

Finally, future developments will need to establish clear connections between extinction risk and functional rarity. It is not straightforward to assume that rarity always implies higher extinction risk. While extinction is generally expected not to be a random process, common, instead of rare species, can be lost if their traits make them more susceptible to environmental changes [7]. Previous studies applying species loss simulations on functional diversity/ecosystem functions have assumed extinction orders according to metacommunity nestedness patterns and species response traits (e.g., body size [8] or species palatability to livestock [9]), and not necessarily on their rarity in a community or region [10]. Ecological consequences of species loss are better evaluated in a continuous fashion, using estimations of vulnerability. Such estimations combine functional trait information of species (preferably based on multiple traits, as a proxy for overall functioning) with information on species extinction risk and their expected response to environmental changes [11,12].

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References

- Violle, C. et al. (2017) Functional rarity: the ecology of outliers. Trends Ecol. Evol. 32, 356–367
- Carmona, C.P. et al. (2016) Traits without borders: integrating functional diversity across scales. *Trends Ecol. Evol.* 31, 382–394
- Bennett, J.A. and Pärtel, M. (2017) Predicting species establishment using absent species and functional neighborhoods. *Ecol. Evol.* 7, 2223–2237
- de Bello, F. *et al.* (2017) Decoupling phylogenetic and functional diversity to reveal hidden signals in community assembly. *Methods Ecol. Evol.* http://dx.doi.org/ 10.1111/2041-210X. 12735 Published online March 20, 2017
- de Bello, F. *et al.* (2013) Which trait dissimilarity for functional diversity: trait means or trait overlap? *J. Veg. Sci.* 24, 807–819
- Carmona, C.P. et al. (2016) The density awakens: a reply to Blonder. Trends Ecol. Evol. 31, 667–669
- Laliberté, E. et al. (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecol. Lett. 13, 76–86
- Larsen, T.H. et al. (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecol. Lett. 8, 538–547
- Verón, S.R. et al. (2011) Grazing-induced losses of biodiversity affect the transpiration of an arid ecosystem. Oecologia 165, 501–510
- Sasaki, T. et al. (2017) Differential responses and mechanisms of productivity following experimental species loss scenarios. *Oecologia* 183, 785–795

- Sasaki, T. *et al.* (2014) Vulnerability of moorland plant communities to environmental change: consequences of realistic species loss on functional diversity. *J. Appl. Ecol.* 51, 299–308
- Carmona, C.P. et al. (2017) Assessing vulnerability of functional diversity to species loss: a case study in Mediterranean agricultural systems. *Funct. Ecol.* 31, 427–435

Letter

A Common Toolbox to Understand, Monitor or Manage Rarity? A Response to Carmona *et al.*

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Carmona *et al.* [1] highlight a probabilistic approach to functional rarity as an extension of our integrated framework to functional rarity [2]. The authors argue that it could be considered as a common toolbox for rarity. While we certainly agree with the authors about the necessity to unify the quantification of biodiversity and rarity in a community ecology and biogeography perspective [3], we call for a more operational and pragmatic quantification in a conservation perspective.

Carmona *et al.* [1] question the relevance of categorizing functional rarity instead of providing a continuous quantification. In fact, the integrated view of functional rarity we proposed [2] is not categorized by principle or design. We proposed a set of indices that are continuous and in line with the probabilistic approach promoted by Carmona *et al.* [1] (see also [4]). We defined local and regional scales for the sake of simplicity but the delimitation





calculating the indices for various scales g., top 5 or 10%), potentially useful infor- theoretical and applied ecology is not a can be easily achieved. This set of functional rarity indices can now be calculated using the R package, funrar, available on CRAN (https://cran.r-project.org/web/ packages/funrar/index.html) [5]. We encourage everyone to complement or improve functions available in funrar. Implementing the framework of Carmona et al. [4] in funrar appears to be a natural perspective.

As a byproduct of our quantitative framework for assessing functional rarity, we originally proposed to categorize it through 12 forms of functional rarity, echoing Rabinowitz's seven forms of (taxon) rarity [6]. We argue that this two-step assessment (quantification and then categorization) of functional rarity should not be minimized or ignored. In a conservation perspective, it is essential to keep in mind that any new tool for quantifying different facets of biodiversity will be in the hands of resource managers and decision-makers. Providing continuous and sophisticated metrics for rarity may be mathematically appealing, but will likely be counterproductive in some cases if interpretation of values is unclear. There are strong arguments in favour of treating rarity as a discontinuous or categorical variable rather than as a continuous variable in the conservation literature: 'because for legal and conservation purposes species often need to be categorized as rare or otherwise, a more pragmatic approach is often desirable' [7]. Our 12 forms of functional rarity follow this recommendation. More broadly, there is a growing effort to identify simple and operational metrics to facilitate the monitoring and management of biodiversity and rarity. We consider that the basic categories of functional rarity that we proposed could be easily added to the list of Essential Biodiversity Variables (EBV) [8]. For instance, our approach allows the identification of species that possess

between these two scales is not fixed; the highest degree of functional rarity (e. biodiversity and rarity worldwide. Bridging mation for monitoring and managing new challenge for the field, but we



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Figure 1. Cookbook for the Application of Violle et al.'s Framework to Functional Rarity: When, How and Why Study Functional Rarity? Several fields of (theoretical and applied) biology needs a unified framework to quantify rarity. The funrar R package [5] implements the framework proposed in Violle et al. [2]. Depending on the objectives of the research question in each field, one can be interested to: (i) assess the originality of a single item (e.g., species or habitat) (the red point is original - i.e., rare - compared to the black ones); or (ii) quantify the whole functional rarity of a set of items (e.g., a community or a grid cell) (the sum, or any other integration functions of functional rarity values of each item). In the latter case, functional rarity and functional redundancy are the two sides of the same coin and Carmona et al.'s framework [4] can be easily implemented.



question whether the complexification of science, the emergence of big data and sophisticated approaches to analyse them, although necessary, may separate instead of bridging both sides of ecology.

The concept of (functional) rarity is multifaceted by nature [2], and its application involves at least two forms: an item-byitem (IbI) analysis versus a set-of-items (Sol) analysis (Figure 1). In an Ibl perspective, the interest is to characterise the functional rarity of a species or any item of lower or higher organisation level (e.g., community, habitat, or biome) compared to other items of the same type (e.g., analysing the functional rarity of a given plant species relatively to all other land plant species). In this case, the main questions are: what causes functional rarity; what are the consequences of functional rarity; and what is the link between species' extinction risk and functional rarity? These are crucial questions for conservation ecology, and also for more theoretical fields like functional ecology, macroecology, and evolutionary biology. From a functional ecology or macroecology perspective, an appealing research frontier would be to identify outliers from 'universal laws' of functioning and phenotypic diversification (e.g., the leaf economics spectrum in plants, or allometric relationships in both plants and animals), their causes of persistence in nature, and the reasons why theoretical laws can be violated. As a consequence, beyond the need in conservation, IbI analyses appear also particularly relevant in many fields of biology (Figure 1).

Sol analyses are specifically relevant in a community ecology and biogeography perspective [3,9]. Sol refers to the amount of functional rarity that does exist in a given assemblage, for example, in a community or a biome. Sol functional rarity indices can be compiled by, for example, averaging or summing species-based lbl

indices [5]. It is important to note that Sol indices and functional redundancy analyses are the two sides of the same coin [10] and thus can address complementary topics. Is the functional space of a community saturated? What are the causes of the maintenance of rare phenotypes in a community? Are ecosystem functioning and stability driven by the functions supported by some rare phenotypes, or by functional redundancy? As a unified analytical framework, the trait probability density (TPD) [1,4] approach can be relevant for Sol analyses. Nevertheless, there are some practical limitations in the application of this framework given that it requires ideal and precise descriptions of continuous trait distributions (within species, communities, etc), which are rarely available.

There have been many attempts to mathematically unify and integrate the different facets of biodiversity and rarity [4,11]. This is valuable given that single biodiversity (rarity) metrics can be provided. We proposed one of them through a multiplicative framework [2,5], echoing abundanceweighted evolutionary distinctiveness scores [12]. TPD can be used for assemblage-level analyses. In any case, we call for simplicity and pragmatism when navigating the jungle of rarity indices, so as to remain useful for the conservation and monitoring of biodiversity whose objectives are tightly linked to rarity issues within the global context of extinction of both species and functions.

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References

- Carmona, ->C. et al. (2017) Towards a common toolbox for rarity: a response to Violle et al. Trends Ecol. Evol. 32, 889–891
- Violle, C. et al. (2017) Functional rarity: the ecology of outliers. Trends Ecol. Evol. 32, 356–367
- Violle, C. et al. (2014) The emergence and promise of functional biogeography. Proc. Natl. Acad. Sci. U. S. A. 111, 13690–13696
- Carmona, C.P. et al. (2016) Traits without borders: integrating functional diversity across scales. Trends Ecol. Evol. 31, 382–394
- Grenie, M. et al. (2017) funrar: an R package to characterize functional rarity. *Diversity Distrib.* http://dx.doi.org/ 10.1111/ddi.12629 Published online September 11, 2017
- Rabinowitz, D. (1981) Seven forms of rarity. In *The Biological Aspects of Rare Plant Conservation* (Synge, H., ed.), pp. 205–217, Wiley
- 7. Gaston, K. (1994) Rarity, Chapman & Hall
- Pereira, H.M. *et al.* (2013) Essential biodiversity variables. Science 339, 277–278
- Enquist, B.J. *et al.* (2015) Scaling from traits to ecosystems: developing a general Trait Driver Theory via integrating trait-based and metabolic scaling theories. *Adv. Ecol. Res.* 52, 249–318
- Ricotta, C. et al. (2016) Measuring the functional redundancy of biological communities: a quantitative guide. *Methods Ecol. Evol.* 7, 1386–1395
- Cadotte, M.W. et al. (2013) The ecology of differences: integrating evolutionary and functional distances. Ecol. Lett. 16, 1234–1244
- Cadotte, M. and Davies, T. (2010) Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Divers. Distrib.* 16, 376–385