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Vegetation ecology meets ecosystem science: Permanent grasslands as a functional biogeography case study

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HIGHLIGHTS

- We present the rationale and first results of a Functional Biogeography exercise
- We collated 51,486 botanical relevés in French permanent grasslands
- We combined botanical relevés, seven key functional traits and environmental layers
- We provide country-wide predictions of forage digestibility through trait mapping
- We discuss the next challenges for functional biogeography

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ABSTRACT

The effect of biodiversity on ecosystem functioning has been widely acknowledged, and the importance of the functional roles of species, as well as their diversity, in the control of ecosystem processes has been emphasised recently. However, bridging biodiversity and ecosystem science to address issues at a biogeographic scale is still in its infancy. Bridging this gap is the primary goal of the emerging field of functional biogeography. While the rise of Big Data has catalysed functional biogeography studies in recent years, comprehensive evidence remains scarce. Here, we present the rationale and the first results of a country-wide initiative focused on the C_3 permanent grasslands. We aimed to collate, integrate and process large databases of vegetation relevés, plant traits and environmental layers to provide a country-wide assessment of ecosystem properties and services which can be used to improve regional models of climate and land use changes. We outline the theoretical background, data

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availability, and ecoinformatics challenges associated with the approach and its feasibility. We provide a case study of upscaling of leaf dry matter content averaged at ecosystem level and country-wide predictions of forage digestibility. Our framework sets milestones for further hypothesis testing in functional biogeography and earth system modelling.

1. Introduction

Functional trait-based ecology has opened new avenues to help elucidate the assembly processes leading to the structure of ecological communities on the one hand (McGill et al., 2006; Weiher et al., 2011) and to link biodiversity and ecosystem processes on the other hand (Chapin et al., 2000; Diaz and Cabido, 2001; Lavorel and Garnier, 2002; Eviner and Chapin, 2003; Cadotte et al., 2011). Ultimately, a trait-based approach has the potential to provide a comprehensive framework to link community assembly with ecosystem functioning. Most work in this field has been conducted at local scales (Lavorel and Garnier, 2002; Garnier and Navas, 2012), and we still lack proof-of-concept for the benefit of functional approaches at a larger spatial scale (but see e.g., Reich, 2012; Swenson et al., 2012; Lamanna et al., 2014). The emerging discipline of functional biogeography – i.e., the study of the geographical distribution of the functional attributes of organisms – attempts to fill this knowledge gap (Violle et al., 2014).

The distribution of functional traits in communities depicts the diversity and abundance of ecological strategies displayed by co-occurring species. Theoretical expectations suggest a link between the properties of this trait distribution and ecosystem functioning and dynamics (Enquist et al., 2015). In particular, the mean trait value of a community (Community-Weighted Means or CWM: the average value of species traits weighted by their relative abundance in the community) is expected to provide an accurate snapshot of ecosystem properties relevant to biogeochemical cycling (Garnier et al., 2004). This hypothesis is based on the "mass ratio hypothesis": a species' trait will impact ecosystem properties in proportion to the local abundance/biomass of the species within the community (Grime, 1998). The mass ratio hypothesis has been tested by examining relationships between CWM of plant traits and a number of ecosystem properties. For example, significant relationships have been established empirically between leaf chemistry and litter decomposition (Cornwell and Ackerly, 2009), between species relative growth rate, leaf structure and ecosystem net primary productivity (Garnier et al., 2004; Vile et al., 2006; Reich, 2012), between leaf dry matter content and forage digestibility (Gardarin et al., 2014). This framework therefore provides conceptual and practical guidelines to scale up from individual organs to ecosystem properties and, ultimately, to understand how changes in community functional structure can impact ecosystem functioning (Lavorel and Garnier, 2002). A functional perspective to biogeography needs to extend this framework to large spatial scales in order to provide proxies of ecosystem properties at any point on earth (Violle et al., 2014). In this perspective, a key milestone would be to provide continuous maps of CWMs per biome. Ultimately, this information could help parameterize process-based Land Surface Models based on the functional characteristics of vegetation surface (Van Bodegom et al., 2014).

How to proceed to design these CWM maps? Theoretically, a taxon-free approach could be applied through intense sampling of traits of organisms at a coarse geographic scale without any prior information about taxonomy, but this approach is practically almost intractable. A sensible alternative at these scales is to infer local CWMs metrics from species' mean traits (Swenson and Weiser, 2010; Albert et al., 2011; Swenson et al., 2012). While the importance of accounting for intraspecific phenotypic variation in functional biogeography is still debated (Albert et al., 2011; Reich et al., 2014), extracting mean species trait values from global databases appears a reasonable procedure at least for most traits classically used in functional ecology (Kazakou et al., 2014). The mapping of CWMs, and more generally of any moment of the trait distribution (Enquist et al., 2015), requires a combination of species' trait information with local floristic composition (Lavorel et al., 2011). A main challenge thus consists in combining large heterogeneous databases, notably: *species* × *sites* matrices, trait databases and environmental layers (Violle et al., 2014). Interestingly, the amount of plot-based vegetation data (complete lists of species occurrence and abundance) – hereafter vegetation relevés – collected by environmental agencies, land-use managers and researchers (Schaminée et al., 2007, 2009) is a real gold mine for functional biogeography. The time is ripe for vegetation ecology to meet ecosystem science since the raw data and modelling frameworks are now available to provide spatially distributed vegetation parameters at a regional scale and to use them to scale up to biogeochemical cycling (Reichstein et al., 2014).

In this paper we present the rationale and first results of the DIVGRASS project conducted at the CESAB, the French Centre for the Synthesis and Analysis of Biodiversity. DIVGRASS aims to (i) integrate and share existing knowledge about both taxonomic and functional plant diversity, as well as about ecosystem properties and functioning of the C_3 French permanent grasslands, and (ii) combine this information to examine how plant functional diversity impacts biogeochemical cycling. To our knowledge, there has been no previous attempt to integrate vegetation ecology and ecosystem science at this spatial scale. The next sections of the paper illustrate the main work flow of the DIVGRASS initiative and include (i) a presentation of the targeted C_3 grasslands and the specific questions we addressed on these ecosystems; (ii) the data availability for vegetation relevés and plant traits and the methodological challenges we faced to collate and integrate these databases; and (iii) a functional biogeography case study showing the mapping of the CWM of a key functional trait (leaf dry matter content, LDMC $mg \cdot g^{-1}$) and its use for modelling a particular ecosystem property, namely forage digestibility for ruminants, at a country-wide scale. Finally, we provide perspectives for functional biogeography including the predictions of other ecosystem processes (e.g., Net Primary Productivity) using Land Surface Models parameterized with spatially distributed CWMs, and highlight their relevance to evaluate ecosystem services and to inform conservation policies.

2. Permanent grasslands as a case study

Permanent grasslands are broadly defined as "Land on which vegetation is composed of perennial or self-seeding annual forage species which may persist indefinitely. It may include either naturalized or cultivated forages" (Allen et al., 2011). According to European Union laws, this definition is further restricted to grasslands that have been used for at least five years to produce forage, and which have not been ploughed nor re-seeded during this period (Plantureux et al., 2012). In France, permanent grasslands are mainly found in regions producing fodder where they account for more than 20% of the total land area: namely the Pyrénées, Alps, Jura, Vosges, Massif Central for mountainous areas; Normandy, Loire lower valley, Loraine, Champagne-Ardenne and the marshes of Atlantic coast for plains (cf. Fig. 1A). The land area devoted to permanent grasslands increased considerably between 1860 and 1970, mainly in the lowlands (Plantureux et al., 2012). This increase was related to the regression of fallow and heathland, the increasing ability to export dairy and meat products, and the necessity to cope with agricultural disasters (e.g., phylloxera) (Huyghes, 2009). The area occupied by grasslands has steadily decreased since 1970 as a consequence of the development of other fodder resources like maize silage