leathwick, J.R. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics* 40: 677–697.

Fajardo, A., & Piper, F.I. 2011. Intraspecific trait variation and covariation in a widespread tree species (Nothofagus pumilio) in southern Chile. *New Phytologist* 189: 259–271.

Fielding, A., & Bell, J. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38–49.

Fonseca, C.R., Overton, J.M., Collins, B., & Westoby, M. 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology* 88: 964–977.

Givnish, T.J. 1987. Comparative Studies of Leaf Form : Assessing the Relative Roles of Selective Pressures and Phylogenetic Constraints. *New Phytologist* 106: 131–160.

Groom, P.K., & Lamont, B.B. 1999. Which common indices of sclerophylly best reflect differences in leaf structure? *Ecoscience* 6: 471–474.

Guisan, A., & Thuiller, W. 2005. Predicting species distribution: Offering more than simple habitat models. *Ecology Letters* 8: 993–1009.

Guisan, A., & Zimmerman, N.E. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186.

Higgins, S.I., O'Hara, R.B., & Romermann, C. 2012. A niche for biology in species distribution models. *Journal of Biogeography* 39: 2091–2095.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., & Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., & Muller, S. 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology* 98: 1134–1140.

Keddy, P. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3: 157–164.

Klein, T. 2015. Drought-induced tree mortality: from discrete observations to comprehensive research. *Tree Physiology* 35: 225–228.

Laforest-Lapointe, I., Martínez-Vilalta, J., & Retana, J. 2014. Intraspecific variability in functional traits matters: Case study of Scots pine. *Oecologia* 175: 1337–1348.

Lavorel, S., Díaz, S., Cornelissen, J.H.C., Garnier, E., Harrison, S.P., Mcintyre, S., Pausas, J.G., Catherine, N.P., Carlos, R., Roumet, C., Natalia Pérez-harguindeguy, & Urcelay, C. 2007. Plant functional types: are we getting any closer to the Holy Grail? In Canadell, J.G., Pataki, D.E., & Pitelka, L.F. (eds.), *Terrestrial Ecosystems in a Changing World*, pp. 149–160. Springer-Verlag, Berlin, Heidelberg,DE.

Li, L., McCormack, M.L., Ma, C., Kong, D., Zhang, Q., Chen, X., Zeng, H., Niinemets, Ü., & Guo, D. 2015. Leaf economics and hydraulic traits are decoupled in five species-rich tropical-subtropical forests. *Ecology Letters* 18: 899–906.

Maharjan, S.K., Poorter, L., Holmgren, M., Bongers, F., Wieringa, J.J., & Hawthorne, W.D. 2011. Plant functional traits and the distribution of West African rain forest trees along the rainfall gradient. *Biotropica* 43: 552–561.

Maherali, H., Pockman, W., & Jackson, R. 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* 85: 2184–2199.

Maire, V., Gross, N., Hill, D., Martin, R., Wirth, C., Wright, I.J., & Soussana, J.F. 2013. Disentangling Coordination among Functional Traits Using an Individual-Centred Model: Impact on Plant Performance at Intra- and Inter-Specific Levels. *Plos One* 8: 1–16.

Manzoni, S. 2014. Integrating plant hydraulics and gas exchange along the drought-response trait spectrum. *Tree Physiology* 34: 1031–1034.

Markesteijn, L., Poorter, L., Paz, H., Sack, L., & Bongers, F. 2011. Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell and Environment* 34: 137–48.

Martinez-Vilalta, J., Poyatos, R., Aguadé, D., Retana, J., & Mencuccini, M. 2014. A new look at water transport regulation in plants. *New Phytologist* 204: 105–115.

McDowell, N.G. 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology* 155: 1051–1059.

McGill, B., Enquist, B., Weiher, E., & Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21: 178–185.

Mereu, S., Salvatori, E., Fusaro, L., Gerosa, G., Muys, B., & Manes, F. 2009. A whole plant approach to evaluate the water use of mediterranean maquis species in a coastal dune ecosystem. *Biogeosciences Discussions* 6: 2599–2610.

Micco, V. De, & Aronne, G. 2012. Morpho-anatomical traits for plant adaptation to drought. In Aroca, R. (ed.), *Plant Responses to Drought Stress*, pp. 37–61. Springer Berlin Heidelberg, Berlin, Heidelberg, DE.

Miranda, J.D.D., Padilla, F.M., Martínez-Vilalta, J., & Pugnaire, F.I. 2010. Woody species of a semi-arid community are only moderately resistant to cavitation. *Functional Plant Biology* 37: 828–839.

Nardini, A., Lo Gullo, M. a., Trifilò, P., & Salleo, S. 2014. The challenge of the Mediterranean climate to plant hydraulics: Responses and adaptations. *Environmental and Experimental Botany* 103: 68–79.

Niinemets, Ü. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* 82: 453–469.

Normand, S., Treier, U. a., Randin, C., Vittoz, P., Guisan, A., & Svenning, J.-C. 2009. Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. *Global Ecology and Biogeography* 18: 437–449.

Panagos, P., Van Liedekerke, M., Jones, A., & Montanarella, L. 2012. European Soil Data Centre: Response to European policy support and public data requirements. *Land Use Policy* 29: 329–338.

Pearman, P.B., D’Amen, M., Graham, C.H., Thuiller, W., & Zimmermann, N.E. 2010. Within-taxon niche structure: Niche conservatism, divergence and predicted effects of climate change. *Ecography* 33: 990–1003.

Pearman, P., Guisan, A., Broennimann, O., & Randin, C.F. 2008. Niche dynamics in space and time. *Trends in Ecology & Evolution* 23: 149–158.

Pollock, L.J., Morris, W.K., & Vesk, P. a. 2012. The role of functional traits in species distributions revealed through a hierarchical model. *Ecography* 35: 716–725.

Poorter, H., Niinemets, U., Poorter, L., Wright, I.J., & Villar, R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *The New Phytologist* 182: 565–88.

Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A., & Milyutin, L.I. 2002. Intraspecific responses to climate in Pinus sylvestris. *Global Change Biology* 8: 912–929.

Reich, P. 2014. The world-wide "fast–slow"plant economics spectrum: a traits manifesto. *Journal of Ecology* 102: 275–301.

Reich, P.B., Walters, M.B., & Ellsworth, D.S. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America* 94: 13730–13734.

Reich, P., Wright, I., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M., & Walters, M. 2003. The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences* 164: 143–164.

Rivas-Martínez, S. 1987. *Memoria del mapa de series de vegetación de España*. Ministerio de Agricultura Pesca y Alimentación, Madrid,SP.

Stahl, U., Reu, B., & Wirth, C. 2014. Predicting species ' range limits from functional traits for the tree flora of North America. *Proceedings of the National Academy of Sciences of the United States of America* 111: 13739–13744.

Sultan, S.E. 2000. Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science* 5: 537–542.

Thuiller, W., Lavorel, S., Midgley, G., Lavergne, S., & Rebelo, T. 2004. Relating plant traits and species distributions along bioclimatic gradients for 88 Leucadendron taxa. *Ecology* 85: 1688–1699.

Valverde-Jimenez, A., & Lobo, J.M. 2007. Threshold criteria for conversion of probability of species presence to either – or presence – absence. *Acta Oecologica* 31: 361–369.

Vilagrosa, A., Chirino, E., Peguero-Pina, J.., Barigah, T.S., Cochard, H., & Gil-Pelegrín, E. 2012. Xylem Cavitation and embolism in plants in water -limited ecosystems. In Aroca, R. (ed.), *Plant Responses to Drought Stress*, pp. 63–109. Springer Berlin Heidelberg, Berlin, Heidelberg, DE.

Violle, C., & Jiang, L. 2009. Towards a trait-based quantification of species niche. *Journal of Plant Ecology* 2: 87–93.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.

Warton, D.I., Wright, I.J., Falster, D.S., & Westoby, M. 2006. Bivariate line-fitting methods for allometry. *Biological reviews of the Cambridge Philosophical Society* 81: 259–91.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P. a., & Wright, I.J. 2002. Plant ecological strategies : Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.

Westoby, M., Reich, P., & Wright, I. 2013. Understanding ecological variation across species: area-based vs mass-based expression of leaf traits. *New Phytologist* 199: 322–323.

Westoby, M., & Wright, I.J. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* 21: 261–268.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A. a, & Langham, G. 2008. Towards an Integrated Framework for Assessing the Vulnerability of Species to Climate Change. *Plos Biology* 6: 2621–2626.

Woodward, F., & Williams, B. 1987. Climate and plant distribution at global and local scales. *Vegetatio* 69: 189–197.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Warton, D.I., & Westoby, M. 2005. Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography* 14: 411–421.

Wright, I., Reich, P., & Westoby, M. 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high-and low-rainfall and high-and low-nutrient habitats. *Functional Ecology* 15: 423–434.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., & Villar, R. 2004. The worldwide leaf economics spectrum. *Nature* 12: 821–827.

Zimmermann, N.E., Yoccoz, N.G., Edwards, T.C., Meier, E.S., Thuiller, W., Guisan, A., Schmatz, D.R., & Pearman, P.B. 2009. Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences of the United States of America* 106: 19723–19728.

Supporting Information

Appendix 3.1: Species trait values used and data sources

Appendix 3.2: Pairwise correlation matrix among functional traits

Appendix 3.3: Correlation matrix among functional traits and species niche

Appendix 3.1

Table 3.1.1:Traits values used in the analysis. Maximum photosynthetic rate per unit leaf mass (A_{mass}), and per unit leaf area (A_{area}), maximum stomata conductance (G_{max}), intrinsic Water Use Efficiency (WUE), Leaf Area (LA), Specific Leaf Area (SLA), Leaf LifeSpan, (LLS), nitrogen content per unit leafmass (N_{mass}), Minimum Leaf Water Potential (MLWP), Maximum Height (MH), Seed Dry Weight (SDW), water potential at which 50% of hydraulic conductivity is lost (PLC_{50}), Safety Margin (SM), and Wood Density (WD)

	SLA m^2/kg	SDW mg	LLS days	A_{area} µmol co_2/m^2 seg	G_{max} Mol h_20/m^2 seg	N_{mass} mg/g	WD g/cm^2	LA cm^2	MH m	PLC_{50} mpa	WUE µmol co_2/mol h_20	MLWP mpa	A_{mass} µmol co_2/g seg	SM mpa
Acer monspessulanum	10.7	10.2	180.7	8.8	0.1	19.4	0.7	16.5	11.0	-3.3	67.8	-4.1	93.3	-0.8
Arbutus unedo	6.5	1.9	330.0	13.2	0.3	12.9	0.8	10.1	9.5	-2.2	63.4	-2.8	85.5	-0.6
Erica arborea	7.8	0.2	360.0	11.0	0.2	12.4	0.7	0.0	6.0	-2.7	65.9	-3.6	85.4	-0.9
Erica multiflora	3.7	0.1	300.0	8.4	0.2		0.8	0.1	2.3		67.1	-4.5	31.0	
Juniperus oxycedrus	4.0	60.7	548.2	5.5	0.1	6.6	0.5	0.3	9.0	-9.0	79.5	-3.9	22.0	5.1
Juniperus phoenica	6.3	27.5	897.0	4.9	0.1	8.4	0.6	0.2	6.7		67.9	-5.5	30.7	
Olea europaea	4.7	278.0	912.0	13.5	0.2	19.0	0.9	10.0	10.0	-7.2	96.8	-4.2	63.1	3.0
Pinus halepensis	5.1	22.0	1083.0	7.6	0.1	12.5	0.5	3.0	19.3	-3.1	79.1	-2.6	38.9	0.5
Phyllerea latifolia	7.1	43.9	1007.3	14.3	0.2	17.8	0.9	4.3	8.0	-6.7	73.9	-6.7	101.0	-0.1
Pistacia lentiscus	4.9	21.4	735.0	12.0	0.2	14.5	0.8	1.2	3.0	-5.1	72.0	-5.0	59.3	0.1
Pinus pinea	3.3	718.0	1050.0	9.7	0.2	12.5	0.5	6.0	25.0	-3.7	77.3	-2.5	31.9	1.2
Prunus spinosa	12.5	225.8	157.0	13.0	0.3	21.7	0.9	13.5	4.5	-5.3	55.0		163.0	
Pistacia terebinthus	7.5	13.8	171.8	17.9	0.3	23.1	0.8	8.3	7.5	-8.4	56.2	-3.8	133.9	4.6
Quercus coccifera.	5.4	1446.0	441.0	8.3	0.1	16.6	0.8	0.9	3.3	-6.9	83.3	-6.3	45.3	0.7
Quercus faginea	8.9	1639.0	206.0	14.9	0.2	20.9	0.6	6.4	20.0		69.0	-2.6	132.5	

Table 3.1.1.

(continuation)

	SLA	SDW	LLS	A_{area}	G_{max}	N_{mass}	WD	LA	MH	PLC_{50}	WUE	MLWP	A_{mass}	SM
	m^2/kg	mg	days	µmol co$_2$/m^2 seg	Mol h$_2$0/m^{2}s eg	mg/g	g/cm^2	cm2	m	mpa	µmol co$_2$/mol h$_2$0	mpa	µmol co$_2$/g seg	mpa
Quercus ilex	5.0	1925.7	758.0	13.1	0.2	13.6	0.9	12.7	17.8	-2.0	62.3	-3.1	66.1	-1.1
Quercus pubescens	14.8	729.8	206.0	15.5	0.2	18.4	0.6	25.1	22.4	-2.9	64.5	-3.0	229.7	-0.1
Quercus pyrenaica	9.8	2999.0	162.0	16.8	0.3	24.4	0.8	14.5	20.5	-2.8	46.6	-3.2	164.1	-0.4
Quercues suber	6.5	3249.5	459.3	13.7	0.2	17.6	0.8	8.8	19.5		62.4	-3.2	89.1	
Rhamnus alaternus	7.3	9.1		11.7	0.2	18.1	0.8	8.2	6.0	-8.1	70.2	-4.0	85.3	4.1
Rosmarinus officinalis	4.8	0.5	330.0	9.7	0.1	12.0		0.5	1.8	-9.4	69.8	-4.6	46.3	4.8

<u>*Source used to extract species FT values*</u>

Aboal, J.R., Arévalo, J.R., & Fernández, Á. 2005. Allometric relationships of different tree species and stand above ground biomass in the Gomera laurel forest (Canary Islands). Flora - Morphology, Distribution, Functional Ecology of Plants 200: 264–274.

Adame, P., del Río, M., & Cañellas, I. 2008. A mixed nonlinear height–diameter model for pyrenean oak (Quercus pyrenaica Willd.). Forest Ecology and Management 256: 88–98.

Awada, T., Radoglou, K., Fotelli, M.N., & Constantinidou, H.I. a. 2003. Ecophysiology of seedlings of three Mediterranean pine species in contrasting light regimes. Tree physiology 23: 33–41.

Baquedano, F.J., & Castillo, F.J. 2007. Drought tolerance in the Mediterranean species Quercus coccifera, Quercus ilex, Pinus halepensis, and Juniperus phoenicea. Photosynthetica 45: 229–238.

Barboutis, J. a., & Philippou, J.L. 2007. Evergreen Mediterranean hardwoods as particleboard raw material. Building and Environment 42: 1183–1187.

Calatayud, V., Cerveró, J., & Sanz, M.J. 2007. Foliar, Physiologial and Growth Responses of Four Maple Species Exposed to Ozone. Water, Air, and Soil Pollution 185: 239–254.

Camarda, I., & Valsecchi, F. 2008. Alberi e arbusti spontani della Sardegna. Delfino, Carlo, Sassari.

Castro-Díez, P. 1998. Leaf morphology, leaf chemical composition and stem xylem characteristics in two Pistacia (Anacardiaceae) species along a climatic gradient. Flora 193: 195–202.

Castro-Díez, P., Montserrat-Martí, G., & Cornelissen, J. 2003. Trade-offs between phenology, relative growth rate, life form and seed mass among 22 Mediterranean woody species. Plant Ecology 166: 117–129.

Castro-Diez, P., Puyravaud, J., Cornelissen, J.H.C., & Villar-Salvador, P. 1998. Stem anatomy and relative growth rate in seedlings of a wide range of woody plant species and types. Oecologia 116: 57–66.

Castro-Díez, P., Villar-Salvador, P., Pérez-Rontomé, C., Maestro-Martínez, M., & Montserrat-Martí, G. 1997. Leaf morphology and leaf chemical composition in three Quercus (Fagaceae) species along a rainfall gradient in NE Spain. Trees - Structure and Function 11: 127–134.

Cavender-Bares, J., Cortes, P., Rambal, S., Joffre, R., Miles, B., & Rocheteau, a. 2005. Summer and winter sensitivity of leaves and xylem to minimum freezing temperatures: a comparison of co-occurring Mediterranean oaks that differ in leaf lifespan. The New phytologist 168: 597–612.

Cela, P.G., Gamarra, R.G., & Viñas, J.I.G. 1998. Arboles y arbustos de la Peninsula Iberica e Islas Baleares. Jaguar S.A., Madrid.

Chaideftou, E., Thanos, C.A., & Dimopoulos, P. 2006. Plant functional traits in relation to seedling recruitment and light conditions in sub-Mediterranean oak forests of Greece. In Plant, fungal and habitat diversity investigation and conservation. Proceedings of IV Balkan Botanical Congress, Sofia, pp. 597–601.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., (…) , & Zanne, A.E. 2012. Global convergence in the vulnerability of forests to drought. Nature 491: 752–5.

Cochard, H., Barigah, S.T., Kleinhentz, M., & Eshel, A. 2008. Is xylem cavitation resistance a relevant criterion for screening drought resistance among Prunus species? Journal of plant physiology 165: 976–82.

Corcuera, L., Camarero, J.J., & Gil-Pelegrín, E. 2002. Functional groups in Quercus species derived from the analysis of pressure-volume curves. Trees - Structure and Function 16: 465–472.

Damesin, C., Rambal, S., & Joffre, R. 1997. Between-tree variations in leaf d 13 C of Quercus pubescens and Quercus ilex among Mediterranean habitats with different water availability. Oecologia 111: 26–35.

DRYAD. http://datadryad.org/

Duhme, F., & Hinckley, T.M. 1992. Daily and seasonal variation in water relations of macchia shrubs and trees in France (Montpellier) and Turkey (Antalya). Vegetatio 99-100: 185–198.

El-Bana, M., Shaltout, K., Khalafallah, A., & Mosallam, H. 2010. Ecological status of the Mediterranean Juniperus phoenicea L. Relicts in the desert mountains of North Sinai, Egypt. Flora - Morphology, Distribution, Functional Ecology of Plants 205: 171–178.

Emberson, L.D., Büker, P., & Ashmore, M.R. 2007. Assessing the risk caused by ground level ozone to European forest trees: a case study in pine, beech and oak across different climate regions. Environmental pollution 147: 454–66.

Escudero, a., & Mediavilla, S. 2003. Decline in photosynthetic nitrogen use efficiency with leaf age and nitrogen resorption as determinants of leaf life span. Journal of Ecology 91: 880–889.

Fagúndez, J., & Izco, J. 2010. Seed morphology of the European species of Erica L. sect. Arsace Salisb. ex Benth. (Ericaceae). Acta Botanica Gallica 157: 45–54.

Faria, T., Silvério, D., Breis, E., Cabral, R., Abadia, A., Abadia, J.S., Perreira, J.S., & Chaves, M.M. 1998. Differences in the response of carbon assimilation to summer stress (water deficits, high light and temperature) in four Mediterranean tree species. Physiologia Plantarum 102: 419–428.

Filho, J.T., Damesin, C., Rambal, S., & Joffre, R. 1998. Retrieving leaf conductances from sap flows in a mixed Mediterranean woodland: A scaling exercise. Annales des Sciences Forestieres 55: 173–190.

Gallego, H. a., Rico, M., Moreno, G., & Santa Regina, I. 1994. Leaf water potential and stomatal conductance in Quercus pyrenaica Willd. forests: vertical gradients and response to environmental factors. Tree physiology 14: 1039–1047.

Galmés, J., Flexas, J., Savé, R., & Medrano, H. 2006. Water relations and stomatal characteristics of Mediterranean plants with different growth forms and leaf habits: responses to water stress and recovery. Plant and Soil 290: 139–155.

Gratani, L., & Bombelli, A. 2001. Differences in leaf traits among Mediterranean broad-leaved evergreen shrubs. Annales Botanicci Fennici 38: 15–24.

Gratani, L., & Varone, L. 2004a. Adaptive photosynthetic strategies of the Mediterranean maquis species according to their origin. Photosynthetica 42: 551–558.

Gratani, L., & Varone, L. 2004b. Leaf key traits of Erica arborea L., Erica multiflora L. and Rosmarinus officinalis L. co-occurring in the Mediterranean maquis. Flora 69: 58–69.

Gratani, L., & Varone, L. 2006. Long-time variations in leaf mass and area of Mediterranean evergreen broad-leaf and narrow-leaf maquis species. Photosynthetica 44: 161–168.

Haldimann, P., & Feller, U. 2004. Inhibition of photosynthesis by high temperature in oak (Quercus pubescens L .) leaves grown under natural conditions closely correlates with a reversible heat- dependent reduction of the activation state of ribulose-1 , 5-bisphosphate carboxylase / oxy. Plant Cell and Environment 27: 1169–1183.

Iovi, K., Kolovou, C., & Kyparissis, A. 2009. An ecophysiological approach of hydraulic performance for nine Mediterranean species. Tree physiology 29: 889–900.

Juan, R., Pastor, J., Fernández, I., & Diosdado, J. 2003. Relationships between mature cone traits and seed viability in Juniperus oxycedrus L. subsp. macrocarpa (Sm.) Ball (Cupressaceae). Acta Biologica Cracoviensia 45: 69–78.

KEW. http://www.kew.org/

Kuppers, M. 1985. Carbon relations and competition between woody species. Oecologia 66: 343–352.

Kuppers, M. 1984. Carbon relations and competition between woody species in a Central European Hedgerow. 2. Stomatal responses, water-use, and hydraulic conductivity. Oecologia 64: 344–354.

Lansac, A.R., Zaballos, J.P., & Martin, A. 1994. Seasonal water potential changes and proline accumulation in mediterranean shrubland species. Vegetatio 113: 141–154.

De Lillis, M. 1991. An ecomorphological study of the evergreen Leaf. Braun-Blanquetia 7: 126.

Llorens, L., Peñuelas, J., & Filella, I. 2003. Diurnal and seasonal variations in the photosynthetic performance and water relations of two co-occurring Mediterranean shrubs, Erica multiflora and Globularia alypum. Physiologia plantarum 118: 84–95.

Lloret, F., Casanovas, C., & Peñuelas, J. 1999. Seedling survival of Mediterranean shrubland species in relation to root: shoot ratio, seed size and water and nitrogen use. Functional Ecology 210–216.

Llusia, J., & Penuelas, J. 2000. Seasonal patterns of terpene content and emission from seven Mediterranean woody species in field conditions. American Journal of Botany 87: 133–140.

Loustau, D., Domec, J.C., & Bosc, A. 1998. Interpreting the variations in xylem sap flux density within the trunk of maritime pine (Pinus pinaster Ait.): Application of a model for calculating water flows at tree and stand levels. Annales des Sciences Forestieres 55: 29–46.

Marongiu, B., Porcedda, S., Caredda, A., De Gioannis, B., Vargiu, L., & La Colla, P. 2003. Extraction ofJuniperus oxycedrus ssp.oxycedrus essential oil by supercritical carbon dioxide: influence of some process parameters and biological activity. Flavour and Fragrance Journal 18: 390–397.

Martínez-Vilalta, J., Prat, E., Oliveras, I., & Piñol, J. 2002. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. Oecologia 133: 19–29.

Martínez-Vilalta, J., Sala, A., & Piñol, J. 2004. The hydraulic architecture of Pinaceae–a review. Plant Ecology 171: 3–13.

Mediavilla, S., & Escudero, A. 2003. Mature trees versus seedlings: differences in leaf traits and gas exchange patterns in three co-occurring Mediterranean oaks. Annals of Forest Science 60: 455–460.

Mediavilla, S., & Escudero, A. 2004. Stomatal responses to drought of mature trees and seedlings of two co-occurring Mediterranean oaks. Forest Ecology and Management 187: 281–294.

Mediavilla, S., Escudero, A., & Ecology, S.P. 2003. Relative Growth Rate of Leaf Biomass and Leaf Nitrogen Content in Several Mediterranean Woody Species. Plant Ecology 168: 321–332.

Medlyn, B.E., Loustau, D., & Delzon, S. 2002. Temperature response of parameters of a biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine (Pinus pinaster Ait.). Plant, Cell and Environment 25: 1155–1165.

Mesléard, F., & Lepart, J. 1989. Continuous basal sprouting from a lignotuber:Arbutus unedo L. and Erica arborea L., as woody Mediterranean examples. Oecologia 80: 127–131.

Miralles, J., Martínez-Sánchez, J.J., Franco, J. a., & Bañón, S. 2011. Rhamnus alaternus growth under four simulated shade environments: Morphological, anatomical and physiological responses. Scientia Horticulturae 127: 562–570.

Montesinos, D., García-Fayos, P., & Verdú, M. 2010. Relictual distribution reaches the top: Elevation constrains fertility and leaf longevity in Juniperus thurifera. Acta Oecologica 36: 120–125.

Nardini, A., Battistuzzo, M., & Savi, T. 2013. Shoot desiccation and hydraulic failure in temperate woody angiosperms during an extreme summer drought. New Phytologist 200: 322–329.

Nardini, A., Pedà, G., & Rocca, N. 2012. Trade-offs between leaf hydraulic capacity and drought vulnerability: morpho-anatomical bases, carbon costs and ecological consequences. New Phytologist 196: 788–798.

Navas, M.-L., Ducout, B., Roumet, C., Richarte, J., Garnier, J., & Garnier, E. 2003. Leaf life span, dynamics and construction cost of species from Mediterranean old-fields differing in successional status. New Phytologist 159: 213–228.

Oliveras, I., Martínez-vilalta, J., Jimenez-ortiz, T., Lledó, M.J., Escarré, A., & Piñol, J. 2003. Hydraulic properties of Pinus halepensis , Pinus pinea and Tetraclinis articulata in a dune ecosystem of Eastern Spain. Plant Ecology 169: 131–141.

Otieno, D.O., Schmidt, M.W.T., Kurz-Besson, C., Lobo Do Vale, R., Pereira, J.S., & Tenhunen, J.D. 2007. Regulation of transpirational water loss in Quercus suber trees in a Mediterranean-type ecosystem. Tree physiology 27: 1179–1187.

Paula, S., Arianoutsou, M., Kazanis, Dtavsanoglu, Lloret, F., Buhk, C., Ojeda, F., Luna, B., Moreno, J.M., Rodrigo, A., Espelta, J.M., Palacio, S., Fernandez-Santos, B., Fernandes, P.M., J. G. Pausas, & 1Ceam. 2009. Fire-related traits for plant species of the Mediterranean Basin. Ecology 90: 1420.

Pérez, S., Renedo, C.J., Ortiz, a., Delgado, F., & Fernández, I. 2014. Energy potential of native shrub species in northern Spain. Renewable Energy 62: 79–83.

Quero, J.L., Villar, R., Marañón, T., & Zamora, R. 2006. Interactions of drought and shade effects on seedlings of four Quercus species: physiological and structural leaf responses. The New phytologist 170: 819–33.

Quero, J.L., Villar, R., Marañón, T., Zamora, R., & Poorter, L. 2007. Seed-mass effects in four Mediterranean Quercus species (Fagaceae) growing in contrasting light environments. American Journal of Botany 94: 1795–1803.

Ripullone, F., Guerrieri, M.R., Nole', A., Magnani, F., & Borghetti, M. 2007. Stomatal conductance and leaf water potential responses to hydraulic conductance variation in Pinus pinaster seedlings. Trees 21: 371–378.

Rodriguez-Perez, J., Riera, N., & Traveset, A. 2005. Effect of seed passage through birds and lizards on emergence rate of mediterranean species : differences. Functional Ecology 19: 699–706.

Rubio-Casal, A.E., Leira-Doce, P., Figueroa, M.E., & Castillo, J.M. 2010. Contrasted tolerance to low and high temperatures of three tree taxa co-occurring on coastal dune forests under Mediterranean climate. Journal of Arid Environments 74: 429–439.

Sakcali, M.S., & Ozturk, M. 2004. Eco-physiological behaviour of some mediterranean plants as suitable candidates for reclamation of degraded areas. Journal of Arid Environments 57: 1–13.

Tognetti, R., Longobucco, A., & Raschi, A. 1998. Vulnerability of xylem to embolism in relation to plant hydraulic resistance in Quercus pubescens and Quercus ilex co-occurring in a Mediterranean coppice stand in central Italy. New Phytologist 139: 437–447.

Tognetti, R., Minnocci, a, Peñuelas, J., Raschi, a, & Jones, M.B. 2000. Comparative field water relations of three Mediterranean shrub species co-occurring at a natural CO(2) vent. Journal of experimental botany 51: 1135–46.

Traveset, A. 1994. Cumulative effects on the reproductive output of Pistacia terebinthud (Anacardiaceae). Oikos

Tsahar, E., Friedman, J., & Izhaki, I. 2002. Impact on fruit removal and seed predation of a secondary metabolite , emodin , in Rhamnus alaternus fruit pulp. Oikos 99: 290–299.

Tsiouvaras, C.N. 1967. Ecology and Managment of Kermes Oak(Quercus coccifera L.) Shrubland in Greece: A review. Journal of Range Management 40: 542–564.

Varone, L., & Gratani, L. 2009. Leaf expansion in Rhamnus alaternus L. by leaf morphological, anatomical and physiological analysis. Trees 23: 1255–1262.

Vilà, M., Stoll, P., & Weiner, J. 1998. Effects of Rosmarinus officinalis neighbors on resprouting of Erica multiflora individuals. Plant Ecology 136: 167–173.

Vilagrosa, A., Bellot, J., Vallejo, V.R., & Gil-Pelegrin, E. 2003. Cavitation, stomatal conductance, and leaf dieback in seedlings of two co-occurring Mediterranean shrubs during an intense drought. Journal of experimental botany 54: 2015–24.

Voulgaridis, E., & Passialis, C. 1995. Characteristics and technological properties of the wood of Mediterranean evergreen hardwoods. In Foret Méditerranéenne, pp. 3–12.

De Vries, W., Reinds, G.J., Gundersen, P., & Sterba, H. 2006. The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. Global Change Biology 12: 1151–1173.

Warren, C.R., & Adams, M.A. 2000. Trade-offs between the persistence of foliage and productivity in two Pinus species. Oecologia 124: 487–494.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., (…) & Villar, R. 2004. The worldwide leaf economics spectrum. Nature 12: 821–827.

Appendix 3.2

Table 3.2.1 Pearson correlation coefficients between functional traits. * represent significant relationships between traits (P value < 0.05). Maximum photosynthetic rate per unit leaf mass (A_{mass}), and per unit leaf area (A_{area}), maximum stomata conductance (G_{max}), intrinsic Water Use Efficiency (WUE), Leaf Area (LA), Specific Leaf Area (SLA), Leaf Life Span, (LLS), nitrogen content per unit leaf mass (N_{mass}), Minimum Leaf Water Potential (MLWP), Maximum Height (MH), Seed Dry Weight (SDW), water potential at which 50% of hydraulic conductivity is lost (PLC_{50}), Safety Margin (SM), and Wood Density (WD).

	LA	LLS	SLA	A_{mass}	A_{area}	G_{max}	N_{mass}	WUE	WD	PLC_{50}	MLWP	SM	SDW
LLS	-0.27												
SLA	0.62*	-0.59*											
A_{mass}	0.74*	-0.56*	0.88*										
A_{area}	0.65*	-0.37	0.5*	0.85*									
G_{max}	0.39	-0.51*	0.46*	0.68*	0.76*								
N_{mass}	0.67*	-0.51*	0.64*	0.83*	0.79*	0.64*							
WUE	-0.34	0.62*	-0.56*	-0.57*	-0.46*	-0.7*	-0.4						
WD	0.27	-0.27	0.18	0.43	0.51*	0.54*	0.57*	-0.24					
PLC_{50}	0.42	0	0.29	0.29	0.15	0.19	0.03	-0.34	-0.05				
MLWP	0.46*	-0.19	0.13	0.23	0.26	0.22	0.08	-0.29	-0.35	0.55*			
SM	-0.3	0.07	-0.39	-0.36	-0.16	-0.25	-0.07	0.36	-0.27	-0.89*	-0.16		
SDW	0.54*	0.12	0.21	0.29	0.34	0.06	0.37	-0.01	-0.02	0.18	0.19	-0.12	
MH	0.61*	0.17	0.24	0.3	0.32	0.06	0.18	-0.1	-0.4	0.61*	0.67*	-0.36	0.64*

Appendix 3.3

Table 3.3.1 R squared between functional traits and niche characteristics (using traits as explanatory variables).* significant relationships (P values < 0.05). Between bracket the sign of the relationships. . Maximum photosynthetic rate per unit leaf mass (A_{mass}), and per unit leaf area (A_{area}), maximum stomata conductance (G_{max}), intrinsic Water Use Efficiency (WUE), Leaf Area (LA), Specific Leaf Area (SLA), Leaf LifeSpan, (LLS), nitrogen content per unit leafmass (N_{mass}), Minimum Leaf Water Potential (MLWP), Maximum Height (MH), Seed Dry Weight (SDW), water potential at which 50% of hydraulic conductivity is lost (PLC_{50}), Safety Margin (SM), and Wood Density (WD).

	SLA	LLS	LA	N_{mass}	A_{mass}	A_{area}	G_{max}	WUE	WD	PLC_{50}	MLWP	SM	MH	SDW
APopt	0.44*	(-) 0.11	0.38*	0.22*	0.53*	0.3*	0.33*	(-) 0.18	0.13	0.32*	0.05	(-) 0.51*	0.14	0.07
APmin	0.67*	(-) 0.22*	0.35*	0.13	0.49*	0.12	0.11	(-) 0.18	0.01	0.22	0.03	(-) 0.3*	0.08	0.01
APmax	0.22*	(-) 0.27*	0.04	0.11	0.21*	0.09	0.34*	(-) 0.32*	0.09	0.28*	0.03	(-) 0.4*	0.01	(-) 0.03
APrng	0.05	(-) 0.19	0	0.06	0.08	0.05	0.32*	(-) 0.26*	0.1	0.21	0.02	(-) 0.3*	0	(-) 0.05
PDQopt	0.32*	(-) 0.06	0.08	0.01	0.19	0.01	0.07	(-) 0.07	0	0.26*	0	(-) 0.44*	0	(-) 0.01
PDQmin	0.4*	(-) 0.21*	0.22*	0.1	0.25*	0.05	0.09	(-) 0.14	(-) 0	0.06	0.04	(-) 0.03	0.01	0.03
PDQmax	0.31*	(-) 0.34*	0.15	0.15	0.22*	0.06	0.2*	(-) 0.28*	0.02	0.14	0.02	(-) 0.18	0	(-) 0.01
PDQrng	0.01	(-) 0.12	0	0.03	0.01	0.01	0.11	(-) 0.14	0.05	0.06	0	(-) 0.18	(-) 0.01	(-) 0.16
AMTopt	(-) 0.43*	0.24*	(-) 0.1	(-) 0.11	(-) 0.21*	(-) 0.03	(-) 0.13	0.34*	0.01	(-) 0.08	(-) 0.02	0.16	(-) 0.06	(-) 0.1
AMTmin	(-) 0.53*	0.23*	(-) 0.08	(-) 0.03	(-) 0.22*	(-) 0.01	(-) 0.05	0.22*	0.04	(-) 0.12	(-) 0.03	0.17	(-) 0.05	(-) 0.01
AMTmax	(-) 0.57*	0.42*	(-) 0.26*	(-) 0.27*	(-) 0.36*	(-) 0.07	(-) 0.19	0.31*	(-) 0	(-) 0.17	(-) 0.1	0.23	(-) 0.08	(-) 0.05
AMTrng	0.25*	(-) 0.05	0	(-) 0.02	0.06	(-) 0.01	(-) 0	(-) 0.07	(-) 0.11	0.04	0	(-) 0.06	0.01	(-) 0

Table 3.3.1 (continuation)

	SLA	LLS	LA	Nmass	Amass	Aarea	Gmax	WUE	WD	PLC50	MLWP	SM	MH	SDW
pHopt	(-) 0.14	0.03	(-) 0.2*	(-) 0.13	(-) 0.28*	(-) 0.27*	(-) 0.36*	0.22*	(-) 0.05	(-) 0.4*	(-) 0.1	0.36*	(-) 0.22*	(-) 0.06
pHmin	(-) 0	0.07	(-) 0.06	(-) 0.15	(-) 0.14	(-) 0.29*	(-) 0.42*	0.11	(-) 0.33*	(-) 0.16	(-) 0.04	0.27*	(-) 0.01	0
pHmax	(-) 0.18	0.11	(-) 0.05	(-) 0.1	(-) 0.24*	(-) 0.17	(-) 0.24*	0.24*	(-) 0.03	(-) 0.23	(-) 0.06	0.29*	(-) 0.11	(-) 0.02
pHrng	(-) 0.04	0.01	0.03	0.09	0.02	0.17	0.24*	(-) 0.01	0.36*	0.03	0.01	(-) 0.07	(-) 0.01	(-) 0.03
a2opt	(-) 0	0.01	0.07	0.04	0.05	0.19	0.14	(-) 0.01	0.08	0.21	0.06	(-) 0.13	0.12	0.02
a2min	(-) 0.12	0.03	(-) 0.03	0	(-) 0.01	0.04	0.04	0	0.04	0.01	0.02	(-) 0.01	0	(-) 0
a2max	(-) 0.04	0	0.01	0.04	0.02	0.19	0.15	(-) 0.01	0.29*	0.08	0.01	(-) 0.12	0	(-) 0
a2rng	0	0.01	(-) 0.1	(-) 0.14	(-) 0.12	(-) 0.3*	(-) 0.22*	0.03	(-) 0.49*	(-) 0.12	(-) 0	0.24	0	0

Chapter 4. Functionally diverse forest stabilize productivity against inter-annual climatic variability

Abstract

Increasing concern for the impacts of global change on biodiversity has recently reopen the interest to understand the effects of diversity on the stability of ecosystem functioning. Despite the great evidence of this positive effect on grass communities much less is known for forest. Here, we use data from the Quebec Forest Survey and the Enhanced Vegetation Index from MODIS (i.e. our proxy of productivity) for assess the effect of functional diversity on the temporal stability of forest productivity. Results showed, after controlling for climatic effects, that stability was due to the positive effect of functional diversity and functional identity of communities (i.e. dominant trait values within communities). These findings provide new information about the diversity-stability effect on forest which is of clear interest for forest managers and mitigation strategies for climate change.

Introduction

The unprecedented rate of loss of species raises concerns for the possible consequences on ecosystem functions and stability and future provision of ecosystem services (Isbell et al. 2011; Lavorel 2013; Balvanera et al. 2014). Consensus is building over the idea that loss of biodiversity may impact ecosystem functions at an order of magnitude comparable to that of other environmental drivers of global change (Cardinale et al. 2012; Hooper et al. 2012; Tilman et al. 2012). In the last 25 years, research on Biodiversity and Ecosystem Function (BEF) relationships has produced an increasing body of evidence and mathematical theory of how biodiversity and functional diversity have an effect on ecosystem processes (Balvanera et al. 2006; Cardinale et al. 2012). A positive effect of diversity on productivity has been widely observed across environmental gradients and over different ecosystem types, e.g. grasslands, aquatic systems and forests. Indeed, in forest ecosystems it was found that mixed species stands have a greater above-ground productivity (Morin et al. 2011; Paquette & Messier 2011; Ruiz-Benito et al. 2014) store higher amounts of carbon below ground (Gamfeldt et al. 2013), and in general have a 25% higher productivity (Zhang et al. 2012).

Although less represented in the literature, diversity is thought to also affect the stability of ecosystems (Cottingham et al. 2001; Jiang & Pu 2009; Hector et al. 2010). Yachi & Loreau (1999) proposed the insurance hypothesis as a theoretical background to explain why more diverse ecosystems would be more stable over time (also refer as statistical averaging, portfolio effect or species asynchrony, Doak et al. 1998; Tilman et al. 2006; Hector et al. 2010). They stated that "biodiversity insures ecosystems against declines in their functioning because many species provide greater guarantees that some will maintain functioning even if others fail". Indeed, Allan et al. (2011) observed in grass communities that diversity promoted stability because species relative contribution to a given function (i.e. productivity) changed over time. Yachi & Loreau (1999) also pointed that strength of the insurance effect depend on species individual responses to environmental fluctuations, asynchronicity of these responses, and the shape of these responses. Other mechanism suggested to promote a positive diversity-stability effect is overyielding (Tilman et al. 1999). Overyielding refers when species mixtures perform better than expected from their constituent species on monocultures. Thus, since variability (the complementary term of stability) is commonly measured by the coefficient of variation of a time series (i.e. standard deviation/mean), mechanisms buffering productivity in relation to its variability will promote stability. Indeed, this mechanism was observed in forest and grass communities (Tilman et al. 2006; Hector et al. 2010; Jucker et al. 2014).

It has been suggested that stability can also depend on the responses of dominant species to environmental fluctuations (Hillebrand et al. 2008). Referred as “the selection effect”, the hypothesis states that natural selection might promote dominant species being more stable over time. Thus, stability of ecosystem functions may largely depend on the stability of dominant species (Grime 1998). Indeed, Sasaki & Lauenroth (2011) handling the relative abundances of dominants, observed that stability scaled with their abundances but not with diversity. The effect of dominants on stability has also lead to try to understand which functional traits (i.e. morphological, physiological, and phonological plant attributes, Violle et al. 2007) might determine stability. For instance, Májeková et al. (2014) and Polley et al. (2013) found in grasses that communities with greater LDMC were more stable (i.e. the functional identity effect). They suggested that conservative slow growing species will be more stable since they respond slowly to environmental fluctuations (i.e. storage effect; Chesson 2000; Májeková et al. 2014).

The concept of ecosystem stability actually embraces the concept of resistance to perturbations, resilience (i.e. the ability of a system to return its equilibrium after a perturbation) and dynamic stability (i.e. the ability of a system to sustain a constant function despite small environmental perturbations). Biodiversity was found to increase the resistance, resilience and dynamic stability of grassland ecosystem productivity to climate extremes across a wide range of climatic zones (Isbell et al. 2015). As other ecosystem types, more diverse forests are found to be less prone to pest attacks (Jactel & Brockerhoff 2007) and more resistant to drought (but not always, see Grossiord et al. 2014). Diversity was also found to have a positive effect on stability of ecosystems (Cardinale et al. 2013), but to the best of our knowledge, the effect of diversity on dynamic stability has being tested only once in forest ecosystems by Jucker et al. (2014) using tree ring data.

The difficulty in obtaining annual measurements of productivity may be overcome using remote sensing products as Normalized Vegetation Index (NDVI) or the Enhanced Vegetation Index (EVI). These products have been previously used to assess ecosystem productivity (Yang et al. 2008; Gaitán et al. 2013; Gaitán et al. 2014) and have been successfully linked to seasonal and inter-annual variations of gross primary production (Dong et al. 2003; Sjöström et al. 2011), while Fang et al. (2001) observed that inter annual variability of productivity in different biomes was correlated with the variability of precipitations. The more common index used is the NDVI which is based on visible and near infrared bands to detect plant activity. Drawbacks using NDVI, e.g. signal saturation over dense vegetation covers, lead to use other vegetation index as EVI. EVI also uses information in the blue band to remove atmospheric and soil influences. Thus, EVI respond better to canopy structural variations as leaf area index (LAI), canopy type, plant physiognomy, and canopy architecture (Gao et al. 2000; Huete et al. 2002) .

The aim of the present study was to assess the importance of functional diversity on the stability of forest productivity. We used data from the Quebec (eastern Canada) forest Inventory and remote sensing product as proxy of productivity (i.e. EVI) to test the hypothesis that i) The inter-annual productivity of more functionally diverse forest ecosystems is more stable than low diversity forests, ii) Community Weighted Mean Functional traits are also determinant of stability, and iii) The effect of diversity is independent of the climatic conditions.

Materials and Methods

Stand composition and functional structure

The stand species composition and species-specific basal area of each plot of the Quebec Forest Survey (QFS) were used to compute Functional Diversity indexes and the Community Weighted Mean. QFS covers the Temperate and Boreal climatic zones (dfb and dfc Koppen biozones, respectively) with plots randomly distributed across each region. New plots are added every year, while older one are measured approximately every ~10 years (Duchesne & Ouimet 2008). From the over ~36.000 plot measurements available we selected pairs of plots that were not affected by neither important natural disturbances nor human intervention (see Paquette & Messier 2011 for further details). Of the remaining 12,324, only those plots measured after 1997 were used for further analysis (7,172).

Stand above ground biomass increments of the remaining 7,172 pairs of plots over the period embracing 2000-2007 were computed as:

$$Y = \frac{\sum_{i=1}^{n} b_{i-t_2} - b_{i-t_1}}{t_2 - t_1}$$

where *Y* is the yearly increment of total aboveground biomass of live trees between a pair of measurements at times t_1 and t_2 for a given plot, and *b* is the biomass of tree *i* present at both sampling times (see Paquette &Messier 2011 for further details). Individual biomasses *b* of trees were computed using d.b.h. and published equations for aboveground stem and branch biomass (Lambert et al. 2005).

The Functional Diversity indexes used are those computed in Paquette & Messier (2011), with demonstrated impact on productivity. Briefly, Functional diversity was computed with the Functional Dispersion (FDis) index (Laliberté & Legendre 2010) using wood density (WD), maximum height (maxH), seed dry weight (SDW), leaf mass area (LMA) and nitrogen leaf content (N_{mass}). This index was calculated using single traits and specific combinations of 3 (i.e. WD, SDW and maxH; FDis_3) and 5 traits (i.e. all traits; FDis_5). For avoid redundancy on results and for allowing comparisons with the work of Paquette & Messier (2011) we only showed results for FDis_3 calculated with presence-absence data (hereafter referred as FD). For each plot, the averaged mean value of each trait weighted by species abundance was also calculated (i.e. Community Weighted Mean, CWM).

Climatic zone classification and stand climatic data (i.e. annual mean temperature, AMT, and annual precipitation, AP) were also retrieved from Paquette & Messier (2011). Mean monthly air temperatures, annual mean temperature (AMT) and annual precipitations (AP) for each year over the period 2000-2007 were retrieved from the Centre For Climatic Research at resolution of 0.5 degrees (http://climate.geog.udel.edu/~climate/). These data were used to compute the coefficient of variation of those variables across the studied period, i.e. CV AP and CV AMT. Data were also used to compute the growing season length (GSL) for each year and plot and its variation across the studied period (SD GSL). Growing season was defined following Agri-Food Canada Science and Technology Branch (http://www.agr.gc.ca/) as the months for which average air temperature was above 5 °C.

Stand annual productivity and its variability across the studied period

The sum of the monthly values of the Enhanced Vegetation Index (EVI) over the growing season was used as a proxy for annual productivity. EVI was retrieved from the Moderate Resolution Imaging Spectroradiometer (MODIS) and is considered to reflect canopy structural variations as leaf area index (LAI), canopy type, plant physiognomy, and canopy architecture better than the more commonly used NDVI (Gao et al. 2000; Huete et al. 2002). The MODIS product MOD13Q1 provides EVI data every 16 days (23 images per year) at a resolution of 250 meters. EVI data from the period 2000 to 2007 were downloaded from http://modis.gsfc.nasa.gov/ and assigned to their corresponding plots (23 x 8 EVI values for each plot). MOD13Q1 product also provides the MODIS Quality Assessment Science Data Sets (QA SDS) which supplies information about the conditions under which measures were obtained (e.g. snow presence, aerosol quantity, atmospheric correction, cloud cover) classifying EVI data into different quality categories. To ensure the accuracy and integrity of data used in the analysis only EVI values with the highest quality and without snow presence (since it might increase EVI values, Huete et al. 2002) were retained for next steps (Fig. 4.1).

Since quality filtering generated “missing values” in some plots at specific dates and years, a value imputation method was applied. First, the half-monthly data were converted to monthly values in order to have one EVI value per month and year calculating the mean of the two values (one from the ~1st day and the other from ~16th day of the month). Then, the mean and the standard deviation of EVI was calculated for each plot and month of the studied period. Finally, the “missing-values” were filled with a value equal to the mean of the plot for the specific month plus a random value between +- the standard deviation (48,381 EVI values were filled, i.e. ~12% of EVI values). When plots had missing values for the same month for all years it was not possible to compute a mean and a standard deviation and thus these plots were removed from the analysis: from the initial 7,172 plots, 5,538 were conserved. Plots with a negative correlation between annual EVI and AMT were also removed (913 plots were removed).

In order to estimate the goodness of the annual EVI as a proxy for annual productivity, the average of the annual EVI over the period 2000-2007 was regressed against the stand biomass increments. All plots that were deviated more than 4 times the standard deviation from the regression curve were considered outliers and eliminated from the analysis (44 plots were removed).

Finally, the inverse of the coefficient of variation of EVI over the period 2000-2007 was used as a proxy for dynamic stability:

$$Stability = \frac{EVI_{\mu}}{EVI_{\sigma}}$$

where EVI is the sum of EVI over the growing season for each year between 2000 and 2007, whereas μ is the average of EVI for the period 2000-2007 and σ is the standard deviation over the same period.

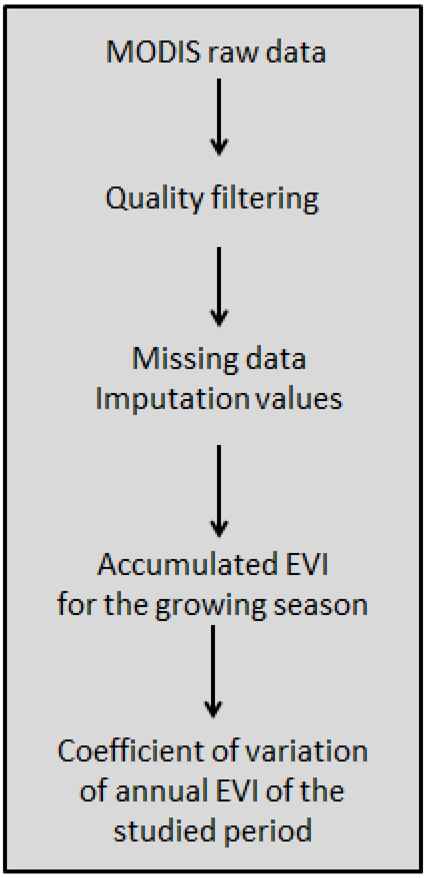


Figure 4.1: Workflow for obtaining plot stability

Data analysis

Linear regressions were used to test the association between stability and single biotic and abiotic predictors. Pearson correlation coefficients between predictors were analysed to detect the strength and direction of those associations. Structural Equation Modelling (SEM) was used to unmask common causes among predictors and stability, which potentially might bias the diversity–stability effect. The conceptual model accounted for climatic (ATM and GSL) and biotic effects (FD and CWM) on stability based on previous studies that suggested their potential effects (Fang et al. 2001; Hector et al. 2010; Májeková et al. 2014). To assess the effect of the different traits on the conceptual model it was alternatively fitted with the different CWM. Since the often used chi-squared test underperforms at large sample sizes, the Bentler Comparative Fit

Index (CFI) and the Root Mean Squared Error of Approximation (RMSEA) were used to assess the quality of the model because accounts for sample size effect. The model was run with the both Temperate and Boreal biomes datasets jointly and separately as previous work highlighted important differences in BEF relationships between the two. Data preparation and analysis were conducted on R software (R Core Team 2015) using Lavaan package for path analysis (Rosseel 2012).

Results

EVI as proxy of stability

The computed mean annual accumulated EVI over the growing season was significantly correlated with the mean annual biomass accumulation of the corresponding plot of the QFS (Fig. 4.2). The best fit was achieved with an exponential curve, however the r of this fit was 0.59 as compared to the 0.58 of the linear fit. This latter was used to compute outliers which were eliminated for the analysis.

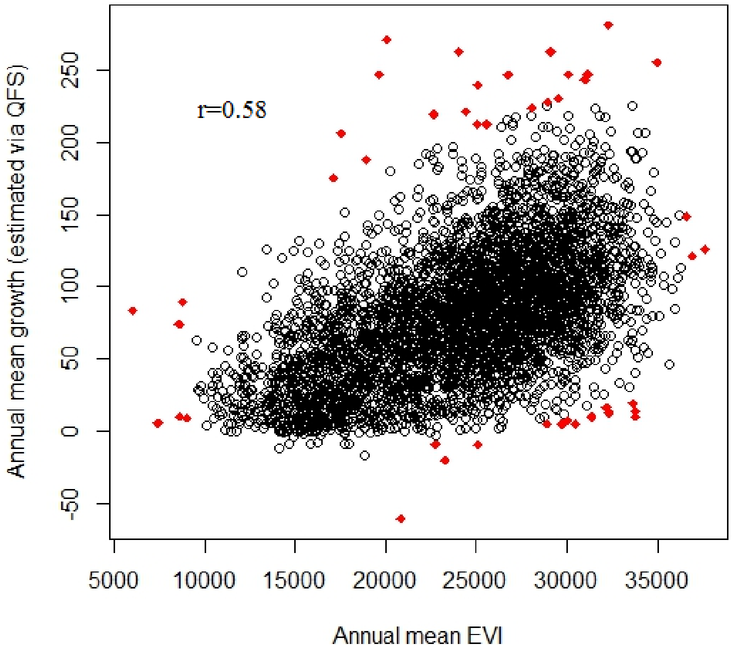


Figure: 4.2. Scatterplot between mean annual EVI retrieved from MODIS (our proxy of productivity) and mean annual growth retrieved from the Quebec forest survey (QFS). Red data points are outliers

Single relationships among stability and biotic and abiotic factors

Of all the biotic and abiotic variables tested against stability the most strongly correlated resulted to be the AMT and the standard deviation of the growing season length (i.e. SD GSL, proxy for climatic variability; Table 4.1). All community mean traits were significantly ($p<0.05$) correlated with stability. Communities mainly composed of species with higher WD, N_{mass}, SDW, maxH, and low LMA tend to be more stable. Functional diversity (FD) was also significantly related with stability, with more diverse communities also more stable (Table 4.1). However, FD was also highly correlated with AMT (Table 4.2).

When both biomes were analysed separately all correlations remained significant (Table 4.1). The influence of climatic factors on stability decreased more strongly in the Temperate zone whereas the strength of the correlation between SD GSL and stability increased in Boreal communities. In general, the significance of the correlations of stability with CWM traits and FD decreased when analysing the two climatic zones separately, disappearing in the cases of CWM WD and SDW in boreal zones.

Correlations between abiotic and biotic factors (Table 4.2) showed how warmer climates tend to have communities with a higher WD, maxH and, SM. Furthermore these warmer communities are characterized by a higher functional diversity (Figure 4.3).

Comparison of the Boreal biome with the Temperate revealed how the two significantly differ for all abiotic and biotic variables considered. Specifically, the Temperate biome is characterised by a much more stable climate, a higher and more stable annual productivity and more diverse communities. Temperate biomes are also characterized by an average slightly higher CWM WD, but the variance of this variable is much higher in the Temperate biome.

Table 4.1: Pearson coefficient of correlation among EVI variability (coefficient of co-variation) and biotic and abiotic factors for the complete data set and each biome separately. * indicate significant correlations (P value < 0.05). Annual mean temperature and its coefficient of variation across the studied years (AMT and CV AMT, respectively), evapotranspiration and precipitation coefficients of variation (CV ET and CV AP, respectively), standard deviation of the growing season length (SD GSL), community weighted mean (CWM) of maximum height, wood density, seed mass, leaf mass area, nitrogen per unit of leaf mass (maxH, WD, SDW, LMA, N_{mass}, respectively), Species richness and diversity (SR and SD, respectively), and functional diversity (FD) regarding three traits with presence-absence data.

	All data set	Boreal	Temperate
AP	-0.19*	-0.08*	-0.07*
AMT	-0.46*	-0.38*	-0.27*
CV AMT	0.47*	0.38*	0.28*
CV AP	-0.09*	0.05	0.03
SD GSL	0.45*	0.62*	0.25*
CWM maxH	-0.3*	-0.17*	-0.2*
CWM WD	-0.21*	-0.02	-0.19*
CWM SM	-0.26*	-0.01	-0.21*
CWM LMA	0.39*	0.2*	0.26*
CWM N_{mass}	-0.33*	-0.2*	-0.19*
FD	-0.36*	-0.18*	-0.22*

Table 4.2: Correlation coefficients among climatic variables and community traits. Abbreviations as in Table 4.1.

	AMT	CV AMT	CWM maxH	CWM WD	CWM SM	CWM LMA	CWM N_{mass}	FD
AMT			0.50*	0.30*	0.52*	-0.61*	0.47*	0.56*
CV AMT	-0.63*		-0.36*	-0.24*	-0.34*	0.42*	-0.34*	-0.39*
SD GSL	-0.09*	0.34*	-0.03	0.00	0.03	0.08*	-0.09*	-0.05*

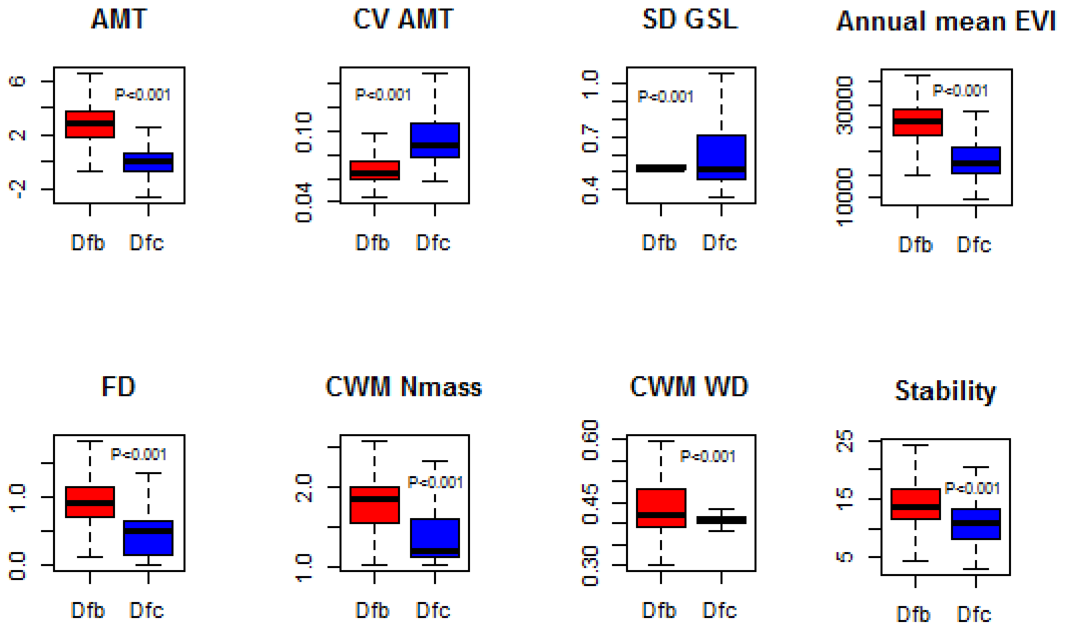


Figure: 4.3. Functional and environmental differences among Koppen climatic zones. Annual mean temperature (AMT), coefficient of variation of AMT (CV AMT), standard deviation of the growing season length (SD GSL), functional diversity (FD), Community weighted mean of wood density and N mass (CWM WD and CWM N_{mass}, respectively), annual mean EVI, and Stability (i.e. 1/ coefficient variation of EVI). P represents the p-value retrieved from ANOVA.

Conceptual models of inter-annual variations of productivity

The variables that correlated the most with stability were used to construct a general model using SEM. Several model structures were tested which included or excluded a number of variables and hypothesis. The variables included in the conceptual model represented in Fig. 4.4 allowed for all links to be significant and fit values were inside those considered adequate for SEM analysis (Hu & Bentler 1999). CFI remained satisfactory even when the model was fitted to the temperate or boreal datasets separately. Climate variability (SD GSL) retained a high explanatory power (i.e. the path coefficient) over stability in all models but it was lower in the temperate (-0.32) zone alone and higher for the boreal zone (-0.56). Both CWM WD and FD significantly explained stability when the entire dataset was analysed. However, the significance of both FD and CWM WD was lost when only the Boreal dataset was considered, while its strength increased for the Temperate dataset (0.1). When using CWM N_{mass} instead of CWM WD the path remained significant, being communities characterised of high N_{mass} more stable (Appendix 4.1).

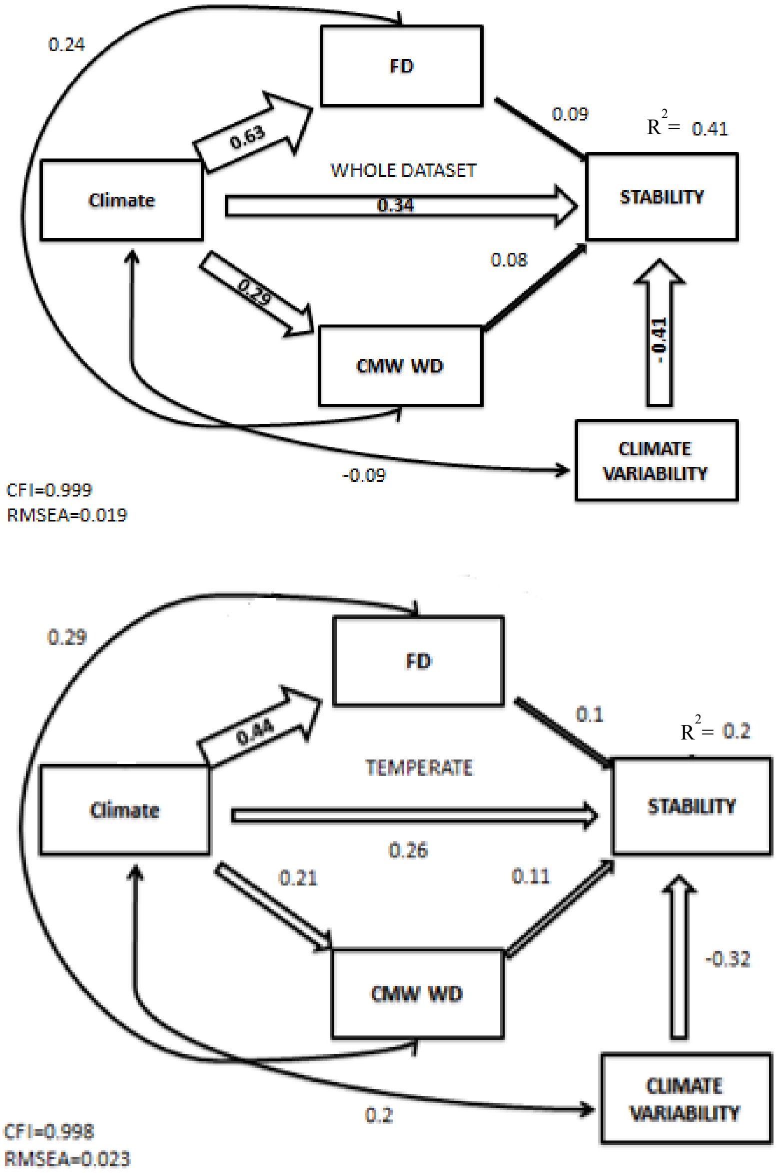


Figure 4.4.A: Structural Equation Models (SEM) with path coefficients. The variance explained for stability (i.e. R^2) and SEM fitting values (i.e. CFI and RMSEA) are also reported. Abbreviations as in Table 4.1.

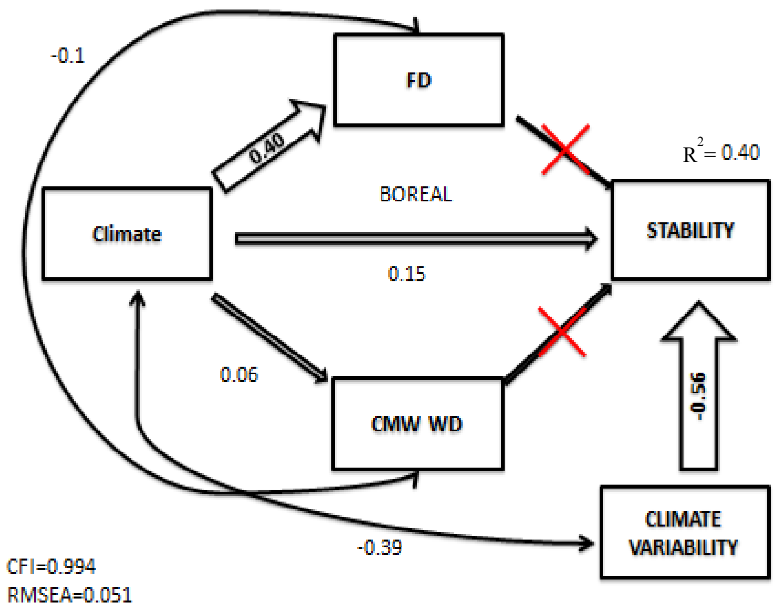


Figure 4.4.B: Structural Equation Models (SEM) with path coefficients. The variance explained for stability (i.e. R^2) and SEM fitting values (i.e. CFI and RMSEA) are also reported. Abbreviations as in Table 4.1.

Discussion

Our results showed that in general functional diversity promotes stability in forest communities. It is in agreement with theory that states that diversity buffers productivity since species might respond differently to climatic fluctuations, which improves temporal stability (i.e. species asynchrony, Yachi & Loreau 1999; Loreau & de Mazancourt 2013). Indeed, studies in grass communities already observed that effect (Tilman et al. 2006; Isbell et al. 2009; Allan et al. 2011). Instead, forest communities have been much less studied and there is little evidence of such influence. Our results are in agreement with those of Jucker et al. (2014) which observed that in forest communities mixed-species stands were more stable than pure stands.

Results of SEM showed that the diversity effect, despite still being significant, might be reduced when controlling for other factors that can affect both stability and diversity.

CWM could be seen as a measure of the functional identity of communities. Previous studies also reported relationships among traits and stability in grass communities (Polley et al. 2013). Indeed, Májeková et al. (2014) observed that grass communities characterised by traits values related with conservative strategies (i.e. high LMA or low N_{mass}) were more stable over time. It has been suggested that slow growing species are advantageous under unfavourable conditions, i.e. the storage effect (Chesson 2000). Our results showed that traits values related with slow life histories as high WD (Adler et al. 2014) improved stability. Indeed, those trait values are usually assigned to late successional species (Poorter et al. 2008; Larjavaara & Muller-Landau 2010) so our results will be in agreement with the storage effect (Chesson 2000). When CWM LMA and N_{mass} were used in the model, was in contradiction with the storage effect, i.e. high N_{mass} communities were more stable. However, these traits tend to distinguish conifers form broadleaves more than representing a gradient of a function. Additionally, low N_{mass} and high LMA are also associated with cold locations (Reich et al. 2003) suggesting that those traits might be are not representing slow-fast strategies but adaptations to cold climates.

Climate and its inter-annual variability were also important drivers of temporal fluctuations in productivity. The effect of climatic factors such as precipitation on ecosystem functions has been already noted (Yang et al. 2008). Indeed, Fang et al. (2001) observed in different biome groups (i.e. forest, grasslands, desert, alpine vegetation, and croplands) that above ground net primary productivity and its inter-annual variability were close related with precipitation and its variability. Hallet et al. (2014) suggested that mechanisms providing stability vary along environmental gradients. It was suggested that in limiting environments species asynchrony would play a major role whereas at more optimal conditions the portfolio effect should be more important. However, it has been also suggested that the diversity effect over even more stressed conditions might be limited. Indeed, Jucker et al.(2014) observed in Spanish and Finish forests (Mediterranean and Boreal climates, respectively) that species asynchrony was much lower than in other less constraining sites . In fact, our results revealed no diversity effect on Boreal forests once the effect of climate of diversity was accounted for. Boreal forests were less functionally diverse than Temperate suggesting that the greater functional similarity might be limiting the range of different responses (DeClerck et al. 2006; Hector et al. 2010). Indeed, DeClerck et al. (2006) observed that conifers in Mountainous California respond similarly to climatic variability limiting functional compensation.

It was initially surprising the lack of effect of diversity on Boreal forest since its positive effects on productivity have been previously observed (overyielding is poitned as mechanism provinding stability, Paquette & Messier 2011). Hooper et al. (2005) suggested a trade-off between the effect of FD on stability and producitivity, while Cardinale et al. (2013) reported that biodiversity does not need to improve simultaneously productivity and stability, arguing that the mechanism operating over these functions may be independent (i.e. complementarity and species asynchrony). Here we find that FD promoted stability of the Temperate biome where previous studies (Paquette & Messier, 2011) found a lack of effect on productivity. The opposite can be said for the Boreal biome where an effect of FD on biomass increments was found by the same authors, but not for stability in this work.

Conclusions

A general positive effect of functional diversity on the stability of ecosystem productivity of Quebec forests was found. However, more detailed analysis revealed how this effect only exists in the Temperate biome and is missing in the Boreal. Our results are consistent with those of Jucker et al. (2014) that to our knowledge is the only work that has previously assessed the effect of diversity on the stability of forests. Merging the results of this work with those of Paquette & Messier (2011) we come to the conclusion that a forest management promoting diversity is to be always promoted, at minimum, enhances one ecosystem function that supports one or more ecosystem services. Furthermore, the enhancement of either annual productivity or dynamic stability should be seen as tools aiding in the mitigation strategies of climate change or as strategies to promote ecosystem resistance to climate change, as long as the change falls inside the physiological tolerance of the community. However, improving insights on mechanism providing separately both functions emerge as necessary in order to best address these actions.

Bilbiography

Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C., & Franco, M. 2014. Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences of the United States of America* 111: 740–5.

Allan, E., Weisser, W., Weigelt, A., Roscher, C., Fischer, M., & Hillebrand, H. 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proceedings of the National Academy of Sciences* 108: 17034–17039.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., & Schmid, B. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9: 1146–56.

Balvanera, P., Siddique, I., Dee, L., Paquette, A., Isbell, F., Gonzalez, A., Byrnes, J., O'Connor, M.I., Hungate, B. a., & Griffin, J.N. 2014. Linking biodiversity and ecosystem services: Current uncertainties and the necessary next steps. *BioScience* 64: 49–57.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., A.Wardle, D., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., & Naeem, S. 2012. Biodiversity loss and its impact on humanity. *Nature* 489: 326–326.

Cardinale, B.J., Gross, K., Fritschie, K., Flombaum, P., Fox, J.W., Rixen, C., Van Ruijven, J., Reich, P.B., Scherer-Lorenzen, M., & Wilsey, B.J. 2013. Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. *Ecology* 94: 1697–1707.

Chesson, P. 2000. Mechanism of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–358.

Cottingham, K.L., Brown, B.L., & Lennon, J.T. 2001. Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters* 4: 72–85.

DeClerck, F. a J., Barbour, M.G., & Sawyer, J.O. 2006. Species richness and stand stability in conifer forests of the Sierra Nevada. *Ecology* 87: 2787–2799.

Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E., & Thomson, D. 1998. The statistical inevitability of stability-diversity relationships in community ecology. *The American Naturalist* 151: 264–276.

Dong, J., Kaufmann, R.K., Myneni, R.B., Tucker, C.J., Kauppi, P.E., Liski, J., Buermann, W., Alexeyev, V., & Hughes, M.K. 2003. Remote sensing estimates of boreal and temperate forest woody biomass: Carbon pools, sources, and sinks. *Remote Sensing of Environment* 84: 393–410.

Duchesne, L., & Ouimet, R. 2008. Population dynamics of tree species in southern Quebec, Canada: 1970-2005. *Forest Ecology and Management* 255: 3001–3012.

Fang, J., Piao, S., Tang, Z., Peng, C., & Ji, W. 2001. Interannual variability in net primary production and precipitation. *Science* 293: 1723.

Gaitán, J., Bran, D., & Oliva, G. 2014. Plant species richness and shrub cover attenuate drought effects on ecosystem functioning across Patagonian rangelands. *Biology Letters* 10: 1–4.

Gaitán, J.J., Bran, D., Oliva, G., Ciari, G., Nakamatsu, V., Salomone, J., Ferrante, D., Buono, G., Massara, V., Humano, G., Celdrán, D., Opazo, W., & Maestre, F.T. 2013. Evaluating the performance of multiple remote sensing indices to predict the spatial variability of ecosystem structure and functioning in Patagonian steppes. *Ecological Indicators* 34: 181–191.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., & Bengtsson, J. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications* 4: 1340.

Gao, X., Huete, A.R., Ni, W., & Miura, T. 2000. Optical-biophysical relationships of vegetation spectra without background contamination. *Remote Sensing of Environment* 74: 609–620.

Grime, J. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.

Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruelheide, H., Chećko, E., Forrester, D.I., Dawud, S.M., Finér, L., Pollastrini, M., Scherer-Lorenzen, M., Valladares, F., Bonal, D., & Gessler, A. 2014. Tree diversity does not always improve resistance of forest ecosystems to drought. *Proceedings of the National Academy of Sciences* 111: 14812–14815.

Hallett, L.M., Hsu, J.S., Cleland, E.E., Collins, S.L., Dickson, T.L., Farrer, E.C., Gherardi, L. a., Gross, K.L., Hobbs, R.J., Turnbull, L., & Suding, K.N. 2014. Biotic mechanisms of community stability shift along a precipitation gradient. *Ecology* 95: 1693–1700.

Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Scherer-Lorenzen, M., Sphen, E.M., Bazeley-White, E., Weilenmann, M., Caldeira, M.C., Dimitrakopoulus, P.G., Finn, J.A., Huss-Danell, K., Jumpponen, A., Mulder, C.P.H., Palmborg, C., Pereira, J., Siamantziouras, A.S.D., Terry, A.C., Troumbis, A.Y., Schmid, B., & Loreau, M. 2010. General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology* 91: 2213–2220.

Hillebrand, H., Bennett, D.M., & Cadotte, M.W. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89: 1510–1520.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B. a., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., & O'Connor, M.I. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486: 105–108.

Hooper, D.U., Chapin, F.S., Ewel, J.J., & Hector, A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*

75: 3–35.

Hu, L., & Bentler, P.M. 1999. Cutoff criteria for fit indexes in covariance structure analysis: Conventional criteria versus new alternatives. *Structural Equation Modeling: A Multidisciplinary Journal* 6: 1–55.

Huete, a., Didan, K., Miura, T., Rodriguez, E.P., Gao, X., & Ferreira, L.G. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment* 83: 195–213.

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S., & Loreau, M. 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477: 199–202.

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Carl, B., Bezemer, T.M., Bonin, C., Bruelheide, H., Luca, E. De, Ebeling, A., Griffin, J.N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., Meyer, S.T., Mori, A.S., Naeem, S., Niklaus, P.A., Polley, H.W., Reich, P.B., Roscher, C., Seabloom, E.W., Smith, M.D., Thakur, M.P., Tilman, D., Tracy, B.F., van der Putten, W.H., van Ruijven, J., Weigelt, A., Weisser, W.W., Wilsey, B., & Eisenhauer, N. 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*. doi: 10.1038/nature15374

Isbell, F.I., Polley, H.W., & Wilsey, B.J. 2009. Biodiversity, productivity and the temporal stability of productivity: Patterns and processes. *Ecology Letters* 12: 443–451.

Jactel, H., & Brockerhoff, E.G. 2007. Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10: 835–848.

Jiang, L., & Pu, Z. 2009. Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *The American naturalist* 174: 651–659.

Jucker, T., Bouriaud, O., Avacaritei, D., & Coomes, D. a. 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. *Ecology Letters* 17: 1560–1569.

Laliberté, E., & Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305.

Lambert, M.-C., Ung, C.-H., & Raulier, F. 2005. Canadian national tree aboveground biomass equations. *Canadian Journal of Forest Research* 35: 1996–2018.

Larjavaara, M., & Muller-Landau, H.C. 2010. Rethinking the value of high wood density. *Functional Ecology* 24: 701–705.

Lavorel, S. 2013. Plant functional effects on ecosystem services. *Journal of Ecology* 101: 4–8.

Loreau, M., & de Mazancourt, C. 2013. Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters* 16: 106–115.

Májeková, M., de Bello, F., Doležal, J., & Lepš, J. 2014. Plant functional traits as determinants of population stability. *Ecology* 95: 2369–2374.

Morin, X., Fahse, L., Scherer-Lorenzen, M., & Bugmann, H. 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters* 14: 1211–1219.

Paquette, A., & Messier, C. 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography* 20: 170–180.

Polley, H.W., Isbell, F.I., & Wilsey, B.J. 2013. Plant functional traits improve diversity-based predictions of temporal stability of grassland productivity. *Oikos* 122: 1275–1282.

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manriquez, G., Harms, K.E., Licona, J.., Martinez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Peña-Claros, M., Webb, C.O., & Wright, I.J. 2008. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology* 89: 1908–1920.

Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M., & Walters, M.B. 2003. The evolution of plant functional variation: traits, specctra, and strategies. *International Journal of Plant Sciences* 164: 143–164.

Roscher, C., Weigelt, A., Proulx, R., Marquard, E., Schumacher, J., Weisser, W.W., & Schmid, B. 2011. Identifying population- and community-level mechanisms of diversity-stability relationships in experimental grasslands. *Journal of Ecology* 99: 1460–1469.

Rosseel, Y. 2012. lavaan: An R package for structural equation modeling. *Journal of Statistical Software* 48: 1–36.

Ruiz-Benito, P., Gómez-Aparicio, L., Paquette, A., Messier, C., Kattge, J., & Zavala, M.A. 2014. Diversity increases carbon storage and tree productivity in Spanish forests. *Global Ecology and Biogeography* 23: 311–322.

Sasaki, T., & Lauenroth, W.K. 2011. Dominant species , rather than diversity , regulates temporal stability of plant communities. *Oecologia* 166: 761–768.

Sjöström, M., Ardö, J., Arneth, a., Boulain, N., Cappelaere, B., Eklundh, L., de Grandcourt, a., Kutsch, W.L., Merbold, L., Nouvellon, Y., Scholes, R.J., Schubert, P., Seaquist, J., & Veenendaal, E.M. 2011. Exploring the potential of MODIS EVI for modeling gross primary production across African ecosystems. *Remote Sensing of Environment* 115: 1081–1089.

Tilman, D., Ecology, S., & Jul, N. 1999. The Ecological Consequences of Changes in Biodiversity : A Search for General Principles. *Ecology* 80: 1455–1474.

Tilman, D., Reich, P.B., & Isbell, F. 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proceedings of the National Academy of Sciences* 109: 10394–10397.

Tilman, D., Reich, P.B., & Knops, J.M.H. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441: 629–632.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.

Yachi, S., & Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America* 96: 1463–1468.

Yang, Y., Fang, J., Ma, W., & Wang, W. 2008. Relationship between variability in aboveground net primary production and precipitation in global grasslands. *Geophysical Research Letters* 35: L23710.

Zhang, Y., Chen, H.Y.H., & Reich, P.B. 2012. Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. *Journal of Ecology* 100: 742–749.

Supporting Information

Appendix 4.1. SEM with CWM N_{mass}.

Appendix 4.1.

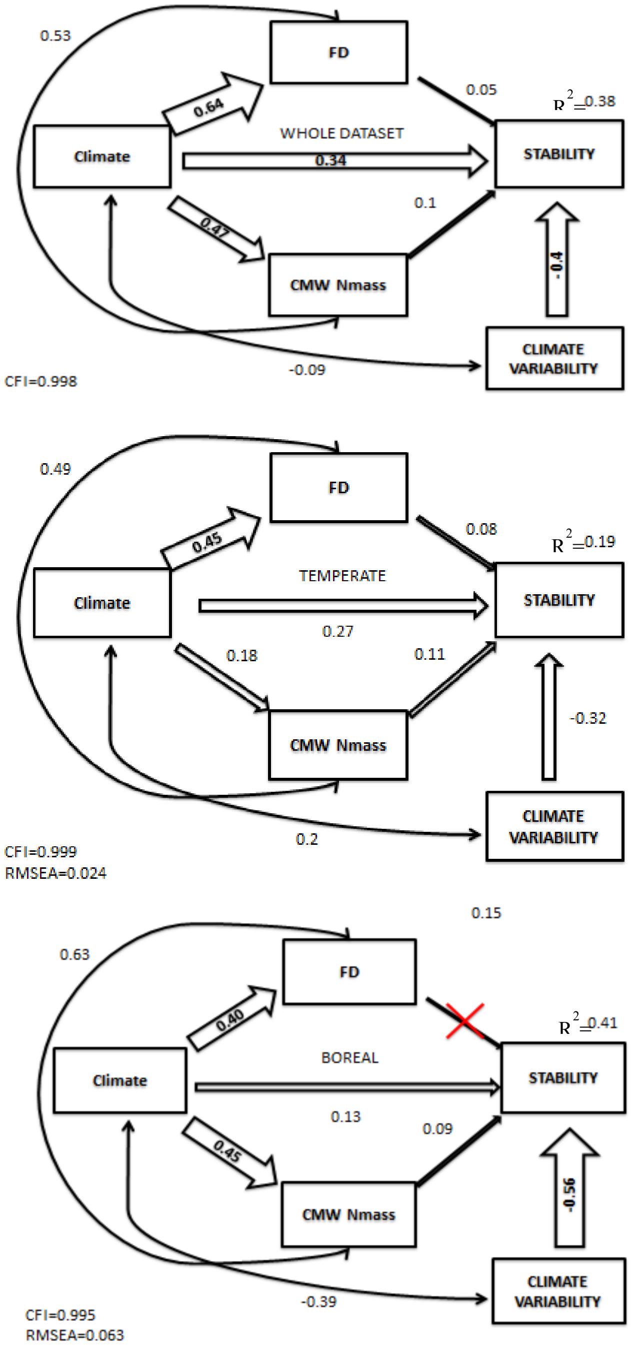


Figure 4.1.1: Structural Equation Models (SEM) with path coefficients. The variance explained for stability (i.e. R^2) and SEM fitting values (i.e. CFI and RMSEA) are also reported. Abbreviations as in Table 4.1.

Chapter 5. Environmental filtering drives community specific leaf area in the Mediterranean and predicts changes under future climatic conditions

Abstract

Ecosystem functions are mediated by species assemblages and their functional traits, and understanding their response to climate change is of main importance to develop appropriate management strategies. The following chapter proposes a novel approach to assess the impacts of climate change on ecosystem based on the assumption that community mean trait values will change as consequence of new climatic conditions (environmental filtering theory). First we assessed how environmental filtering currently operates in the Mediterranean both over the mean and range of community specific leaf area (SLA), second we assessed if actual values of community SLA will be above the limits tolerable over future aridity conditions. Our results showed that aridity is currently driving community SLA values (both mean and range) and that future climatic conditions will alter significantly those values, mainly in communities with high SLA and from humid and mid elevations. In addition, the magnitude of that change (i.e. the change in SLA needed for the community to be adapted to the new conditions) would be higher over those same communities suggesting important changes on ecosystem functions related with SLA. The approach, despite requiring current species composition data, proves useful to be applied in several other regions where forest inventory data are available.

Introduction

Current and future climate change impacts on ecosystem raise concerns for the perpetuation of their functions and the services they provide (Bellard et al., 2012; Grimm et al., 2013; Schröter et al., 2005). Since it is recognised that ecosystem functions are mediated by species assemblages and their functional attributes (Lavorel et al., 2007), how the functional structure of community will respond to climate change is of main importance to determine optimal management policies to deal whit it (Lavorel, 2013). We present a novel approach, based on environmental filtering theory (Keddy, 1992), to assess climate change impacts on the functional structure of woody plant communities in the Mediterranean.

It is recognised that the functional structure of communities (i.e. the mean traits but also its diversity) strongly affects ecosystems (Loreau et al., 2002). Species traits (i.e. plant morphological, physiological, and phenological attributes) determine the adaptive potential of species to the environment but have also been shown to quantitative correlate with several ecosystem functions (Lavorel et al., 2007). Mass ratio hypothesis states that dominant species, via their dominant attributes, determine in an "overwhelming extent" community primary production(Grime, 1998). Dominants are those species that account for the highest proportion of biomass in the community whereas transients are instable in time and space and account for less biomass (Grime, 1998). Instead, subdominants account for a smaller proportion of the community biomass and thus their contribution to primary production is lower. Community weighted mean trait (i.e. the average trait value according to species abundances, CWM) has been used to test the effect of dominant traits on ecosystem functions. For instance Garnier et al., (2004) showed how leaf traits (i.e. specific leaf area, leaf nitrogen content and leaf dry matter content) correlated with net primary productivity, litter decomposition rate, and soil carbon and nitrogen content. Indeed, they suggested these traits as "functional markers" for scaling up from individuals to ecosystems functions.

Community mean traits are also seen as a “trait expression” of environmental filtering effect on community composition (Shipley et al., 2006). Environmental filtering proclaims that the environment acts as a filter removing those species lacking a specific trait combination (Keddy, 1992). For instance Ackerly et al., (2002) in Mediterranean woody communities, found that solar radiation promoted communities composed by species with low leaf area and SLA. They argued that those trait values enhanced leaf heat loss and wilting resistance, thus species lacking this trait combination might have difficulties to perform properly under arid conditions. Moreover, Pakeman et al., (2009) using data from different locations of Europe observed that variations in community traits values were mainly explained by differences in climatic and soil conditions.

In addition to those constrains on community trait mean values, environmental filtering is also expected to influence the amount of suitable responses along gradients (i.e. the range of CWM observed in each environmental zone). It was suggested that strong filtering operates at less favourable locations promoting greater functional similarity (i.e. constraining the trait values requiered for existence in harsh conditions, Swenson et al., 2012; Weiher and Keddy, 1995). Indeed Swenson and Enquist (2007) analysing data from North, Central and South America, showed that wood density varies much less in communities from Temperate and high elevation zones than those from Tropical and low lands (i.e. more favourable abiotic conditions). Also Swenson et al. (2012) observed that Temperate regions had narrow functional traits distributions suggesting strong environmental filtering over these communities.

Traditionally, studies on climate change focused on its impacts on species distributions underpinning risks for biodiversity loss and on functions and services provided by specific species. For instance, Benito Garzón et al. (2009) assessed the potential effects of climate change on Iberian tree species reporting potential risks for a loss of genetic diversity. However, it is difficult to assess climate change impacts on ecosystem functioning based on the analysis of its impacts over a single species. To evercome this limitation, species have been grouped in different plant functional types (PFT) (Díaz and Cabido, 1997). Dynamic Global Vegetation Models (DGVM, Prentice et al., 2007) and Species Distribution Modelling (SDM, Thuiller et al., 2006) have been the approaches used to assess climate change impacts on ecosystem functioning. For instance, DGVM have been used to model net primary productivity and predict it under future scenarios (Prentice et al., 2007). Instead, SDM have been used to project the future distribution of broad functional groups and it was hypothesised that expected changes from coniferous to deciduous broadleaves forests will alter ecosystem properties as soil biogeochemistry or fire flammability (Thuiller et al., 2006). Despite their usefulness, the drawbacks of these approaches relies on the functional simplifications of communities (Scheiter et al., 2013). For instance, it has been observed that there is greater variation within PFT than among them (Yang et al., 2015). Consequently, the focus is now pointing to model community traits values in order to later project into future conditions. For instance Dubuis et al. (2013) in non-woody communities from the Swiss Alps, used regression models to fit and predict community traits values in order to projected them in a geographical space under different future climatic scenarios. Instead Frenette-Dusault et al. (2013), based on Community Assembly by Traits-Selection approach (CATS, Shipley 2009), predicted changes on community composition for different scenarios. However, the later approach needed to assume that species pool will not change in the future (i.e. no migration of new species in the study area). Indeed, it is an important drawback since changes in species distribution and consequently on species pools are the common conclusion of climate change studies (Bakkenes et al., 2002; Benito Garzón et al., 2009; Thuiller et al., 2006). Here we propose an approach that does not aim to explain if potential changes on community traits will be the consequence of relative changes in species abundances, species trait plasticity, adaptation, or new species arrivals (Bussotti et al., 2014). Instead, the study employs the hypothesis that dominant trait values will change with new conditions suggesting important changes on ecosystem functioning.

Materials and Methods

Study area and climatic and community data

The study area covered the Spanish continental territory, located between 36º N and 44ºN of latitude, and between 10º W and 3 º E longitudes. The main Koppen climatic domains are Dry and Temperate, with annual mean temperatures ranging from ~3 to ~17ºC and precipitations from ~300 to ~2,200 mm/year (Chazarra, 2011).

We classified the studied area into different aridity categories using the aridity index computed at a resolution of 30 arc seconds by Trabucco and Zommer (2009, http://www.csi.cgiar.org). The aridity index is the ratio among annual precipitation and potential evapotranspiration: potential evapotranspiration is calculated using solar radiation, mean monthly temperatures and daily temperatures ranges. Aridity categories were defined by bins of 0.2 (see Table 1).

Species community composition and cover was obtained from the Third Spanish National Forest Inventory (IFN3) (http://www.magrama.gob.es/; Direccion General de Conservacion de la Naturaleza, 2006). IFN3 includes periodical surveys (every ~10 years) of the whole forested area of Spain and reports information on stand composition, structure, and productivity. IFN3 has a regular sampling design with one sample plot every ~1km^2 accounting for more than 90,000 plots in total. We selected those plots composed by species that usually form natural forests in Spain and not classified as plantations by the IFN3 (i.e. we excluded *Eculayptus sp*. and *Pinus radiata* plantations, and plots composed by species like *Acacia sp*. or *Castanea sativa*). In addition, we only used in our analysis those plots in which the stand cover was greater than 90% (the number of species providing the 90% of cover was used as species richness in the analysis). 56,546 plots remained after this filtering process.

Species SLA values were retrieved from the literature (see Appendix 5.1 for data values and sources used). We selected those values that were measured on sun exposed leafs and on adult plants. When more than one value was found for a species, the average of the value was used for further analysis. Community weighted mean SLA (CWM SLA) was calculated as the aggregated SLA value of species inside the community weighted by their relative abundances (Garnier et al., 2004).

Climate change models predictions

The WorldClim dataset (Hijmans R. J. et al., 2005) defines a high resolution (30 arc sec or about 600 m for Spain) interpolation of monthly climate station observations (monthly average over the 1960-2000 period) of temperature (min, max and mean) and precipitation. A combination of 19 Earth System Models (ESM, see appendix) of future climate provided by Phase 5 of the Coupled Model Intercomparison Project (CIMP5; Meehl and Bony, 2011) for the different representative concentration pathways (RCP's; Vuuren et al., 2011) were downloaded from WorldClim and CIAT websites. Data have been previously downscaled using the Delta method (Ramirez and Jarvis, 2010), spatially resolving monthly GCM climate anomalies with the high resolution spatial distribution defined by the WorldClim. Data integrate multiple climate (temperature and precipitation) anomalies projections for 2050 (monthly averages 2035-2065) over WorldClim (i.e. climate model bias is excluded), although assuming that the change in climate is relatively stable over space.

Thus, using the data retrieved from CIMP5 we extracted for each plot both the projected annual precipitation and potential evapotranspiration to calculate the aridity index predicted by each of 19 ESM for the RCP 4.5 and 8.5 scenarios. Implementing such ensemble allowed to assess the uncertainty inherent to GCM simulations and RCP scenarios.

Predicting climate change impacts on plant communities

The method, based on the theory that the environment acts as a filter removing species without specific trait values (Keddy, 1992), firstly sets CWM SLA limits for each aridity class based on current CWM SLA distributions. Later, the method assess for each plot if a change in aridity class is predicted by climatic models and finally, it assess also for each plot if current values of CWM SLA will be above the limit tolerable over future conditions.

The procedure to assess potential changes was as follows: Studied plots were assigned to their relative aridity class. All CWM SLA values falling in one of the aridity classes were used to compute mean values and percentiles for each aridity class. The percentiles of each class were then regressed against aridity classes to assess how CWM SLA changed across aridity classes when using a specific percentile. Finally, based on maximum R^2 and slope stability of these regressions (it was used to note if a specific percentile can accurately represent SLA changes across aridity classes) we determined the percentile to be used as to compute the CWM SLA limit of each aridity class. Since the R^2 and slope became approximately stable above the 75th percentile we decide to run the analysis using different percentiles (i.e. 75th and 90th) thus allowing to assess the sensitivity of the results (i.e. if the predicted changes change regarding the percentile used). In order to further assess the effect of the percentile used to assess climate change impacts, we ran the analysis for all the percentiles using one specific model (i.e. the Coupled Physical Model CM3 since it predicted the greatest changes).

To determine if a change will occur, we defined two conditions that simultaneously were needed to meet: 1) climatic models have to predict a change in aridity class, and 2) current CWM SLA have to be greater than the SLA limit of the new arid class (i.e. a change in CWM SLA is need for adaptation). Thus, the plots in which a change in aridity class were identified for each CC scenario. For the plots in which a change was projected, the current CWM SLA was compared with the limit of the future aridity class (limits defined by the 75th and 90th percentiles). Those plots in which the current CWM SLA fell outside the range of the future aridity class were flagged as positive. Additionally, the difference between present and future CWM SLA was used as a measure of the magnitude of change. Finally, the probability of an expected change was estimated (and mapped) by the number of models predicting change divided by the total number of models. All these patterns were also analysed for different classes of Aridity, SLA, elevation (data extracted from https://ccafs.cgiar.org at a resolution of 30 arc seconds), and species richness.

Data analysis

Linear regression models were used to test the associations among CWM SLA and its range with aridity. All procedure were conducted under R software (R Core Team 2015, http://www.R-project.org/).

Results

Community SLA across arid zones

Both average and range of CWM SLA increased significantly across aridity classes (Fig. 5.1). Thus, communities from more humid zones tended to have higher CWM SLA and especially higher variability of CWM SLA values (the regression slope was higher for the range). Indeed, humid zones showed longer tails towards the upper end (positive skewness).

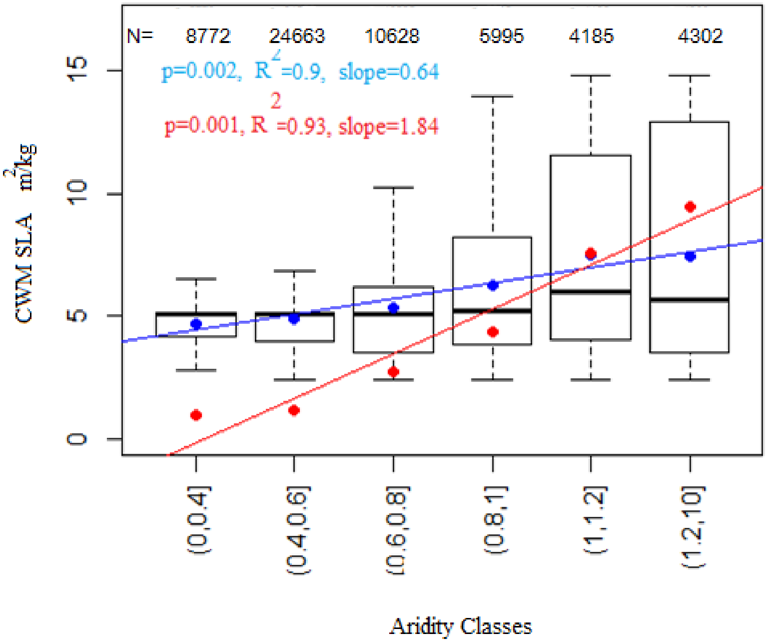


Figure 5.1: Community weighted mean SLA across aridity classes. Hinges represent the first and third quartiles and whiskers ± 1.5 the interquartile range. The blue line represents the regression line of CWM SLA average across classes (blue points). Instead, the red line represents the regression line of CWM SLA range (i.e. the difference between the 25th and 75th percentile) across aridity classes.

Percentile selection for determining CWM SLA limits and the sensibility of that decision

Regressions among limits of CWM SLA across aridity classes showed that the strength of the relationships (R2) decreased when using percentiles from the 25th to 45th. It rapidly increased up to the 60th percentile and tended to stabilize after the 75th (R2 remained around 0.9, Fig. 5.2). The slope of the regressions increased with a maximum at the 80th percentile with and slightly decreased after it (from the 75th to 90th slope values were around 1.7). The sensitivity of using a specific percentile for setting CWM SLA limits showed that the variation of the results was minimal within the range of 65th and 80th percentile for all aridity classes (Fig. 5.3).

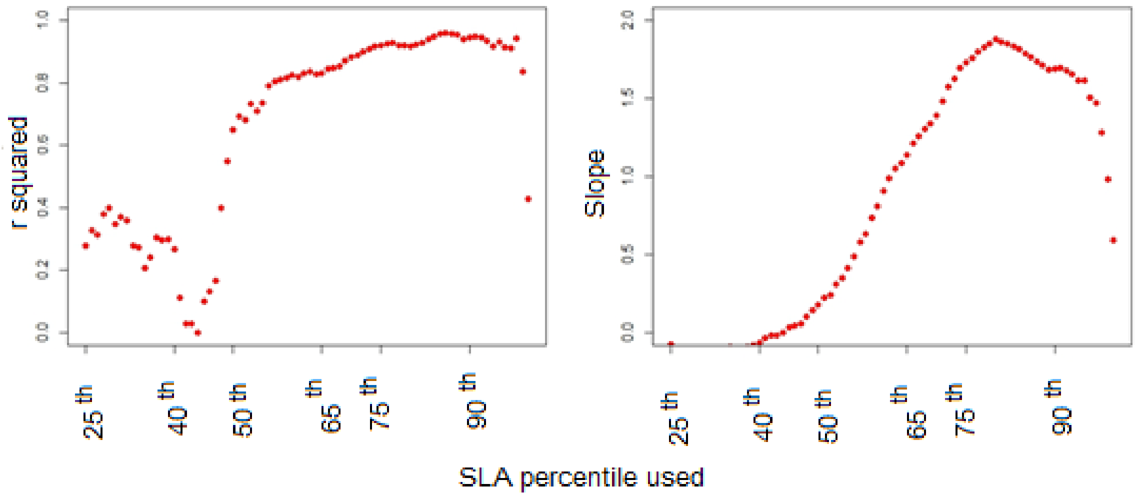


Figure 5.2: R square and slope values for regressions among SLA limits for different aridity classes

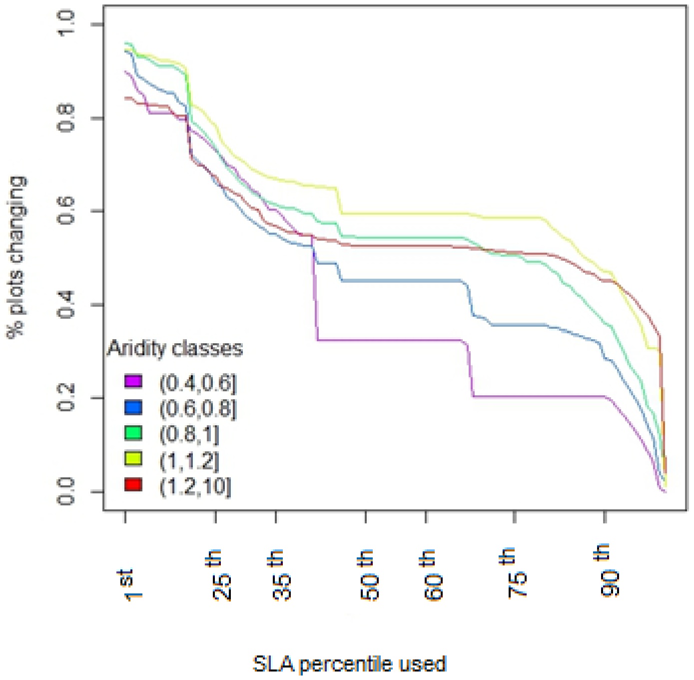


Figure 5.3: Sensitivity of using a specific percentile for set CWM SLA limits. A first Plateau is reached for most aridity classes between 80th and 65th. I.e. percentile choice between these two values has a minor effect on the results.

Expected changes were more frequent in communities characterised by an aridity index between 0.8 and 1.2 (i.e. those communities occupying less arid locations, Table 5.1). However, the magnitude of the change was greater for those locations with an aridity index between 1-1.2 and 0.6-0.8 when using percentile 75th and 90th for setting CWM SLA limits, respectively (Fig. 5.4). The other aridity classes remained approximately with the same magnitude of change independently of the percentile used. The fraction of plots with an expected change and the magnitude of change increased with the CWM SLA. Thus, more changes and with higher magnitude were predicted for communities composed of high SLA species. Elevation classes also followed that pattern with more and greater changes on high altitudes locations. Instead, the number of species composing the communities (1, 2, or 3 species) did not influence the magnitude of change, but monocultures were expected to suffer less proportion of changes.

The maps showed that regardless the RCP scenario and SLA limit used, expected changes in CWM SLA were wide spread across the whole Spanish territory excepting the south-eastern part (Fig. 5.5). Indeed, in this region almost none change were projected. Instead, regarding the magnitude of those changes, it was predicted greater for the northern part.

Table 5.1: Fraction of plots with predicted change for different community characteristics. 75th and 90th represent the results according the percentile used to set CWM SLA limits. Mean refers to the mean fraction of plots with predicted change across models. The 5th and 95th represents the fraction of plots predicted to change for the models located at those percentiles (after sorting the percentages projected by each model).

		75th						90th					
	N	RCP 4.5			RCP 8.5			RCP 4.5			RCP 8.5		
Total	56,546	5th	Mean	95th	5th	Mean	95th	5th	Mean	95th	5th	Mean	95th
Aridity class													
(0.4-0.69)	24,663	0.05	**0.10**	0.18	0.03	**0.13**	0.20	0.05	**0.10**	0.18	0.03	**0.13**	0.20
(0.6-0.8)	10,628	0.09	**0.21**	0.34	0.08	**0.25**	0.36	0.05	**0.12**	0.19	0.04	**0.15**	0.23
(0.8-1)	5995	0.11	**0.28**	0.38	0.08	**0.31**	0.44	0.03	**0.09**	0.14	0.02	**0.11**	0.21
(1-1.2)	4186	0.15	**0.34**	0.45	0.11	**0.36**	0.47	0.09	**0.22**	0.29	0.07	**0.24**	0.30
(1.2-10)	4302	0.07	**0.21**	0.35	0.05	**0.25**	0.36	0.02	**0.08**	0.17	0.02	**0.12**	0.27
Species richness													
1	28,357	0.06	**0.12**	0.18	0.05	**0.14**	0.19	0.03	**0.07**	0.12	0.03	**0.09**	0.15
2	20,724	0.08	**0.17**	0.27	0.07	**0.21**	0.30	0.06	**0.12**	0.20	0.05	**0.15**	0.23
3	9465	0.06	**0.18**	0.29	0.06	**0.22**	0.35	0.04	**0.10**	0.17	0.04	**0.13**	0.21

Table 5.1 (continuation)

		75th						90th					
		RCP 4.5			RCP 8.5			RCP 4.5			RCP 8.5		
	N	5th	Mean	95th	5th	Mean	95th	5th	Mean	95th	5th	Mean	95th
CWM SLA class													
(4-6)	28,565	0.02	**0.05**	0.08	0.02	**0.06**	0.10	0.01	**0.03**	0.05	0.01	**0.04**	0.06
(6-8)	5878	0.21	**0.48**	0.75	0.17	**0.57**	0.84	0.13	**0.27**	0.44	0.09	**0.34**	0.55
(8-10)	6434	0.28	**0.56**	0.86	0.21	**0.65**	0.93	0.15	**0.33**	0.57	0.13	**0.42**	0.69
(10-12)	2677	0.19	**0.55**	0.83	0.15	**0.63**	0.88	0.15	**0.49**	0.76	0.12	**0.57**	0.83
(12-14)	2868	0.26	**0.68**	0.97	0.18	**0.75**	0.98	0.19	**0.51**	0.77	0.14	**0.59**	0.91
(14-16)	57	0.05	**0.66**	0.98	0.30	**0.77**	0.97	0.05	**0.66**	0.98	0.30	**0.77**	0.97
Elevation class													
(0-250)	4727	0.06	**0.13**	0.19	0.04	**0.15**	0.22	0.04	**0.05**	0.07	0.01	**0.06**	0.11
(250-500)	9002	0.05	**0.14**	0.21	0.03	**0.16**	0.22	0.03	**0.09**	0.14	0.02	**0.11**	0.16
(500-1000)	27,339	0.07	**0.15**	0.23	0.05	**0.18**	0.25	0.05	**0.10**	0.15	0.04	**0.12**	0.18
(1000-1500)	15,042	0.07	**0.17**	0.29	0.05	**0.21**	0.32	0.04	**0.12**	0.22	0.03	**0.15**	0.26
(1.500-2000)	2356	0.04	**0.08**	0.12	0.03	**0.09**	0.13	0.03	**0.06**	0.08	0.02	**0.06**	0.09

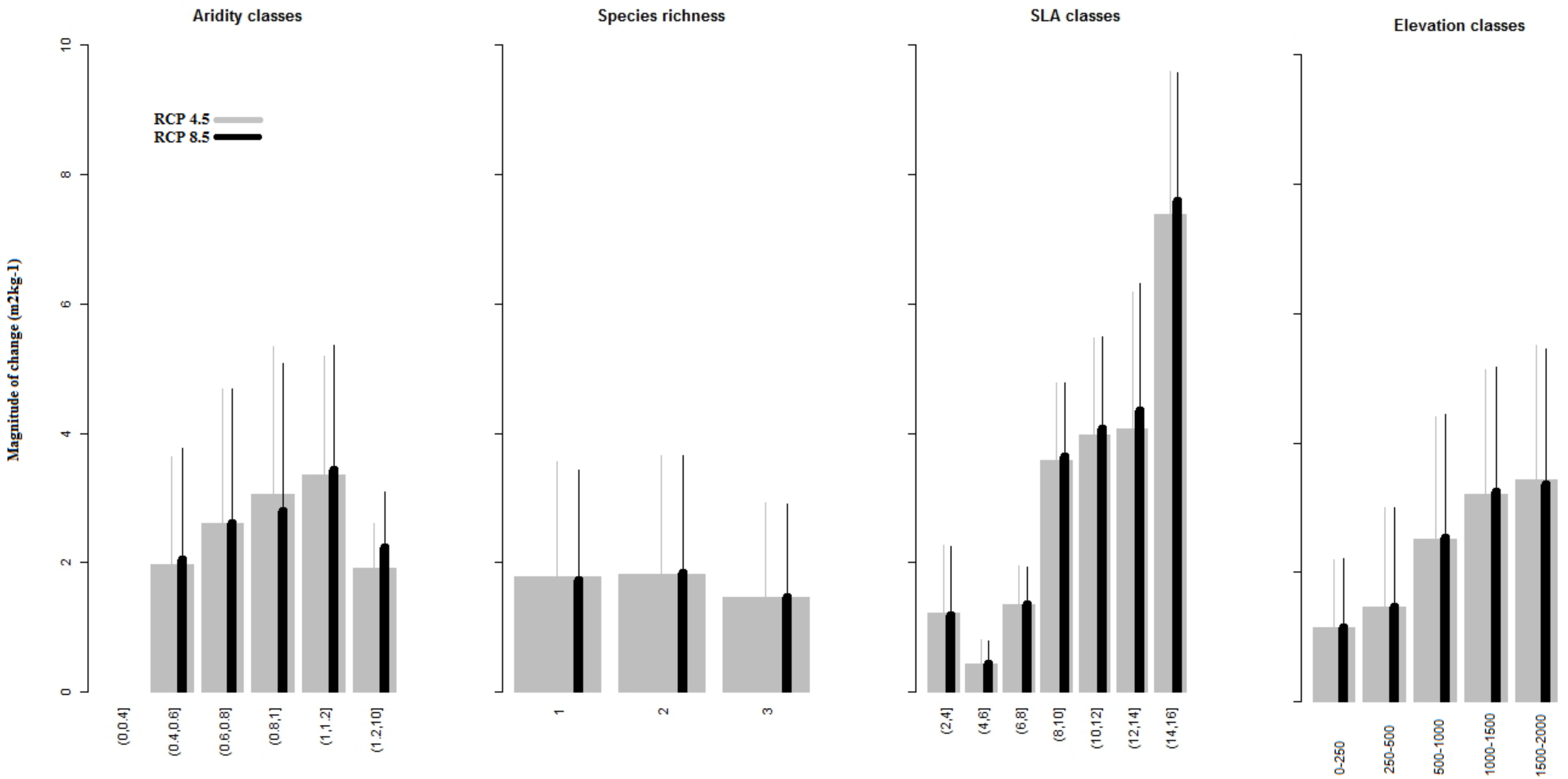


Figure 5.4.A: Magnitude of change (i.e. the difference between current CWM SLA and the limit for the future aridity class) when using the 75th percentile for setting CWM SLA limits. It is showed the mean value and its variability (i.e. standard deviation, thin lines) across different community characteristics.

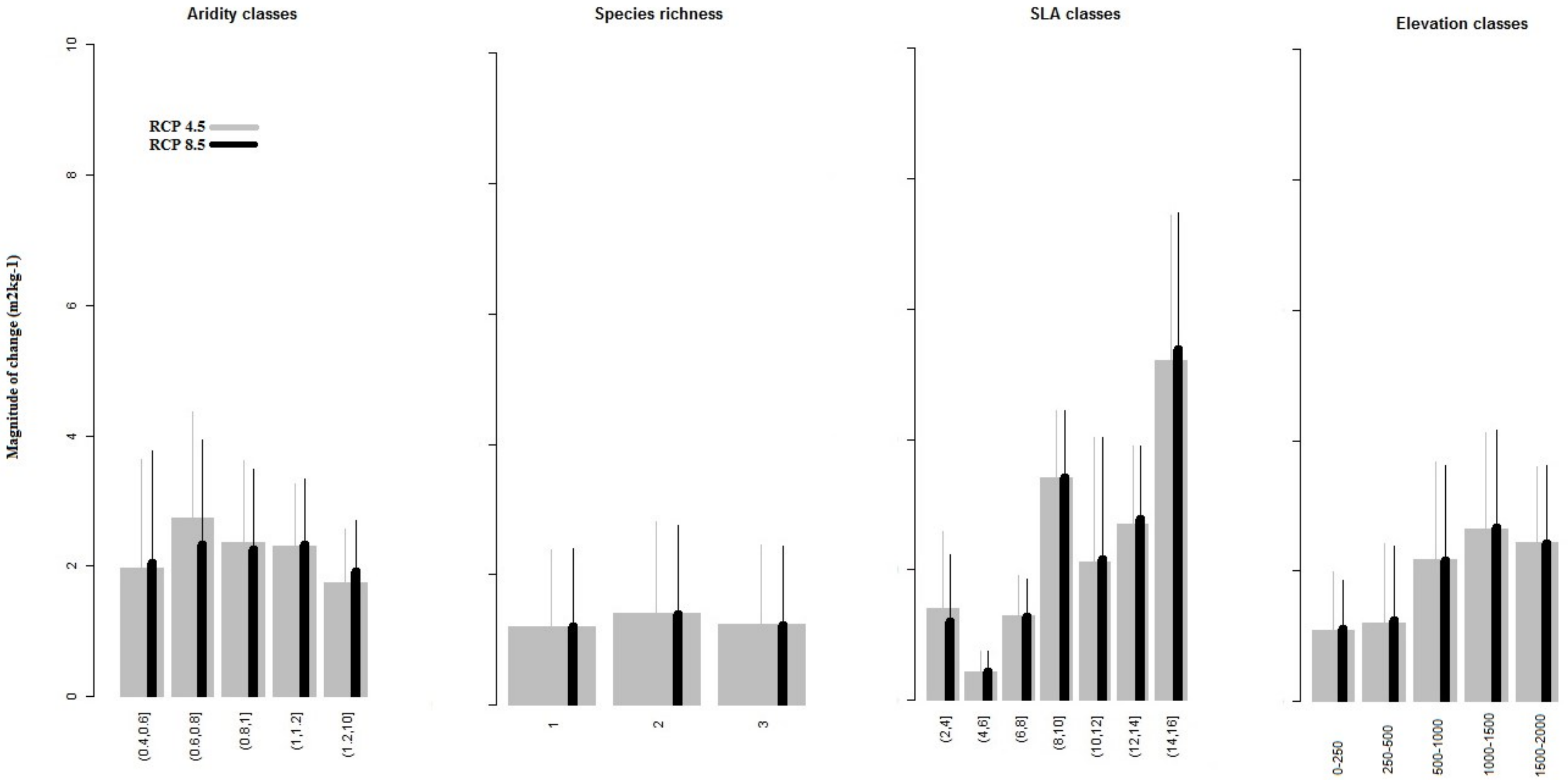


Figure 5.4.B: Magnitude of change (i.e. the difference between current CWM SLA and the limit for the future aridity class) when using the 90th percentile for setting CWM SLA limits. It is showed the mean value and its variability (i.e. standard deviation, thin lines) across different community characteristics.

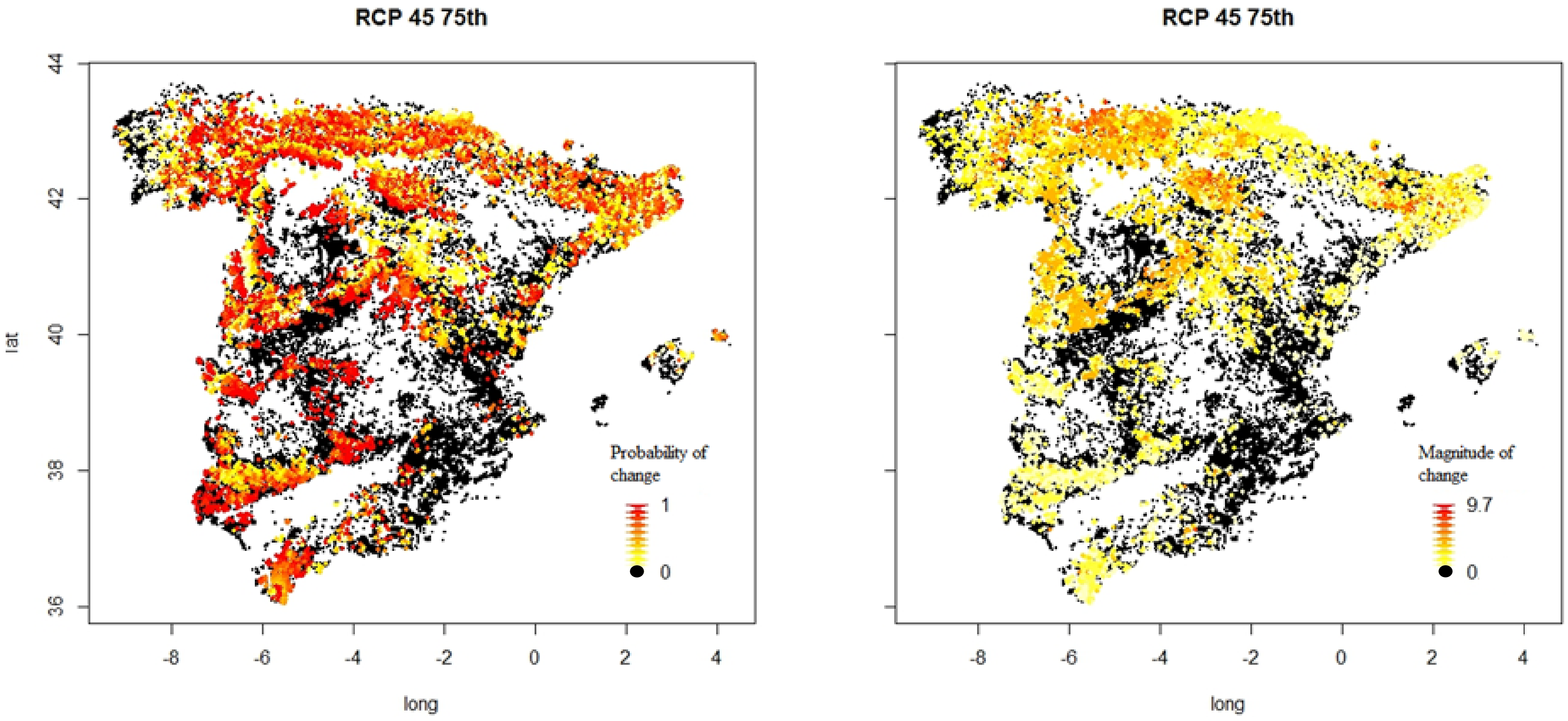


Figure 5.5.A: Maps with the probability of change (i.e. the fraction of models predicting change) and the magnitude of that change (i.e. the difference between current CWM SLA and that needed to be adapted on future conditions) for scenarios RCP 4.5 when using the 75th percentile for setting CWM SLA limits.

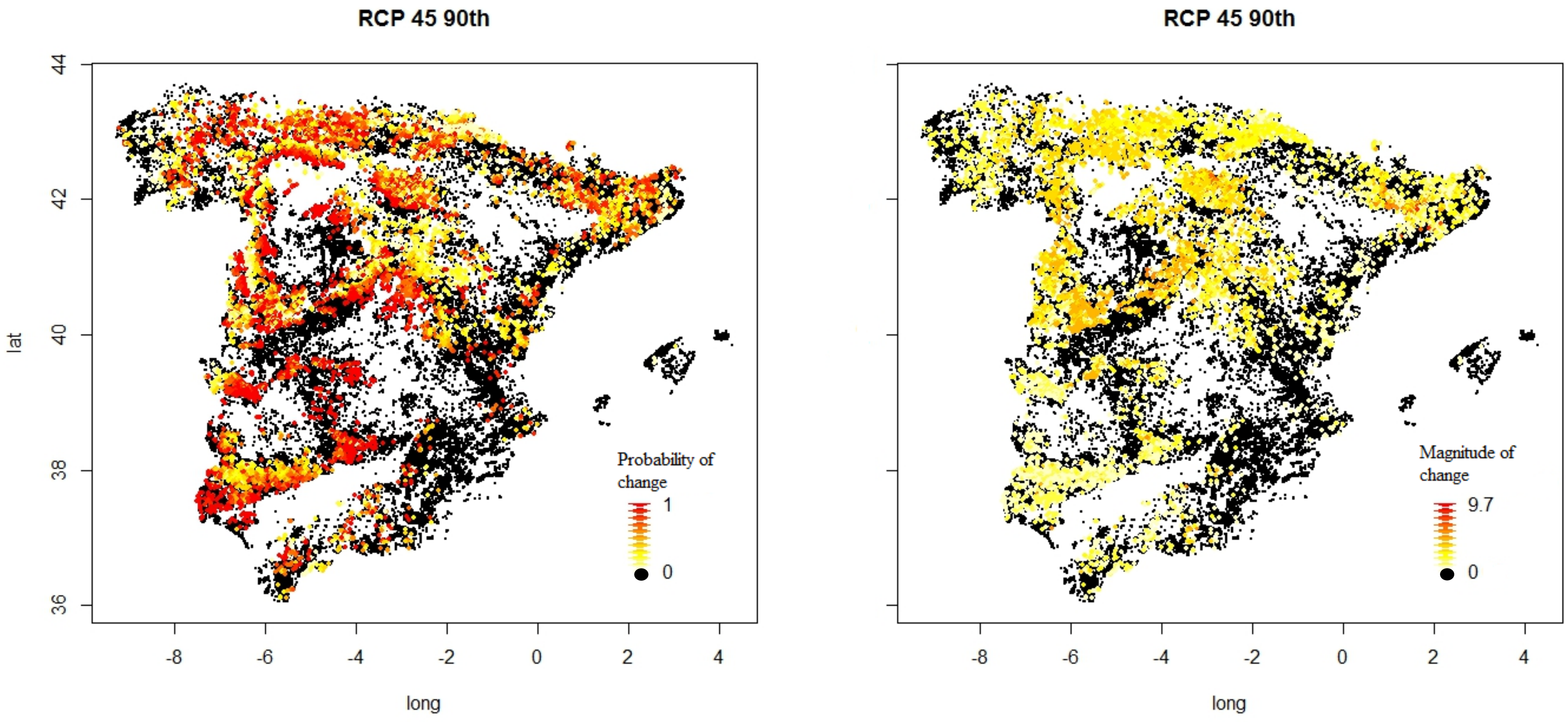


Figure 5.5.B: Maps with the probability of change (i.e. the fraction of models predicting change) and the magnitude of that change (i.e. the difference between current CWM SLA and that needed to be adapted on future conditions) for scenarios RCP .5 when using the 90th percentile for setting CWM SLA limits.

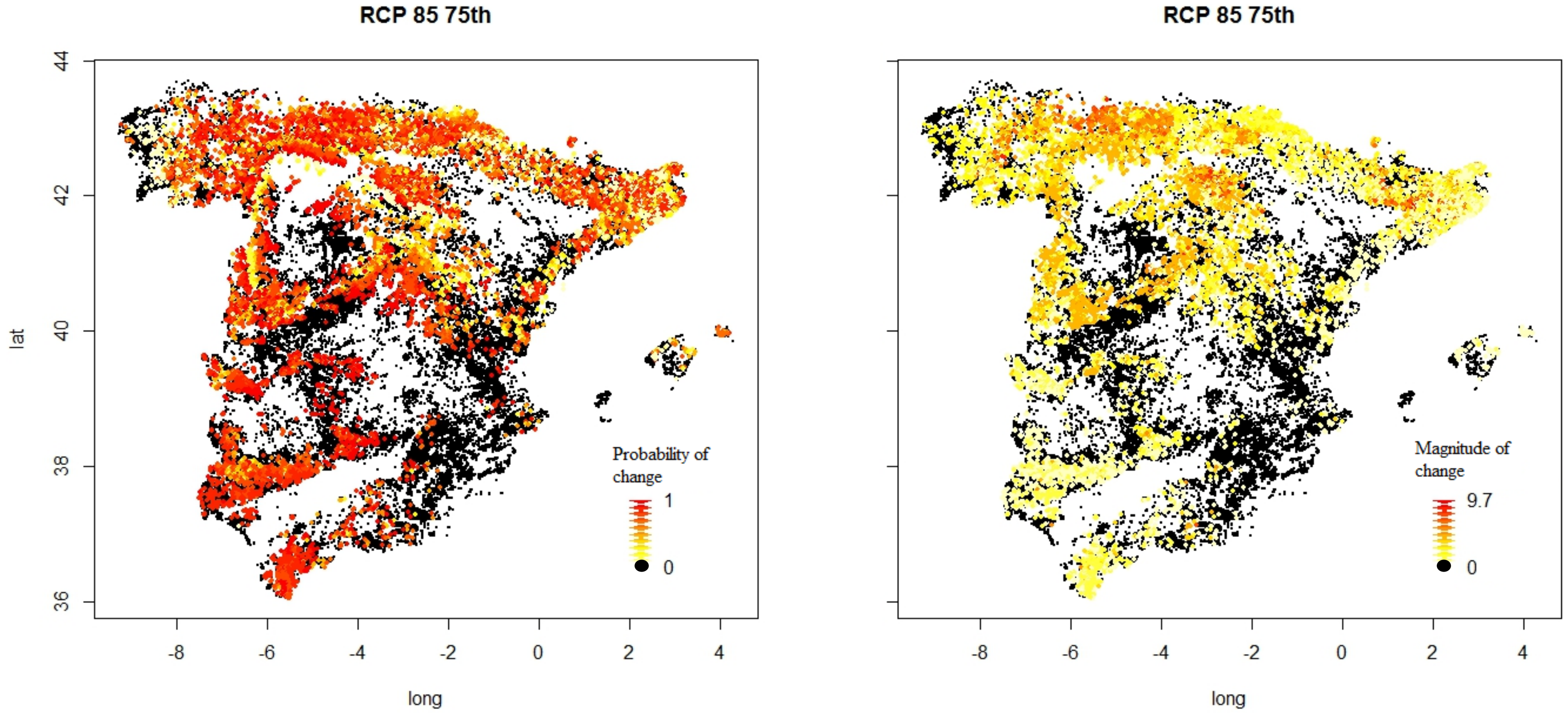


Figure 5.5.C: Maps with the probability of change (i.e. the fraction of models predicting change) and the magnitude of that change (i.e. the difference between current CWM SLA and that needed to be adapted on future conditions) for scenarios RCP 8.5 when using the 75th percentile for setting CWM SLA limits.

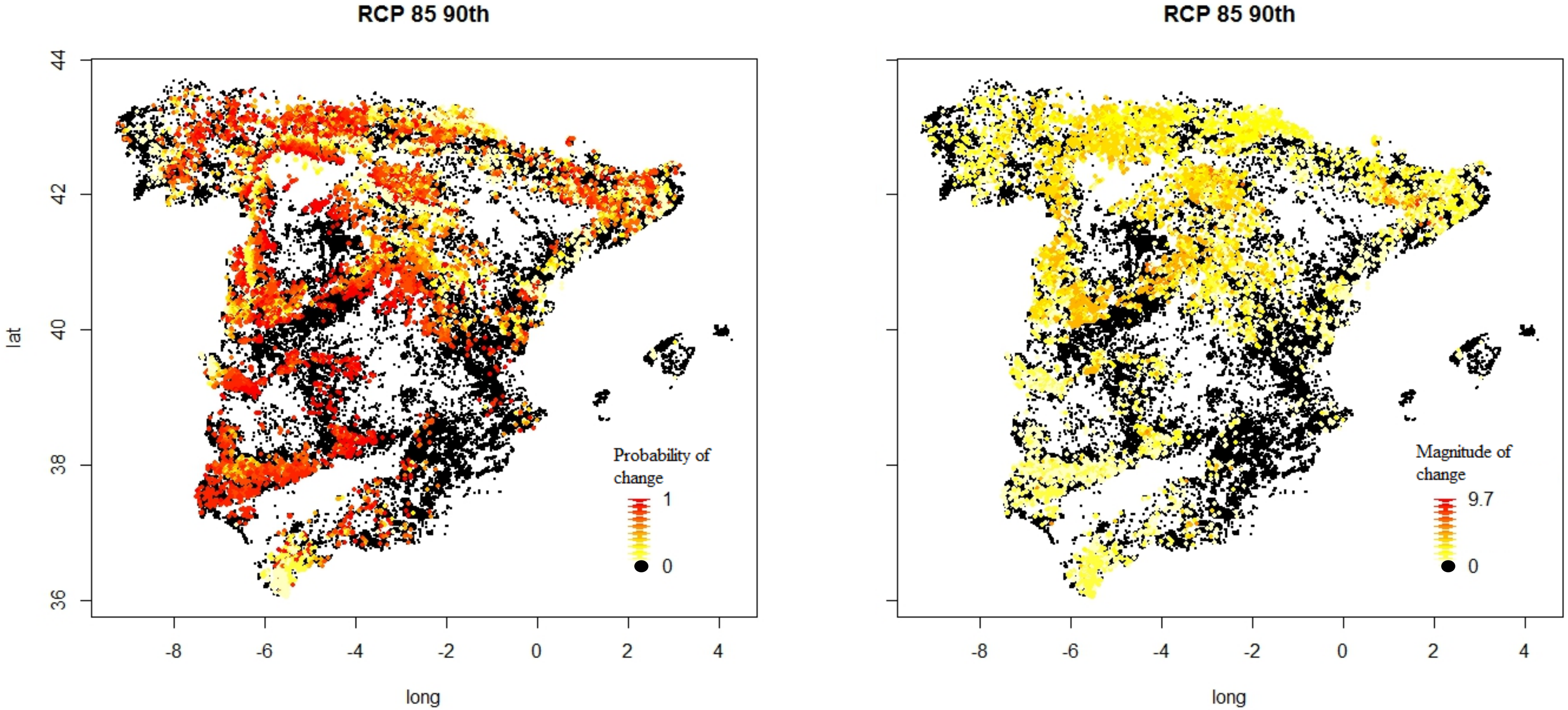


Figure 5.5.D: Maps with the probability of change (i.e. the fraction of models predicting change) and the magnitude of that change (i.e. the difference between current CWM SLA and that needed to be adapted on future conditions) for scenarios RCP 8.5 when using the 90th percentile for setting CWM SLA limits.

Discussion

Environmental filtering acting on community SLA

CWM SLA distribution across aridity classes evidenced the current filtering imposed by drought. Thus, since SLA represents species capacity to resist drought (Micco and Aronne, 2012), it was expected that increasing aridity will reduce the SLA values that allow species to exist in that locations. Indeed, Ackerly et al., (2002) found that increasing solar radiation promoted communities with low SLA in dry environments. Results also showed that in humid locations a wider spectrum of functional strategies coexists (greater CMW SLA range) whereas in arid sites the range of strategies was narrower. It is consistent with theory that predicts that filtering operates strongly in low resource environments limiting the range of strategies (i.e. limiting variability on trait values within communities, Weiher and Keddy, 1995). Indeed, Swenson et al., (2012) identified in America, that for SLA and wood density the range of values that can be observed are smaller at low mean temperatures and high latitudes sites suggesting the same trends at community level (i.e. low variability on CWM SLA and wood density.

Our results also showed that in the Mediterranean climate change will impact on community SLA values due to the overwhelming effect of environmental filtering. Studies conducted in other climatic zones and vegetation types also predict changes on community traits values due to the impositions created by future climatic conditions (Moor et al., 2015). For instance Dubuis et al., (2013), predicted increments in CWM height and SLA with warming in the Swiss Alps. However, in the Mediterranean region the expected changes are completely different from those on Temperate or Boreal zones since warming will be accompanied by a reduction of precipitations (Giorgi and Lionello, 2008). Thus, greater aridity will promote species with leaves adapted to resist drought (i.e. low SLA, Micco and Aronne, 2012). Indeed, our results projected a significant decrease in CWM SLA for some communities. Communities from humid and mid elevation locations, and with high SLA were predicted to suffer the greatest changes. Our community level analysis is in agreement with the results found by other authors working at species level, e.g. studies that analysed climate change impacts on species distribution in Spain observed that species like *Fagus sylvatica*, *Quercus petraea* or *Quercus pryrenaica*, characterised by high SLA and mainly located in mountainous regions, will suffer the greatest impacts whereas species better adapted to drought, i.e. *Pinus hapensis* or *Quercus ilex*, would be expected to increase their geographical ranges (Benito Garzón et al., 2009; Ruiz-Labourdette et al., 2012).

Our results also projected that the magnitude of the change (i.e. the difference among the current CWM SLA and the maximum tolerated over future conditions) will be greater also over communities from humid and mid elevation locations, and with high CWM SLA. Indeed, studies conducted at species level suggested that trend. For instance , Peñuelas et al., (2007) already observed that *Quercus ilex* (with SLA values between 4-7) is replacing *Fagus sylvatica* (SLA values between 12-14) in Catalonia mountains (north eastern Spain) consequence of global change.

Thus, our results jointly with those at species levels (despite the latter do not directly link with functions) suggest significant alterations on those ecosystem process related with SLA. Indeed, SLA together with climate, soil resources and other closely related traits (i.e. N content and photosynthetic rate, Wright et al., 2004) determine functions as net primary productivity (NPP, Chapin et al., 2009). With SLA being positively correlated with NPP. Therefore, big changes on high SLA communities (both in number and magnitude) imply a bigger reduction in NPP than similar changes in low SLA communities. In addition, other ecosystem functions are also closely related with SLA and this spectrum of traits, as litter decomposition (Cornwell et al., 2008; Garnier et al., 2004), suggests that impacts on traits values dominating communities might set off changes on ecosystem functioning.

An environmental filtering method for climate change assessment

The approach proposed in this study changes the focus from species to traits, allowing to overcome species-specific responses to environmental changes, i.e. adaptation, plasticity, or migration (Bussotti et al., 2014). Thus, the approach does not need to account for future species pools as other methods do (e.g. CATS, Frenette-Dussault et al., 2013) which is an important drawback since it is the common conclusion of many studies on climate change (Bakkenes et al., 2002; Benito Garzón et al., 2009; Thuiller et al., 2006).

Despite the approach simply relies on the maximum trait value that can overcome the climatic filtering (i.e. environmental filtering, Keddy, 1992), defining that limit is an uncertain task since it is difficult to determine which would be the “trait threshold” limiting species to be included in a given community under specific climatic conditions. However, testing different percentiles to set this limit allows to assess the sensibility of the approach but also the consequences of climate change under different “trait response scenarios”. Our results showed that, obviously, by setting higher CWM SLA limits less changes would be expected. However, our results also showed that under different percentiles the expected change remained stable suggesting consequently the stability of the impacts.

An important aspect of the approach is to select the trait driven by climate and assumptions taken regarding other factors that might affect that trait. However, accumulated evidence exists about the importance of different traits across climatic regions (Cornwell and Ackerly, 2009; Díaz et al., 2004; Maharjan et al., 2011). For instance, for our example on Spain we considered aridity as the unique driver of CWM SLA, since its strong influence on species distribution across an aridity gradient has been previously noticed (Costa-Saura et al, under revision, chapter 3 of this thesis). However, SLA has been shown to be also influenced by nutrient availability on tropical forest, suggesting that combining variables to determine trait distribution might improve the accuracy of the approach. Trait plasticity, which would be also interesting to include in further studies, needs more effort for being integrated since it requires specific knowledge on single species traits variation across gradient.

Conclusions

Based on environmental filtering theory (Keddy 1992), our approach provides an easy but logic way to predict climate change impacts on community mean trait values overcoming the drawbacks of approaches conducted at species levels. In addition, our approach proves useful for more directly link vegetation impacts with those on ecosystem functioning since loss of a species does not necessarily imply a change in ecosystem functioning as it could be replaced by another species performing the same function.

The approach, despite requiring current species composition data, proves useful to be applied in several other regions where forest inventory are a common practice. Indeed, in Europe at least 32 countries have their national forest inventory and Canada, United States and other countries from Central and South America, Asia and Africa also have it.

Bibliography

Ackerly, D., Knight, C., Weiss, S., Barton, K., & Starmer, K. 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia* 130: 449–457.

Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R., & Latour, J.B. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology* 8: 390–407.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters* 15: 365–377.

Benito Garzón, M., Sánchez de Dios, R., & Sainz Ollero, H. 2009. Effects of climate change on the distribution of Iberian tree species. *Applied Vegetation Science* 11: 169–178.

Bussotti, F., Pollastrini, M., Holland, V., & Bruggemann, W. 2014. Functional traits and adaptive capacity of European forests to climate change. *Environmental and Experimental Botany* 111: 91–113.

Chazarra, A. 2011. *Atlas Climático Ibérico*. Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid,SP.

Cornwell, W.K., & Ackerly, D.D. 2009. Community Assembly and Shifts in Plant Trait Distributions across an Environmental Gradient in Coastal California. *Ecological*

Monographs 79: 109–126.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D. a., Wright, I.J., Aerts, R., Allison, S.D., Van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J. a., Read, J., Reich, P.B., Soudzilovskaia, N. a., Vaieretti, M.V., & Westoby, M. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11: 1065–1071.

Díaz, S., & Cabido, M. 1997. Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science* 8: 463–474.

Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., & Zak, M.R. 2004. The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* 15: 295–304.

Direccion General de Conservacion de la Naturaleza. 2006. *Tercer Inventario Forestal Nacional 1997-2006*. Ministerio de Medio Ambiente, Madrid, SP.

Dubuis, A., Rossier, L., Pottier, J., Pellissier, L., Vittoz, P., & Guisan, A. 2013. Predicting current and future spatial community patterns of plant functional traits. *Ecography* 36: 1–11.

Frenette-Dussault, C., Shipley, B., Meziane, D., & Hingrat, Y. 2013. Trait-based climate change predictions of plant community structure in arid steppes. *Journal of Ecology* 101: 484–492.

Garnier, E., Cortez, J., Billès, G., & Navas, M. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630–2637.

Giorgi, F. 2006. Climate change hot-spots. *Geophysical Research Letters* 33: 1–4.

Giorgi, F.., & Lionello, P.. 2008. Climate change projections for the Mediterranean region. *Global and Planetary Change* 63: 90–104.

Grime, J. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.

Grimm, N.B., Chapin, F.S., Bierwagen, B., Gonzalez, P., Groffman, P.M., Luo, Y., Melton, F., Nadelhoffer, K., Pairis, A., Raymond, P. a., Schimel, J., & Williamson, C.E. 2013. The impacts of climate change on ecosystem structure and function. *Frontiers in Ecology and the Environment* 11: 474–482.

Hijmans R. J., Cameron, A., Parra, J.L., Jones, P.G., & Jarvis, A. 2005. The WorldClim interpolated global terrestrial climate surfaces. *http://www.worldclim.org*.

Keddy, P. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3: 157–164.

Lavorel, S. 2013. Plant functional effects on ecosystem services. *Journal of Ecology* 101: 4–8.

Lavorel, S., Díaz, S., Cornelissen, J.H.C., Garnier, E., Harrison, S.P., Mcintyre, S., Pausas, J.G., Catherine, N.P., Carlos, R., Roumet, C., Natalia Pérez-harguindeguy, & Urcelay, C. 2007. Plant functional types: are we getting any closer to the Holy Grail? In Canadell, J.G., Pataki, D.E., & Pitelka, L.F. (eds.), *Terrestrial Ecosystems in a Changing World*, pp. 149–160. Springer-Verlag, Berlin, Heidelberg,DE.

Loreau, M., Downing, A., Emmerson, M., Gonzalez, A., Hughes, J., Inchausti, P., Joshi, J., Norberg, J., & Sala, O.E. 2002. A new look at the relationship between diversity and stability. In Loreau, M., Naeem, S., & Inchausti, P. (eds.), *Biodiversity and ecosystem functioning: synthesis and perspectives*, pp. 79–91. Oxford University Press, Oxford, UK.

Maharjan, S.K., Poorter, L., Holmgren, M., Bongers, F., Wieringa, J.J., & Hawthorne, W.D. 2011. Plant functional traits and the distribution of West African rain forest trees along the rainfall gradient. *Biotropica* 43: 552–561.

Micco, V. De, & Aronne, G. 2012. Morpho-anatomical traits for plant adaptation to drought. In Aroca, R. (ed.), *Plant Responses to Drought Stress*, pp. 37–61. Springer Berlin Heidelberg, Berlin, Heidelberg, DE.

Moor, H., Hylander, K., & Norberg, J. 2015. Predicting climate change effects on wetland ecosystem services using species distribution modeling and plant functional traits. *Ambio* 44: 113–126.

Niinemets, Ü. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* 82: 453–469.

Pakeman, R.J., Lepš, J., Kleyer, M., Lavorel, S., Garnier, E., & Vista, C. 2009. Relative climatic , edaphic and management controls of plant functional trait signatures. *Journal of Vegetation Science* 20: 148–159.

Peñuelas, J., Ogaya, R., Boada, M., & S. Jump, A. 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography* 30: 829–837.

Prentice, I.C., Bondeau, A., Cramer, W., Harrison, S.P., Hickler, T., Lucht, W., Sitch, S., Smith, B., & Sykes, M.T. 2007. Dynamic global vegetation modelling : quantifying terrestrial ecosystem responses to large-scale environmental change. In Canadell, J., Pataki, D.E., & Pitelka, L.F. (eds.), *Terrestrial Ecosystems in a Changing World*, pp. 175–192. Springer Berlin Heidelberg, DE.

Ruiz-Labourdette, D., Nogués-Bravo, D., Ollero, H.S., Schmitz, M.F., & Pineda, F.D. 2012. Forest composition in Mediterranean mountains is projected to shift along the entire elevational gradient under climate change. *Journal of Biogeography* 39: 162–176.

Savage, V.M., Webb, C.T., & Norberg, J. 2007. A general multi-trait-based framework for studying the effects of biodiversity on ecosystem functioning. *Journal of*

Theoretical Biology 247: 213–29.

Scheiter, S., Langan, L., & Higgins, S. 2013. Next generation dynamic global vegetation models: learning from community ecology. *New Phytologist* 198: 957–969.

Schröter, D., Cramer, W., Leemans, R., Prentice, I.C., Araújo, M.B., Arnell, N.W., Bondeau, A., Bugmann, H., Carter, T.R., Gracia, C. a, de la Vega-Leinert, A.C., Erhard, M., Ewert, F., Glendining, M., House, J.I., Kankaanpää, S., Klein, R.J.T., Lavorel, S., Lindner, M., Metzger, M.J., Meyer, J., Mitchell, T.D., Reginster, I., Rounsevell, M., Sabaté, S., Sitch, S., Smith, B., Smith, J., Smith, P., Sykes, M.T., Thonicke, K., Thuiller, W., Tuck, G., Zaehle, S., & Zierl, B. 2005. Ecosystem service supply and vulnerability to global change in Europe. *Science* 310: 1333–1337.

Shipley, B., Vile, D., & Garnier, É. 2006. From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science* 314: 812–814.

Stuart Chapin III, F., McFarland, J., David McGuire, a., Euskirchen, E.S., Ruess, R.W., & Kielland, K. 2009. The changing global carbon cycle: linking plant-soil carbon dynamics to global consequences. *Journal of Ecology* 97: 840–850.

Swenson, N., & Enquist, B. 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany* 94: 451–459.

Swenson, N.G., Enquist, B.J., Pither, J., Kerkhoff, A.J., Boyle, B., Weiser, M.D., Elser, J.J., Fagan, W.F., Forero-Montaña, J., Fyllas, N., Kraft, N.J.B., Lake, J.K., Moles, A.T., Patiño, S., Phillips, O.L., Price, C. a., Reich, P.B., Quesada, C. a., Stegen, J.C., Valencia, R., Wright, I.J., Wright, S.J., Andelman, S., Jørgensen, P.M., Lacher Jr, T.E., Monteagudo, A., Núñez-Vargas, M.P., Vasquez-Martínez, R., & Nolting, K.M. 2012. The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography* 21: 798–808.

Thuiller, W., Lavorel, S., Sykes, M.T., & Araújo, M.B. 2006. Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions* 12: 49–60.

Weiher, E., & Keddy, P. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos* 74: 159–164.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., & Villar, R. 2004. The worldwide leaf economics spectrum. *Nature* 12: 821–827.

Yang, Y., Zhu, Q., Peng, C., Wang, H., & Chen, H. 2015. From plant functional types to plant functional traits: A new paradigm in modelling global vegetation dynamics. *Progress in Physical Geography* 39: 514–535.

Supporting Information

Appendix 5.1. SLA values and sources used.

Appendix 5.2. Global circulation models integrated in the CMIP5 program.

Appendix 5.1

Table 5.1.1: Species SLA values used

Species	SLA (m^2kg^{-1})
Acer monspessulanum	10.7
Arbutus unedo	6.5
Buxus sempervirens	5.9
Crataegus monogyna	9.9
Erica arborea	7.8
Fraxinus angustifolia	10.7
Fagus sylvatica	13.0
Juniperus oxycedrus	4.0
Olea europaea	4.7
Pinus halepensis	5.1
Phyllerea latifolia	7.1
Pinus nigra	3.1
Pinus pinaster	2.4
Pinus pinea	3.3
Prunus spinosa	12.5
Pinus sylvestris	3.5
Pistacia terebinthus	7.5
Quercus faginea	8.9
Quercus ilex	5.0
Quercus petraea	13.5
Quercus pubescens	14.8
Quercus pyrenaica	9.8
Quercus robur	14.0
Quercues suber	6.5
Rhamnus alaternus	7.3

<u>*Sources used for species SLA data:*</u>

Bauer, G., Schulze, E.D., & Mund, M. 1997. Nutrient contents and concentrations in relation to growth of Picea abies and Fagus sylvatica along a European transect. Tree physiology 17: 777–86.

Cavender-Bares, J., Cortes, P., Rambal, S., Joffre, R., Miles, B., & Rocheteau, a. 2005. Summer and winter sensitivity of leaves and xylem to minimum freezing temperatures: a comparison of co-occurring Mediterranean oaks that differ in leaf lifespan. The New phytologist 168: 597–612.

Chaideftou, E., Thanos, C.A., & Dimopoulos, P. 2006. Plant functional traits in relation to seedling recruitment and light conditions in sub-Mediterranean oak forests of Greece. In Plant, fungal and habitat diversity investigation and conservation. Proceedings of IV Balkan Botanical Congress, Sofia, pp. 597–601.

Escudero, a., & Mediavilla, S. 2003. Decline in photosynthetic nitrogen use efficiency with leaf age and nitrogen resorption as determinants of leaf life span. Journal of Ecology 91: 880–889.

Faria, T., Silvério, D., Breis, E., Cabral, R., Abadia, A., Abadia, J.S., Perreira, J.S., & Chaves, M.M. 1998. Differences in the response of carbon assimilation to summer stress (water deficits, high light and temperature) in four Mediterranean tree species. Physiologia Plantarum 102: 419–428.

Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelier, P., Ducout, B., Roumet, C., & Navas, M. 2001. Consistency of species ranking based on functional leaf traits. 152: 69–83.

Gratani, L., & Bombelli, A. 2001. Differences in leaf traits among Mediterranean broad-leaved evergreen shrubs. Annales Botanicci Fennici 38: 15–24.

Gratani, L., & Varone, L. 2004. Leaf key traits of Erica arborea L., Erica multiflora L. and Rosmarinus officinalis L. co-occurring in the Mediterranean maquis. Flora 69: 58–69.

Gratani, L., & Varone, L. 2006. Long-time variations in leaf mass and area of Mediterranean evergreen broad-leaf and narrow-leaf maquis species. Photosynthetica 44: 161–168.

Gulías, J., Flexas, J., Abadía, a, & Madrano, H. 2002. Photosynthetic responses to water deficit in six Mediterranean sclerophyll species: possible factors explaining the declining distribution of Rhamnus ludovici-salvatoris, an endemic Balearic species. Tree physiology 22: 687–97.

Lansac, A.R., Zaballos, J.P., & Martin, A. 1994. Seasonal water potential changes and proline accumulation in mediterranean shrubland species. Vegetatio 113: 141–154.

Mediavilla, S., & Escudero, A. 2003. Mature trees versus seedlings: differences in leaf traits and gas exchange patterns in three co-occurring Mediterranean oaks. Annals of Forest Science 60: 455–460.

Mediavilla, S., Escudero, A., & Ecology, S.P. 2003. Relative Growth Rate of Leaf Biomass and Leaf Nitrogen Content in Several Mediterranean Woody Species. Plant Ecology 168: 321–332.

Morecroft, M.D., & Roberts, J.M. 1999. Photosynthesis and stomatal conductance of mature canopy Oak (Quercus robur) and Sycamore (Acer pseudoplatanus) trees throughout the growing season. Functional Ecology 13: 332–342.

Nardini, A., Pedà, G., & La Rocca, N. 2012. Trade-offs between leaf hydraulic capacity and drought vulnerability: morpho-anatomical bases, carbon costs and ecological consequences. The New phytologist 196: 788–98.

Robson, T.M., Sánchez-Gómez, D., Cano, F.J., & Aranda, I. 2012. Variation in functional leaf traits among beech provenances during a Spanish summer reflects the differences in their origin. Tree Genetics & Genomes 8: 1111–1121.

Varone, L., & Gratani, L. 2009. Leaf expansion in Rhamnus alaternus L. by leaf morphological, anatomical and physiological analysis. Trees 23: 1255–1262.

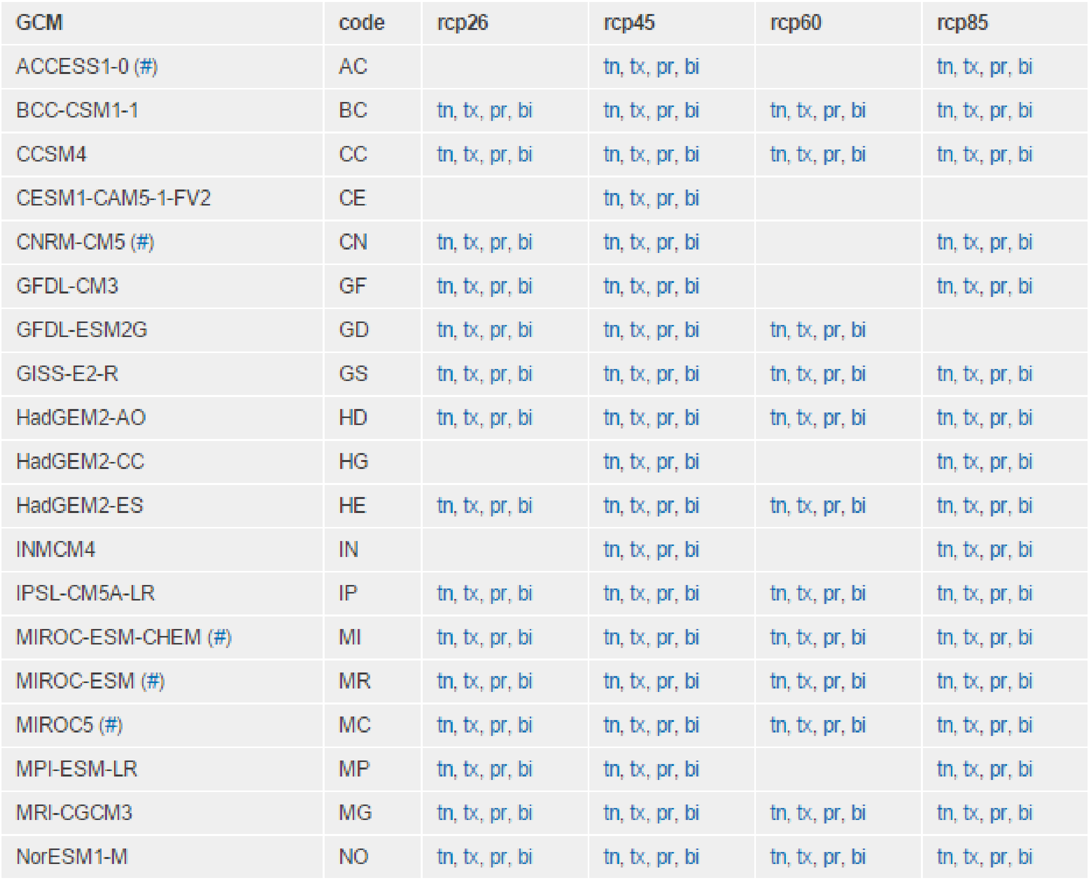
Villar-Salvador, P., & Castro-Díez, P. 1997. Stem xylem features in three Quercus (Fagaceae) species along a climatic gradient in NE Spain. Trees 12: 90–96.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., & Villar, R. 2004. The worldwide leaf economics spectrum. Nature 12: 821–827.

Wuytack, T. 2012. Biomonitoring ambient air quality using leaf characteristics of trees.

Appendix 5.2.

Table 5.2.1: Global circulation models integrated in the CMIP5 program and type of data available. tn, tx, pr and bc refer to monthly average minimum temperature, monthly average maximum temperature, monthly total precipitation and bioclimatic variables, respectively.



GCM	code	rcp26	rcp45	rcp60	rcp85
ACCESS1-0 (#)	AC		tn, tx, pr, bi		tn, tx, pr, bi
BCC-CSM1-1	BC	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi
CCSM4	CC	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi
CESM1-CAM5-1-FV2	CE		tn, tx, pr, bi		
CNRM-CM5 (#)	CN	tn, tx, pr, bi	tn, tx, pr, bi		tn, tx, pr, bi
GFDL-CM3	GF	tn, tx, pr, bi	tn, tx, pr, bi		tn, tx, pr, bi
GFDL-ESM2G	GD	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi	
GISS-E2-R	GS	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi
HadGEM2-AO	HD	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi
HadGEM2-CC	HG		tn, tx, pr, bi		tn, tx, pr, bi
HadGEM2-ES	HE	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi
INMCM4	IN		tn, tx, pr, bi		tn, tx, pr, bi
IPSL-CM5A-LR	IP	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi
MIROC-ESM-CHEM (#)	MI	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi
MIROC-ESM (#)	MR	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi
MIROC5 (#)	MC	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi
MPI-ESM-LR	MP	tn, tx, pr, bi	tn, tx, pr, bi		tn, tx, pr, bi
MRI-CGCM3	MG	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi
NorESM1-M	NO	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi	tn, tx, pr, bi

General Conclusions

This thesis showed that trait based ecology is a useful approach for identify the mechanisms behind important ecological aspects providing relevant information for the management of forests. It was showed that: 1) with few traits is possible to determine species preferences and limitations across environmental gradients, 2) that trait diversity might promote the stability of ecosystems, and 3) that climate change might alter the dominant traits of communities with consequences on ecosystem functioning. From a theoretical perspective the thesis brings new insights on how traits shape species niche and drive ecosystem functions whereas from applied perspective provides a new look on how to address forest management strategies under current and future climatic conditions. For instance, it proves useful for a "mechanism based" selection of species for restoration plans, i.e. the selection of appropriate species genotypes and provenances according to those traits providing adaptation for future climatic conditions. In addition, it provides useful information for "trait oriented" silvicultural practices, i.e. cuttings and thinning focalized to promote trait diversity or specific traits values in order to adapt and mitigate the effects of climate change.

The thesis also showed the close link among species, communities and ecosystems evidencing the usefulness of trait ecology for scaling up the effect of management strategies over these three levels. For instance, how the promotion of specific traits values within communities (i.e. managing species abundances) might simultaneously influence the resistance and resilience of communities but also the productivity and stability of ecosystems.

It was also showed that trait ecology can served on different tools to expand the range of its analysis and for exploring different ecological dimensions. Indeed, it was showed that remote sensing and climate change modelling proved useful for deal with different temporal scales across wide areas whereas SDM allowed for extrapolate analysis into geographical and niche spaces. In fact, since trait ecology offers both explanations and predictions because relies on the mechanism providing a given function, it suggests potential applications over topics like fire behaviour (traits determining flammability) or carbon stock modelling (traits determining carbon residence time).

Further research directions should simultaneously integrate traits influence on species environmental responses but also its effect on different ecosystems functions. Indeed, despite we provided information about "traits aridity tolerance", lack of knowledge still remaining on how these traits perform in terms of "biomass production" across climatic gradients. Thus, future research should relate species traits with species performance across environmental gradients (feasible with data from forest inventory) but simultaneously considering the effect of neighbors and the effects over other ecosystem functions. Thus, an integrative approach including drought adaptation, productivity, and other functions should provide more complete information for later implement the most optimal management actions.

To conclude just remember that *traits, in its biggest sense, are the attributes that inanimate and animated "beings" have to interact with their surroundings and that these "decisions", usually entails unavoidable trade-offs among the way they perform and interact with their surroundings. Being this presumably true for all "beings" across the Universe, it consequently can be extrapolated to humans, which should make us reflect about many different aspects of our lifes.*

Acknowledgments

I would like to thank all persons that in one way or another helped for the development of this Thesis. First of all I have to thank my professor Donatella Spano for give me the opportunity for developing this project and trusting me. Also I warmly thank my tutor Simone Mereu because his enthusiasm, ideas, discussions, guidance and help, were the basis for this work.

I would like also to thank researches and colleagues from the UNISS, CMCC, WSL, CREAF and CEF for their relevant contribution on this work, i.e. Antonio Trabucco, Niklaus Zimmermann, Jordi Martinez Vilalta, Carlo Pensavalle, Tiziano Iddi and Alain Paquette.

Finally I would like to thank all my friends from Sassari and Spain for their confidence and help; to my family because what I am and what I did is in a great part a consequence of what they directly and indirectly taught me; and finally thank Olga because beyond their support during this thesis, she makes me grow and discover new ways for deal and enjoy life.