The emergence and promise of functional biogeography

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Understanding, modeling, and predicting the impact of global change on ecosystem functioning across biogeographical gradients can benefit from enhanced capacity to represent biota as a continuous distribution of traits. However, this is a challenge for the field of biogeography historically grounded on the species concept. Here we focus on the newly emergent field of functional biogeography: the study of the geographic distribution of trait diversity across organizational levels. We show how functional biogeography bridges species-based biogeography and earth science to provide ideas and tools to help explain gradients in multifaceted diversity (including species, functional, and phylogenetic diversities), predict ecosystem functioning and services worldwide, and infuse regional and global conservation programs with a functional basis. Although much recent progress has been made possible because of the rising of multiple data streams, new developments in ecoinformatics, and new methodological advances, future directions should provide a theoretical and comprehensive framework for the scaling of biotic interactions across trophic levels and its ecological implications.

biodiversity | functional trait | predictive ecology

Biogeography is the study of the distribution of species and ecosystems across space and time and of the underlying biotic and abiotic factors, mechanisms, and processes (1). Biogeography is central to synthesizing small- and large-scale patterns of species' responses to global environmental change and providing a window to assess the importance of earth and evolutionary history, as well as changing biotic and abiotic factors that underlie the current distribution of taxa. Historically, biogeography has been rooted in the species concept. Biologists long ago built global maps of species' ranges and species diversity patterns, which allowed scientists to develop, test, and validate prominent ecological theories at the root of biogeography (2, 3). Biogeography, however, has largely developed separately from ecosystem ecology and earth system biology, yet we argue that one of the great challenges of 21st century biogeography is to provide theoretical baselines and tools for the understanding and prediction of ecosystem responses to environmental changes in terms of species composition and biogeochemical cycles (water, carbon, nutrients, and energy).

For the last several decades, new directions in biogeography have been aided by statistical and computational advances (4, 5), and new species distribution models have provided maps of priority areas for conservation and projections of the effects of global change on species diversity patterns for the next century (6–9). Nonetheless, predictions of how ecological communities respond to past and projected future climates have increasingly been challenged (10) due to the limitations of species-based approaches, including conceptual and technical difficulties in incorporating species interactions, dispersal limitations, and species' adaptations into predictive models (11–16). Indeed, if we treat species as qualitative entities, then we need to understand each and every one. In contrast, trait-based biogeography can help model species interactions, dispersal ability, and physiological tolerance more simply and generically (17). More precisely, if we array species along some continuous trait axes (18), then knowing cross-species relationships (19), e.g., between plant physiological tolerance to drought and diameter of xylem vessel (20), can help forecast the change in species composition of ecological communities in response to variation in abiotic conditions like water availability.

Contrary to species-based biogeography, earth science models directly address changes in biogeochemical cycles at a global scale but using a simplistic representation of biodiversity in most cases (21–24): few plant functional types (PFT), characterized by mean ecophysiological characteristics, are used per biome in models dedicated to simulate and forecast the consequences of global changes on biogeochemical cycling (24). However, in biodiversity–ecosystem functioning research (25–27), the taxonomic composition of an ecosystem is identified as a key driver of ecosystem functioning. More recently, the functional component of biodiversity, i.e., the diversity of forms and functions, has been recognized as the missing link between biodiversity patterns and biogeochemical cycles (28–30) and perhaps is a core driver of ecosystem services (31, 32). Given these insights from ecosystem ecology, there is a growing consensus on the need for a better representation of biodiversity—in particular the composition of species, forms, and functions—in earth science models (21, 23, 24), as stressed in this issue by Reichstein et al. (33).

In this Introduction, and in the related special feature, to bridge historical species-based biogeography with earth systems

science, we argue that the time is ripe to advance functional biogeography. We define functional biogeography as the analysis of the patterns, causes, and consequences of the geographic distribution of the diversity of form and function—namely, trait diversity. Indeed treating the biota as a continuous distribution of traits appears pivotal if one is expected to model the biosphere when there are literally millions of separate species. Describing and explaining the global distribution of forms and functions is a long-standing goal for ecologists (34–36). Such attempts have been synthetized under a variety of terms including macrophysiology (19, 37–39). The emergence of functional biogeography pursues this goal but also aims at linking biogeographical patterns of trait diversity to biogeographical patterns of species diversity, ecosystem functioning, and services because of the integration of concepts and methodologies from multiple fields (Fig. 1). Advancing functional biogeography becomes timely with the rise of a predictive era in ecology and the acceleration of societal demand regarding the evaluation and forecast of past, current, and future ecosystem services.

Biogeography Beyond Species: Functional Traits as a Common Currency Across Biological Organizational Levels and Taxonomic Groups

We posit that a useful approach to functional biogeography is to use a common currency, namely functional traits. Functional traits are morphological, physiological, phenological, or behavioral features measured on organisms that can ultimately be linked to their performance (40). In trait-based ecology, it has been shown that it is possible to aggregate functional traits measured on organisms to explain the functioning of populations, communities, ecosystems, and beyond. For instance, at the community level, the use of community-weighed means (CWM, i.e., the average trait value of a community accounting for effects of species abundance within communities) (40, 41) is a promising tool to accurately predict ecosystem functions such as plant primary productivity (41, 42). As a whole, functional traits can be implemented into more or less complex integrative functions (e.g., CWM is a simple integrative function) to scale up from organs to higher organizational levels including ecosystems and biomes (40, 43, 44). Trait-based approaches have also been extensively used to describe the diversity of forms and functions within a study unit—often termed functional diversity *sensu lato*—using different distance metrics (e.g., variance based) (45–55) and how it scales spatially (56–61).

Variation in functional traits within species is also key. For instance, in this special feature, Reich et al. (62) highlight huge intraspecific variation in gymnosperm needle traits with latitude across the vast boreal domain. They note how this variation fits with trait economic theory and model the impacts of trait variation on carbon cycling across the world's boreal forests. They validate the model output against independent data. Studying phenotypic and genotypic variation within species across space (e.g., within the range of species) represents one primary aspect of functional biogeography (63, 64). Future efforts to quantify both intraspecific phenotypic and genetic variation within species' ranges should bring interesting insights into the eco-evolutionary drivers of species' distributions and help bridge functional ecology, spatial ecology, genetics, and evolutionary biology (65) (Fig. 1). The question of accounting for intraspecific variation in cross-species trait-based studies has been extensively discussed for the last 5 years (52, 66, 67). The importance of accounting for intraspecific variation at macroecological scales, when interspecific variations are expected to be large, is still debated (21, 67–69).

A functional trait approach has now been rapidly and extensively developed in plant ecology, aided by the development of standardized protocols and methodologies (70, 71). More recently, similar initiatives have been initiated for microbes and animals (17, 72–74). These initiatives will favor cross-taxonomic group comparisons of trait diversity patterns from local to global and pave the road of an integrated, comprehensive framework for the understanding of ecology at large spatial and temporal scales. In this special feature, Whittaker et al. (75) are able to provide new insights in the field of island biogeography by building functional diversity–area relationships, in complement to species richness–area relationships and compare them across taxonomic groups (here between beetles and spiders). The
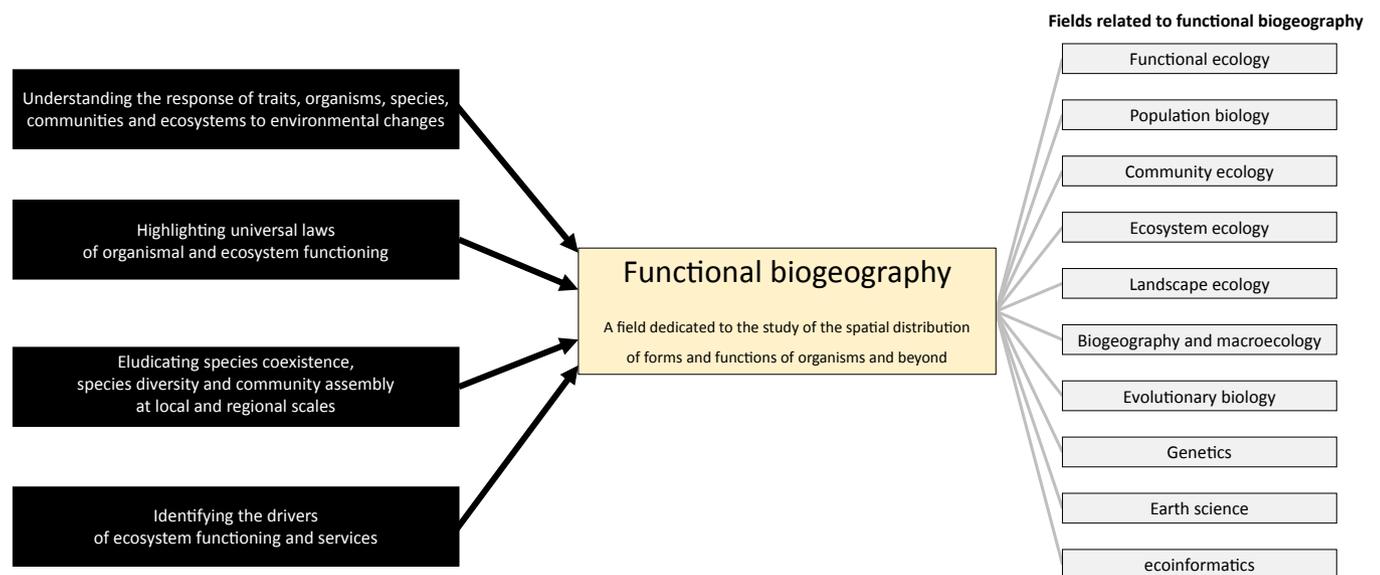

Fig. 1. Functional biogeography: an emergent field at the crossroads of several science fields. Functional biogeography calls for knowledge from multiple fields to answer questions related to the distribution of forms and functions of organisms, populations, communities, ecosystems, and biomes across spatial scales.

analysis of congruence of trait diversities across groups is also timely for better targeting conservation areas, quantifying and explaining multitropic networks and evaluating ecosystem services (76). Interestingly, in this special feature, Kembel et al. (77) demonstrate how phyllosphere bacterial communities impact the performance of plants and the structure of plant communities in a Neotropical forest. The authors propose that the phyllosphere bacterial diversity is a key component of plant functioning and should be considered as a plant functional trait, hence extending our current definition of functional traits (40). This study sheds light on the ecological role of the extended phenotype, still largely ignored in trait-based ecology; in particular, its importance for the adaption of organisms and for the interactions among them. More broadly, such

pioneering studies are a step forward in the quantification of species interactions (including mutualism, competition, facilitation, predation), which remains a priority question in community ecology and biogeography. Identifying the traits involved in species interactions (interaction traits hereafter) is challenging but pivotal for several approaches including network analyses. Considering the interacting communities (the phyllosphere bacterial communities) as traits of other organisms (the plants) is one promising step in that direction.

From Patterns to Predictions

Describing Trait Diversity Across Space. We still lack knowledge of the response of organismal traits to environmental changes for most kingdoms, including plants, which is, however, a prerequisite to make trait-based ecology a predictive science (Fig. 2).

The first trait–environment relationships were established from local studies (78, 79), but site-dependent effects and the restricted range of environmental conditions covered in most studies question the robustness of the results. A functional biogeography approach to this question is a relevant alternative (80). Indeed, examining how species and their functionalities vary geographically can be useful because many of the same drivers of change that occur at every single site on earth have already varied across time and across space. The study from Reich et al. (81) is a notable example. Using a large global biomass dataset, the authors provide biogeographically explicit relationships between biomass partitioning in trees and temperature, elucidating a long-standing ecological question about the variation of plant biomass allocation with increasing stressful conditions.

The establishment of robust trait–environment relationships will help achieve one core goal of functional biogeography: to place measures of the functions of biodiversity on a map (58, 60, 82). Such functional maps are indeed the bases of many questions in functional biogeography and derived fields (57). In this special feature, Bennie et al. (83) elegantly map a core behavioral trait in mammals: the diel time partitioning. They show that the biogeography of this trait is under the influence of thermal constraints but also artificial lighting and other anthropogenic activities. Such a finding is important for improving the modeling of mammals' distribution. Beyond macrophysiological implications on the biogeography of species, mapping the diversity of organismal functions is also central to the quantification of ecosystem functioning and services. Here, van Bodegom et al. (84) show that trait data are now available worldwide to map core traits pertaining to plant functioning (leaf mass per area, stem-specific density, and seed mass in their study) at a global scale. Further, they demonstrate that the spatial variation of these three traits alone explains a large part of observed vegetation types, thus linking trait distributions to dynamic global vegetation models (DGVMs). Ultimately such maps can help refine earth science and land surface models in a more continuous manner, i.e., by replacing the spatial distribution of plant functional types by continuous maps of functional traits as input information in those models (33) provided that data on traits and species occurrences are available (Fig. 3).

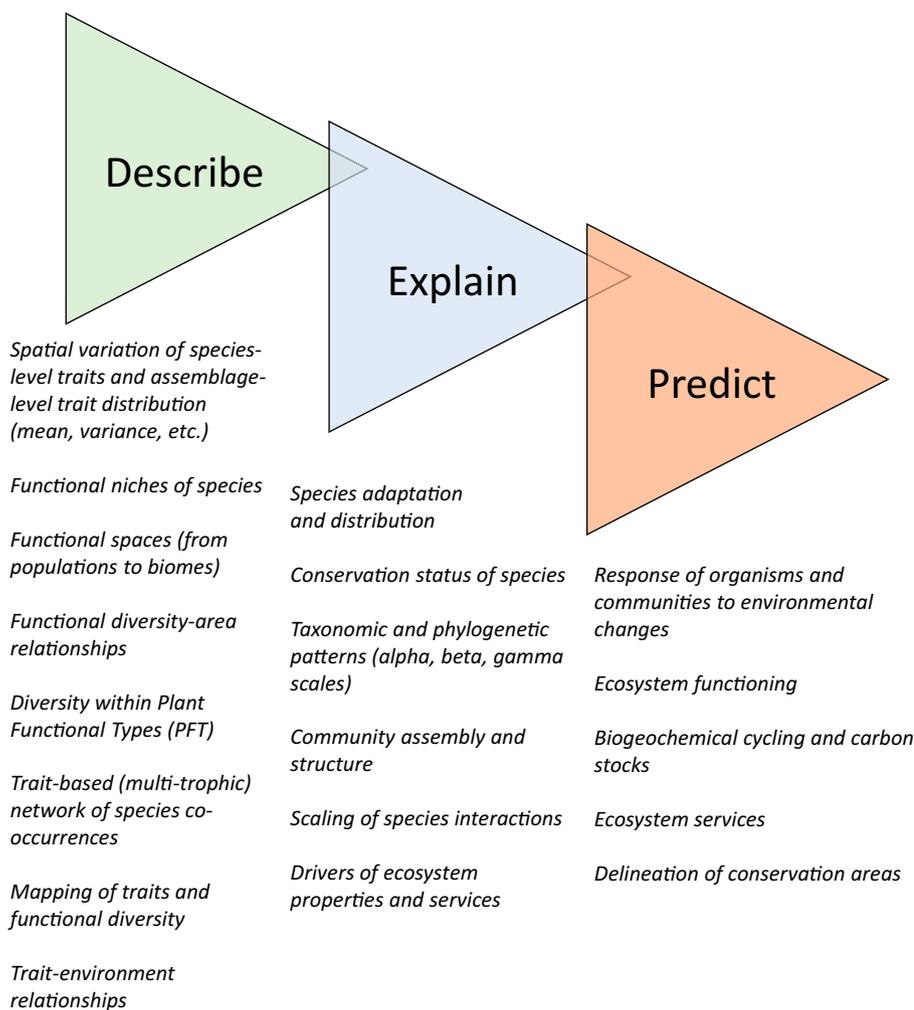Finally, the supposed link between functional traits and resource availabilities offers

Fig. 2. The three tenets of functional biogeography: describe, explain, predict. The first tenet of functional biogeography is to describe the distribution of forms and functions along environmental gradients and across spatial scales. The second is to use this information to explain the geographic distribution of organisms, biodiversity (notably species and phylogenetic diversity) patterns, and ecosystem processes and services. The third is to predict their responses to environmental changes using trait-based predictive functions and models.
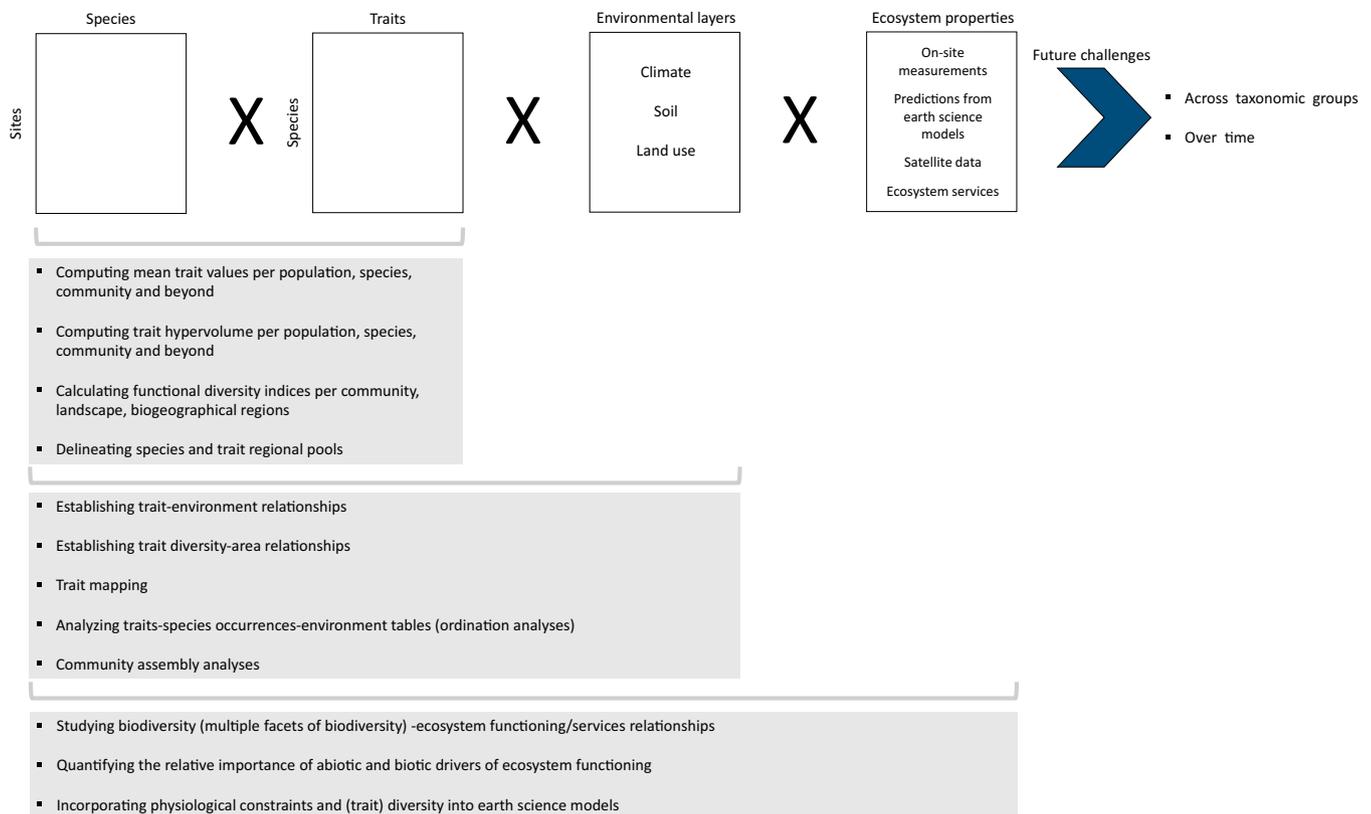
Figure labels:

Describe
Spatial variation of species-level traits and assemblage-level trait distribution (mean, variance, etc.)

Functional niches of species

Functional spaces (from populations to biomes)

Functional diversity-area relationships

Diversity within Plant Functional Types (PFT)

Trait-based (multi-trophic) network of species co-occurrences

Mapping of traits and functional diversity

Trait-environment relationships

Explain
Species adaptation and distribution

Conservation status of species

Taxonomic and phylogenetic patterns (alpha, beta, gamma scales)

Community assembly and structure

Scaling of species interactions

Drivers of ecosystem properties and services

Predict
Response of organisms and communities to environmental changes

Ecosystem functioning

Biogeochemical cycling and carbon stocks

Ecosystem services

Delineation of conservation areas

Fig. 3. General chart for functional biogeography studies using a combination of heterogeneous data sources. Combing organismal traits, species occurrences and abundances, and environmental information allows exploration of the response of organisms, populations, communities, and beyond to environmental changes. In combination with (measured, estimated, modeled, simulated) information about ecosystem properties, one can examine the abiotic and biotic drivers of ecosystem functioning (single processes and multifunctionality) and services and provide predictive outcomes. Although these approaches are increasingly used, the incorporation of time (e.g., biogeography of time series, functional trajectories of ecosystems) and a systematic functional analysis of multitrophic networks are currently lacking.

new insights into the physiological limits of the biogeographical distribution of species and the delineation of their fundamental and realized niches. In this issue, Stahl et al. (85) successfully show that three key functional traits—seed mass, wood density and plant height—explain species' range limits of a continental flora. Maps of functional traits could also be considered as new environmental layers for species distribution modeling (86, 87). Such analyses are a step forward in the definition and quantification of the functional niches of species (18, 88).

Explaining Species Coexistence, Species Diversity, and Community Assembly at Local to Regional and Continental Scales. Functional biogeography can shed light on local species assembly processes and the structure of communities. The idea that local processes depend on regional ones is not new in biogeography (89, 90), but the rising of systematic and standardized descriptions of trait diversity across scales can accelerate quantification of ecological properties and processes and the test of ecological theories on patterns of species diversity

(Fig. 3). For instance, delineating the functional trait space of a region is a way to evaluate the niche space available in this region (18, 86), which should subsequently help explain local species diversity patterns (86, 91, 92). In this special feature, Lamanna et al. (86) recast several biodiversity theories for species richness gradients in terms of variation in functional diversity. As a result, they are able to uniquely assess several trait-based hypotheses for the latitudinal gradient of species richness but from a trait perspective. Based on a large botanical and trait database for woody species in the New World, they find that species occupy a larger functional space in the temperate zone in comparison with the tropics. This finding contradicts several theories that have suggested that there are a greater number of species in the tropics due to larger trait or niche space. In the future we expect more and more powerful tests of biodiversity theories and the elucidation of the biogeographical patterns of species richness by using new botanical and animal trait databases worldwide (Fig. 3). These efforts will

help solidify the development of trait-based biogeography theory.

Functional traits are increasingly used in community ecology to detect and quantify the processes that shape ecological communities (52, 93, 94). With a biogeography perspective, this approach can be applied to understand the spatial scaling of assembly processes across broad gradients. In particular, the scaling of species interactions is the source of one of the most intense debates in biogeography (3, 14, 95–98). Indeed understanding when and how local biotic interactions influence the biogeographical distribution of species is crucial for species distribution modeling (13, 15). Further, the intensity of species interactions (competition in particular) has long been supposed to vary along environmental and latitudinal gradients (e.g., less competition expected in harsh environments and/or higher latitude), which could explain the latitudinal patterns of species richness (3, 95). Mapping traits directly involved in species interactions (82, 99) can help us to understand the scaling of species interactions. For instance, one can expect past intense competition

in biogeographical areas characterized by greater variance in interaction traits (58) as a result of limiting similarity processes (100).

Elucidating the Drivers of Ecosystem Functioning and Services Across Space. Functional biogeography offers a unique window to explain the variation of ecosystem functioning at large scales (33). Elucidating the drivers of ecosystem functioning at this scale is of high priority for policymakers from the perspective of modulating the impacts of human-driven global changes and adjusting conservation policies (101). Past functional biogeography exercises successfully linked the mean functional characteristics of ecosystems to resource cycling (102), but the functional structure of communities, i.e., the distribution of trait values within communities, was not fully characterized. More recent advances in functional ecology have provided tools to quantify both mean functional characteristics (e.g., CWM) and functional dispersion (e.g., Rao's entropy) within ecosystems. Today it is urgent to disentangle effects of both facets of trait diversity in driving ecosystem functioning (103, 104). In particular, functional dispersion could be considered as a proxy of the result of biotic interactions (see above); thus, its quantification can provide insights into the importance of species interactions in the modulation of ecosystem functioning.

Latitudinal gradients, often considered as natural laboratories (105), are particularly appropriate tools for functional biogeography exercises and are of particular relevance to the analysis of large-scale patterns in trait diversity and how it is related to observed or inferred ecosystem processes. In the next few years, relating the functional structure of ecosystems to ecosystem functional features inferred from remote sensing outputs will be particularly valuable to provide continuous maps of functional traits, as well as highly resolved proxies for ecosystem functioning (Fig. 3), as revealed by recent successful attempts (106, 107).

Collectively, a better understanding and quantification of the functional drivers of ecosystem functioning across biogeographical gradients will help refine plant functional types, or eliminate their need entirely, for earth science modeling (24). Practically, providing well-resolved continuous maps of functional traits is a first important step in that direction (84).

The same line of reasoning can be applied to ecosystem services given that ecosystem functions are the biological bases of ecosystem services. Interestingly, as shown by Lamarque et al. (108), it is possible to evaluate ecosystem services bundles and tradeoffs using a trait-

based empirical model. Using mountain grasslands in the French Alps as a case study, the authors are able to disentangle the direct and indirect effects of climate and land use on ecosystem services, including water quality, aesthetic value, and fodder quality and quantity, through a scenario-based study.

Toward Predictions in a Changing World. Because functional biogeography links organismal functions to their environment, it is theoretically possible to predict the response of organisms, communities, and ecosystems to environmental changes from functional traits (43, 44, 109). Ultimately, it appears possible to predict bundles of ecosystem services based on theoretical and empirical knowledge and the mapping of different facets of functional diversity (108, 110).

The stacking of different maps (e.g., taxonomic, phylogenetic functional diversity, carbon stocks, ecosystem productivity, aesthetic values, socio-ecological mapping of species' favorable habitats) (Fig. 3) will help refine conservation areas because there is little reason for a perfect overlapping of species, functional, and phylogenetic rarity (111). For instance, in this special feature, Mouillot et al. (112) show that the functional vulnerability—defined as a potential decrease of functional diversity following species loss—of fish fauna on tropical reefs can be high in areas characterized by high species diversity. Conversely, functional redundancy is discovered in low species diversity areas. Together, this suggests that conserving hotspots of species diversity is not sufficient if one also aims at targeting the functional insurance of biota.

The Rise of Specific Tools and Resources
Functional biogeography will advance faster if large heterogeneous datasets and computing tools are combined and brought to bear in a spatially explicit context (Fig. 3). These datasets are now available or will emerge soon. They encompass a global coverage of geo-referenced species occurrences (113–115), the functional characteristics of species (21, 73, 116, 117), and more and more precise environmental layers (118, 119). Ecoinformatics accelerated the development of datasets structured in a complex and consistent fashion by the means of ontologies for ecology (120, 121), methods for model–data integration (122, 123), and the calculation of the n-dimensional hypervolume (55, 86). Computing and mathematical science are developing approaches to spatial data mining and the extrapolation of information from incomplete datasets (124). For instance, using Bayesian statistics, it will be possible to fill

gaps in trait databases for a given trait and a given species with information from other traits and other species (125, 126). Similarly, in a spatial context, missing information in a grid cell can be filled based on information contained in surrounding grids (124).

Future Perspectives
Functional biogeography should help improve our understanding of the biogeographical patterns of species diversity and, ultimately, may allow us to predict the consequences of global changes for ecosystem functions and services. However, the development of expectations specific to functional biogeography is in its infancy. Indeed, although functional biogeography is inherently process based, theory is still lacking. To make functional biogeography a predictive science, it will be important to include the eco-evolutionary dynamics of organisms, communities, ecosystems, and beyond (10). Some recent findings suggest a tight linkage between functional traits and demography (127), which represents a promising step in the development of an integrative and dynamical theory to functional biogeography.

Another priority avenue is to provide insights into trophic or food web models, first by providing maps of functions of primary producers. To do so, it is urgent to better characterize traits across taxonomic groups and their interrelationships (32, 128), as well as to identify and quantify interaction traits. Rapid progress has been made in ecoinformatics, but global coverage of functional traits, even for plants, is still sparse. Until greater coverage is achieved, it will be impossible to achieve an accurate estimation of trait diversity at a global scale and to account for some facets of trait diversity, including functional rarity. Further efforts in ecoinformatics should also provide relevant ontologies, including trait ontologies that are proving themselves indispensable for functional biogeography exercises.

A functional perspective to biogeography can easily integrate intraspecific trait variation to assess the importance of local adaptation and phenotypic plasticity in the modulation of large-scale processes. Nevertheless, although recent debates in functional ecology have advanced our understanding of the importance of intraspecific variation at local scales (52, 66, 129, 130), it is urgent to evaluate its importance at large scales. It has been assumed that species turnover and interspecific variations predominate over intraspecific variation at large scales (66), but empirical tests are scarce and mostly come from the plant kingdom (68, 69). Further, there are some

specific areas of functional biogeography where intraspecific variation should be accounted for, in particular when characterizing the functional space of a given species (18) and its phenotypic variation within its distribution range (63). A better evaluation of intraspecific trait variation within species' ranges, in complement to a quantification of genetic variation, should bring novel insights into the eco-evolutionary drivers of species' biogeography and functional niches.

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