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Environmental filtering drives community specific leaf area in Spanish forests and predicts relevant changes under future climatic conditions

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ABSTRACT

How functional traits at community level relate with environmental conditions is of great relevance to assess potential effects of climate change on ecosystem functioning. Species' specific leaf area (SLA) is well recognised to be closely correlated with species drought resistance and with other forest functions such as productivity. Here, we used tree species abundance data from 44 501 forest plots from the Third Spanish National Forest Inventory and species SLA values from literature to assess how community weighted mean SLA (CWM_{SLA}) and SLA diversity within communities ($FDis_{SLA}$) of Spanish forests correlate with aridity. Later, using 19 climate change projections and following an approach that limits the values of CWM_{SLA} along an aridity gradient, we assessed the potential climatic effects on CWM_{SLA} for 2050 under the representative concentration pathways (RCP) 4.5 and 8.5. Results showed that CWM_{SLA} and $FDis_{SLA}$ decreased significantly with aridity (deviance explained was 22 and 9%, respectively) suggesting an effect of climatic filtering at community level constraining the diversity of co-occurring strategies at harsher conditions. Up to 25% of plots were predicted to suffer changes in CWM_{SLA} with these impacts being more common and of a greater magnitude in communities characterised by a high CWM_{SLA} and located at humid and mid-altitude zones. Instead, communities already striving in arid areas appeared to be more resilient. The study proves useful for orienting forest management practices in current permanent forest stands based on trait ecology (e.g. promoting communities species composition with specific trait values), to increase their mitigation potential and adaptive capacity to current and future changing climate conditions.

1. Introduction

Global change poses a threat to forest ecosystems and for the services they provide such as carbon sequestration, water regulation or nutrient cycling (Bartczak et al., 2014; Lindner et al., 2010; Schröter et al., 2005). Indeed, recent climate change is already influencing wood production and carbon storage of forests across biomes. Although this influence might be positive in several colder biomes that are experiencing warmer and wetter condition (e.g. increasing productivity, Briceño-Elizondo et al., 2006; Eggers et al., 2008), the effects of climate change are clearly negative in the Mediterranean region (e.g. decreasing tree growth and carbon stocks, Vayreda et al., 2012; Ruiz-Benito et al., 2014a). In fact, among different regions, the Mediterranean basin is considered exceptionally vulnerable to climatic change (Lindner et al., 2010; Schröter et al., 2005) because of its location within the transitional zone between temperate and arid climates (i.e. between central Europe and north Africa) where a reduction in precipitation and a strong increase in temperatures is expected (Giorgi,

2006). Since ecosystem services of Mediterranean are in great extent determined by the functional attributes of communities (see Ruiz-Benito et al., 2014b) how they may respond to climate change is extremely relevant to determine optimal management policies to increase resilience and optimize functionalities (Lavorel, 2013).

A trait-based approach (i.e. based on plant morphological, physiological, or phenological attributes, Violle et al., 2007) is a powerful approach to assess climate change impacts, since traits represent both species adaptation to the environment and their effects on ecosystems (Lavorel et al., 2007). Both functional diversity (FD) and Community Weighted Mean (CWM) of functional traits have been shown to be relevant for ecosystem functioning at the community level (Jucker et al., 2014; Mokany et al., 2008; Paquette and Messier, 2011). CWM is based on the mass ratio hypothesis (Grime, 1998), which states that dominant species can determine, to a great extent, some ecosystem functions such a productivity via their dominant attributes (Lavorel et al., 2011; Roscher et al., 2012). In this context, dominant species are those that account for the highest proportion of biomass in the community

whereas transients species are those instable in time and space and account for less biomass (Grime, 1998). Thus, dominant traits combined in the form of CWM have been used to test the effect of different species compositions on ecosystem functions (Debouk et al., 2015; Lavorel et al., 2011). For instance, Garnier et al. (2004) studying Mediterranean successional series following vineyard abandonment showed how CWM traits (i.e. community specific leaf area and leaf nitrogen content) were positively correlated with functions such as net primary productivity and litter decomposition rate. Accordingly, they suggested these traits as functional markers for scaling up from species organs to ecosystems functions. FD (i.e. trait diversity within communities) has also been found to positively influence ecosystem functioning through mechanisms such as complementary and facilitation resource use (Hooper et al., 2005). For instance, it was observed that FD might improve functions such as productivity and stability across different forest systems (Jucker et al., 2014; Paquette and Messier, 2011; Ruiz-Benito et al., 2014b).

Community mean traits are also seen as a trait expression of the environmental filtering effect on community composition (i.e. environmental selection at community level; Shipley et al., 2006). This means that environmental factors act as a filter by removing those species lacking a specific combination of traits (Keddy, 1992), and thus species of a given community at a given environmental condition tend to converge on specific trait values, but note that a certain degree of trait divergence is also expected for species coexistence because of niche differentiation (Chesson, 2000; Maire et al., 2012). For instance, Ackerly et al. (2002) found that in Mediterranean climates, solar radiation promoted communities mostly composed by species with low leaf area and low specific leaf area (SLA). They argued that species lacking this trait combination might have difficulties to perform properly under arid conditions. Indeed, low SLA values are commonly related with more tightly packed cells with thicker cell walls and few air spaces which might enhance leaf wilting resistance and reduce water losses (Poorter et al., 2009; Micco and Aronne, 2012; De la Riva et al., 2016a). Moreover, Pakeman et al. (2009) using data from different vegetation types across locations in Europe observed that variations in community traits values were mainly explained by differences in climatic and soil conditions. However, sometimes CWM might not entirely reflect species optimal strategies because the environment might more strongly constrain multivariate than univariate traits (Muscarella and Uriarte, 2016).

In addition, environmental filtering is also expected to influence the variation of suitable functional responses along climatic gradients (i.e. a lower FD but also a narrower range of CWM values). It has been suggested that strong filtering operates at less favourable locations promoting greater functional similarity (i.e. constraining the trait values required 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 less in forest communities from temperate and high elevation zones than those from tropical and low lands with more favourable abiotic conditions.

Studies on climate change traditionally have focused on its impact on species distributions and the risk of specific species being lost including their functions and services they provide (e.g. Hanewinkel et al., 2013). For instance, Garzón et al. (2008) reported potential losses of genetic diversity of Iberian tree by some species reducing their range as a consequence of climate change. However, in general it is difficult to assess climate change impact on ecosystem functioning based on a single species analysis. An alternative approach used to overcome this limitation is to group species in plant functional types (PFT), assuming that a set of species share a similar eco-physiology and thus affect ecosystems in a similar way (Díaz and Cabido, 1997). Dynamic Global Vegetation Models (DGVM, Prentice et al., 2007) and Species Distribution Modelling (SDM, Thuiller et al., 2006) approaches have been used to translate climate change impacts on PFT into consequences for

ecosystem functioning. For instance, DGVM have been used to model and predict net primary productivity under future scenarios (Prentice et al., 2007) and SDM to project future distributions of functional groups exploring potential effects on ecosystem properties such as soil biogeochemistry or fire flammability (Thuiller et al., 2006). Despite their usefulness, one of the limitations of these approaches is that they rely on the functional simplifications of communities (Scheiter et al., 2013), wherein Yang et al. (2015) observed that there might be greater variations within PFT (in terms of functional responses and effects) than among them. To overcome these methodological limits, research is now pointing to model community traits values as a whole and later project these under future conditions, in order to assess more accurately how the impacts of climate change on vegetation translate into changes in ecosystem functioning. For instance, Frenette-Dussault et al. (2013), based on the Community Assembly by Traits-Selection approach (CATS, Shipley, 2009), predicted shifts from ruderal to stress-tolerant sub-shrub communities on Morocco steppes, which might reduce the pastoral value of vegetation. However, CATS approach needs to assume that species pool from the studied area will not change in the future (i.e. no migration of new species from other areas). This assumption is an important drawback since migration of new species and consequently changes in species pools are common output from most studies on the effects of climate change in species distribution (Bakkenes et al., 2002; Garzón et al., 2008; Thuiller et al., 2006). Here, we propose an approach that does not need to articulate potential changes on community mean traits considering relative changes in species abundances, species trait plasticity, adaptation, or new species arrivals (note, that all mechanism may lead to changes on CWM; Bussotti et al., 2014). Instead, based on the environmental filtering theory (Keddy, 1992), our study stresses the hypothesis that dominant trait values will vary with climatic conditions leading to changes in ecosystem functioning. Indeed, similar approaches have already credited potential impacts on ecosystem functioning as a consequence of climatic filtering effects on community traits over non woody alpine plant systems (Dubuis et al., 2013), Tasmanian forest communities (Mokany et al., 2015) and in Swedish wetlands (Moor et al., 2015).

Thus, benefiting from the opportunity of a consolidated and accessible forest inventory data (Tomppo et al., 2010), we assessed climate dependency of CWM_{SLA} for more than 44 000 permanent plots distributed across the whole forested territory of Spain. We used SLA as the main trait expression of environmental filtering, since it is well-recognised that SLA reflects species aridity tolerance (Micco and Aronne, 2012; Niinemets, 2001) and particularly of Mediterranean tree species (Costa-Saura et al., 2016). Before assessing potential climate change effects on communities, we tested the following hypotheses over which our approach is based: 1) CWM_{SLA} would decrease with aridity in the Mediterranean since low SLA values are required for drought adaptation, and 2) FD_{SLA} and the range of CWM_{SLA} would also decrease with aridity since increasing drought severity will constrain the number of suitable strategies. The following step was to assess the potential changes in CMW_{SLA} on Spanish forest communities under multiple climate change scenarios in terms of vulnerability, magnitude of impact and likelihood of change. We hypothesized that communities from humid zones characterised by high CMW_{SLA} will be impacted more frequently and will undergo a greater magnitude of change.

2. Materials and methods

2.1. Study area, community and climatic data

The study area covered the Spanish continental territory, located between 36° N and 44° N of latitude, and between 10° W and 3° E longitude. The main Köppen climatic domains are arid and temperate, with annual mean temperatures (AMT) ranging from ∼3 to ∼17 °C and annual mean precipitations (AMP) from ∼300 to ∼2200 mm/year (Chazarra, 2011).