RESEARCH



On the mathematical properties of spatial Rao's Q to compute ecosystem heterogeneity

Duccio Rocchini^{1,2} · Michele Torresani³ · Carlo Ricotta⁴

Received: 26 September 2023 / Accepted: 26 June 2024 / Published online: 11 July 2024 © The Author(s) 2024

Abstract

Spatio-ecological heterogeneity has a significant impact on various ecosystem properties, such as biodiversity patterns, variability in ecosystem resources, and species distributions. Given this perspective, remote sensing has gained widespread recognition as a powerful tool for assessing the spatial heterogeneity of ecosystems by analyzing the variability among different pixel values in both space and, potentially, time. Several measures of spatial heterogeneity have been proposed, broadly categorized into abundance-related measures (e.g., Shannon's H) and dispersion-related measures (e.g., Variance). A measure that integrates both abundance and distance information is the Rao's quadratic entropy (Rao's Q index), mainly used in ecology to measure plant diversity based on in-situ based functional traits. The question arises as to why one should use a complex measure that considers multiple dimensions and couples abundance and distance measurements instead of relying solely on simple dispersion-based measures of heterogeneity. This paper sheds light on the spatial version of the Rao's Q index, based on moving windows for its calculation, with a particular emphasis on its mathematical and statistical properties. The main objective is to theoretically demonstrate the strength of Rao's Q index in measuring heterogeneity, taking into account all its potential facets and applications, including (i) integrating multivariate data, (ii) applying differential weighting to pixels, and (iii) considering differential weighting of distances among pixel reflectance values in spectral space.

Keywords Biodiversity · Diversity metrics · Ecosystem heterogeneity · Remote sensing · Spatial statistics

Duccio Rocchini and Carlo Ricotta equally contributed to the manuscript.

Duccio Rocchini duccio.rocchini@unibo.it

> Michele Torresani michele.torresani@unibz.it

Carlo Ricotta carlo.ricotta@uniroma1.it

- ¹ BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum University of Bologna, via Irnerio 42, 40126 Bologna, Italy
- ² Czech University of Life Sciences Prague, Faculty of Environmental Sciences, Department of Spatial Sciences, Kamýcka 129, Praha Suchdol, 16500, Czech Republic
- ³ Free University of Bolzano/Bozen, Faculty of Agricultural, Environmental and Food Sciences, Piazza Universitá/Universitätsplatz 1, 39100 Bolzano/Bozen, Italy
- ⁴ Department of Environmental Biology, University of Rome "La Sapienza", 00185 Rome, Italy

Introduction: measuring spatio-ecological heterogeneity

Spatio-ecological heterogeneity plays a significant role in shaping various ecosystem properties, including the distribution of species (Kumar et al. 2006; Cervellini et al. 2020), the habitat structure (Deák et al. 2021), and the variability of ecosystem elements (Turner et al. 2013). From this point of view, remote sensing has been widely acknowledged as a powerful tool to measure the spatial heterogeneity of ecosystems based on pixel variability in space and, potentially, in time (Skidmore et al. 2021; Rocchini et al. 2010).

Numerous methods for assessing spatial heterogeneity have been suggested, and they can be broadly categorized into two groups: those linked to abundance (e.g., Shannon's H, Shannon, 1948) and those linked to dispersion (e.g., Variance). A measure coupling such information is Rao's quadratic entropy (hereafter also referred to as Rao's Q index, (Rao 1982)), in which both the abundance and the pairwise distance of objects is considered (see Eq. 1). The potential of such a measure has been widely acknowledged by ecologists to measure biodiversity, in particular when considering functional diversity measures based on in-situ gathered plant traits (Botta-Dukát 2005). Concerning spatio-ecological heterogeneity measurement, Rocchini et al. (2017) first proposed to extend the Rao's Q index to a spatial (2D) dimension. In practical terms, given any kind of remote sensing data treated as a matrix, a moving window (kernel) can be passed over such a matrix and the Rao's Q index can be calculated in a neighborhood. The founding principle in the translation from plant communities to spatio-ecological diversity is that pixels are thought of as individual units - as biological individuals in Rao (1982) - and their reflectance value is treated as species/class in Rocchini et al. 2022.

Spatial Rao's Q has then been widely used to relate spatial heterogeneity to ecosystem properties like local (Conti et al. 2021) and global (Randin et al. 2020) biodiversity patterns, plant structural properties (Torresani et al. 2023), plant species compositional turnover (Wang et al. 2022), plant functional diversity (Hauser et al. 2021), temporal variations of dissimilarities of plant communities (Rossi et al. 2021), coastal vegetation dynamics (Malavasi et al. 2021), tropical (Pangtey et al. 2023) and alpine (Michele et al. 2018) trees diversity and marine habitat changes (Doxa et al. 2022). The question that emerges is why researchers should opt for the adoption of a complex measure that encompasses multiple dimensions and integrates both abundance and distance measurements, rather than relying on straightforward dispersion-based measures of heterogeneity, such as variance (Graham et al. 2019; Wang et al. 2022).

In this paper, we want to shed light on the spatial Rao's Q index from different perspectives, with a focus on its statistical properties. In particular, our aim is to theoretically demonstrate

the power of the Rao's Q index in measuring heterogeneity accounting for all of its potential facets and applications, such as (i) multivariate data integration, (ii) differential weighting of pixels, and (iii) differential weighting of spectral distances, namely the distances among pixel reflectance values in the space defined by the bands of a remotely sensed image as axes. The flow of the presented formula is available in Fig. 1.

What does the Rao's Q index actually measure?

In the realm of remote sensing applications, the process of discerning the spatial distribution of diversity within a digital image, specifically identifying areas of the image that exhibit higher diversity compared to others, commonly involves the computation of diversity indices. These indices are typically calculated within specific regions of interest or by utilizing moving windows (Fig. 2, (Rocchini et al. 2021)). Accordingly, given a moving window of any size and shape composed of *N* pixels, the Rao's Q index can be defined as the expected spectral dissimilarity between two pixels drawn at random with replacement from the window:

$$Q = \sum_{i,j}^{N} \frac{1}{N} \times \frac{1}{N} \times d_{ij}$$
(1)

where $\frac{1}{N}$ is the probability of drawing pixel *i* (or *j*) out of *N* pixels and d_{ij} is the spectral dissimilarity between pixels *i* and *j* such that $d_{ij} = d_{ji}$ (i.e., d_{ij} is symmetric) and $d_{ii} = 0$ (the spectral dissimilarity of a pixel with itself equals zero).

Therefore, according to Eq. 1, in its simplest formulation, Rao's Q index is nothing more than the mean spectral

Fig. 1 Flowchart of the main formulas described in this paper describing the Rao's O index formula (Eq. 1) and its main properties (Eq. 2 and 3). Starting from the Rao's Q index, pixels can be differentially weighted (Eq. 4) to give more importance to specific landscape characteristics, with the possibility of calculating the contribution of each pixel (Eq. 5) as well as the spectral originality (sensu Ricotta et al. 2016) of N pixels (Eq. 6). Furthermore, one can assign a differential weight to distances, e.g., to larger distances which account for the highest possible turnover (Eqs. 7 and 8)



Fig. 2 Description of the moving window approach to calculate any spatial measure in a neighborhood. The first moving window (red) of 3x3 pixels is passed over the original matrix/ image and used to calculate a measure, in this case the Rao's Q index, which is attached to the central pixel in the output matrix/image. Then, it moves by one step (green and then blue, etc.), and the same approach is applied. The whole process is repeated throughout the entire original matrix/image and leads to a new output with the calculated Rao's Q index. Any odd number of pixels can be used as moving window dimension



dissimilarity among the N pixels in the moving window, including the dissimilarity of one pixel with itself. The dissimilarity d_{ij} can be computed either from a single spectral band as the difference in values between two pixels or in a multivariate spectral space by means of one of the many multivariate dissimilarity coefficients used in exploratory data analysis (see, e.g., Legendre and Legendre 2012). Hence, unlike more standard diversity indices which are calculated on a single band at a time, the Rao's Q index can accommodate multivariate differences between digital numbers (DNs).

It is easily shown that for a fixed number of pixels *N*, the relationship between the Rao's Q index and the expected spectral dissimilarity between two pixels drawn at random without replacement from the window $Q' = \sum_{i \neq j}^{N} \frac{1}{N} \times \frac{1}{N-1} \times d_{ij}$ (i.e., the standard mean dissimilarity among the *N* pixels) is equal to:

$$Q' = \frac{N}{N-1} \times Q \tag{2}$$

In the univariate case, if the dissimilarity in the reflectance values (DNs) of a single spectral band is computed as half the squared Euclidean distance $d_{ij} = \frac{1}{2} \times (DN_i - DN_j)^2$, the Rao's Q index is identical to variance, which is routinely used in remote sensing applications to compute the spatial complexity of digital images (Rocchini et al. 2017):

$$Q = \frac{1}{2} \sum_{i,j}^{N} \frac{1}{N} \times \frac{1}{N} \times (DN_i - DN_j)^2 = \frac{1}{N} \sum_{i}^{N} (DN_i - \overline{DN})^2$$
(3)

where \overline{DN} is the mean spectral reflectance of the *N* pixels: $\overline{DN} = \frac{1}{N} \sum_{i}^{N} DN_{i}$. Accordingly, the Rao's Q index can be interpreted as a distance-based multivariate generalization of the variance of a quantitative variable, such as the DNs of one or more spectral bands. As such, it represents the dispersion of DNs in multivariate space, which can be calculated with a wide variety of dissimilarity measures of choice. Champely and Chessel (2002) further showed that, under particular circumstances, quadratic diversity corresponds to the mean distance of the N pixels from the centroid of the DNs distribution in multivariate space.

Potential applications

Multivariate data integration

Compared to more classical univariate measures, the main advantage of the Rao's Q index is that with quadratic entropy one can calculate landscape complexity using multiple spectral bands of a remotely sensed image simultaneously. By using appropriate dissimilarity measures, this multivariate approach can be further extended to integrate a mixture of different data sources in the index calculation, such as raw multispectral bands, categorical land use types derived from image classification or land use maps, ordinal values of landscape conservation status, surface temperatures obtained from thermal sensors, or LiDAR data on the vegetation structural complexity (Torresani et al. 2020). In addition, among the several dissimilarity coefficients that have been developed to handle mixed data sets (Gower 1971; Carranza et al. 1998; Podani 1999) some of them (see, e.g., Pavoine et al. 2009) allow the inclusion of variable weights for the various data sources such that the different variables may contribute differently to the calculation of multivariate landscape complexity (see Rocchini et al. 2017 for an example). In this way, if some variables are more important than others in determining landscape complexity and functioning, then they should be given greater relevance for the calculation of quadratic diversity (Pavoine et al. 2009).

Differential weighting of pixels

In Eq. 1, the weights w_i associated with each pixel are all equal to $w_i = \frac{1}{N}$, which is the probability of drawing pixel *i* out of the *N* pixels in the moving window. Nonetheless, Rao's quadratic entropy (intended as the mean dissimilarity among the *N* pixels) can also be calculated by weighting pixels differently in a way that depends on the specific user requirements. In this case, Eq. 1 becomes:

$$Q = \sum_{i,j}^{N} w_i \times w_j \times d_{ij}$$
(4)

with $0 \le w_i \le 1$ and $\sum_{i=1}^{N} w = 1$.

The weights associated with the different pixels may reflect properties as diverse as their conservation status, land use, vegetation cover, etc. Hence, according to Eq. 4, the N pixels are not all of the same importance, but some pixels are more important than others in determining land-scape diversity.

In this framework, the contribution of pixel i to the overall spectral diversity of a given region/window (its spectral originality O_i , namely the amount of information added to the main cloud of pixels) can be summarized as the mean dissimilarity between pixel i and a second pixel drawn at random with replacement from the window:

$$O_i = \sum_{j}^{N} w_j \times d_{ij} \tag{5}$$

Accordingly, the Rao's Q index in Eq. 4 can also be interpreted as the mean spectral originality of the N pixels in the moving window (see Ricotta et al. 2016), such that:

$$Q = \sum_{i}^{N} w_{i} \times O_{i} = \sum_{i,j}^{N} w_{i} \times w_{j} \times d_{ij}$$
(6)

Differential weighting of spectral distances: a parametric version of the Rao's Q index

As shown in Eq. 1, the Rao's Q index basically summarizes the mean spectral dissimilarity among the N pixels in a given region/window. However, in some cases, it might be useful to confer to higher distances a higher weight enhancing the highest possible gradient of diversity.

One method for attributing a different relevance to the higher spectral dissimilarities d_{ij} compared to lower dissimilarities has been first proposed by Rocchini et al. (2021). Their proposal starts from the observation of Guiasu and Guiasu (2011) that Rao's Q index can be described as a linear function of the combined probabilities of all pairs of pixels (see Rocchini et al. 2021):

$$Q = \sum_{i,j}^{N} \frac{1}{N} \times \frac{1}{N} \times d_{ij} = \sum_{i,j}^{N} \pi_{ij} \times d_{ij}$$
(7)

where π_{ij} is the combined probability of selecting pixels *i* and *j* in this order (Guiasu and Guiasu 2011). Consequently, based on Eq. 7, quadratic diversity is derived as the arithmetic mean of spectral dissimilarities d_{ij} computed between all pixel pairs *i* and *j*.

In order to assign a different level of relevance to higher dissimilarities compared to lower dissimilarities, a natural way consists of substituting the arithmetic mean in Eq. 7 with a power mean or generalized mean (Hardy et al. 1952):

$$Q_{\alpha} = \left(\sum_{i,j}^{N} \pi_{ij} \times d_{ij}^{\alpha}\right)^{\frac{1}{\alpha}}$$
(8)

with $\alpha > 0$.

Each generalized mean Q_{α} always lies between the smallest and largest of the original values: $\min d_{ij} \leq Q_{\alpha} \leq \max d_{ij}$ and, for increasingly high values of the parameter α , progressively assigns higher relevance to higher dissimilarities in the calculation of quadratic diversity.

In this view, some characteristic values of the parameter α recover some more standard concepts of means. For instance, for α approaching 0, quadratic diversity approaches the geometric mean $Q_0 = \sqrt[N]{\prod_{ij}^N \times \pi_{ij} \times d_{ij}^2}$; for $\alpha = 1$, we get the standard arithmetic mean in Eq. 7; for $\alpha = 2$, we get the cubic mean $Q_2 = \sqrt{\sum_{i,j}^N \pi_{ij} \times d_{ij}^2}$, while for $\alpha \to \infty$, we get $Q_{\infty} \to max d_{ij}$. Hence, the generalized version of quadratic diversity embodies a continuum of potential diversity meas-

diversity embodies a continuum of potential diversity measures that differ in their sensitivity to higher and lower spectral dissimilarities.

Outlook

When using Rao's quadratic entropy, three main important possibilities can be applied: (i) the possibility to use it in a multivariate space and generalize it, (ii) the possibility to differentially weight pixel values, and (iii) the possibility to differentially weight distances in the spectral space.

Concerning the first point, the Rao's Q index is a multivariate notion that puts a number of traditional measures of remotely sensed landscape heterogeneity under the same umbrella. As such, it is not an alternative to more classical measures of remotely sensed landscape complexity, such as variance or the mean spectral dissimilarity among pixels. In fact, a univariate version of the Rao's Q index, calculated on a single digital layer, should reduce to any metric based on data dispersion. On the contrary, the implicit properties of Rao's Q index as a multivariate and potentially generalized measure of heterogeneity would enhance the capabilities of measuring landscape diversity from drone or satellite imagery (see the "Multivariate data integration" section), adding information to the simple contrast derived from univariate measures.

Furthermore, with respect to other information theorybased measures, the Rao's O index allows to differentially weight pixels. When using meaningful landscape variables (e.g., some land use class of interest) or known properties of spectral response in a certain band, a differential weight of pixels suspected to be related to peculiar ecological processes can enhance their strength, relying on, e.g., a spatial weighting matrix (Bauman et al. 2018). This is particularly important, especially under the perspective of information theory in which only abundance and richness are strictly considered. However, once using continuous remotely sensed imagery data, it is expected that neighboring pixels have different values from each other. In these cases, Rao's Q, which considers distances, could weigh in a different manner the relative diversity in the used moving window. Figure 3 represents an example of a Sentinel-2 satellite image of the Sella pass in the Dolomites (46°30'30"N - 11° 46'00"E, datum WGS84, Northern Alps, Italy). As an input set, we made use of NDVI (Normalized Difference Vegetation Index), a spectral index based on the high reflectance in the near infrared and the high absorption in the red



Fig. 3 An example of calculation of the Shannon and the Rao's Q indices, starting from a Sentinel-2 image of the Sella pass in the Dolomites $(46^{\circ}30'30''N - 11^{\circ}46'00''E$, datum WGS84), in Northern Alps (Italy). The achieved output shows the importance of weighting spectral distances among pixels in the calculation. While the Shannon index is only considering relative abundance, Rao's Q is explicitly

considering a matrix of spectral distances in the calculation process. Since pixel continuous values of satellite imagery are expected to be different from each other, Shannon's H will always lead to a saturation of diversity values. This is consistent over different grains of analysis (moving windows)

wavelengths by plants representing plant biomass. In this case, a single layer was used since Shannon's H can only be calculated on univariate variables. The Shannon index and the Rao's Q were applied with different moving windows, i.e., windows moving throughout the whole image at a given spatial grain to make the calculation. Since all pixels have different reflectance values in the original image, the Shannon index always leads to maximum diversity over the whole image. On the contrary, Rao's Q considers not only differences in the relative abundance but also distances among pixel values. Hence, moving windows containing different pixels with a lower spectral distance showed a lower variability while those with pixels with higher spectral distances showed high variability. Hence, in general, the final graphical perception is a wider range of colors when using Rao's Q rather than the Shannon index. This pattern was apparent despite the spatial grain used. The complete code and data to reproduce the example is available at: https://github.com/ ducciorocchini/Theoretical_Ecology_paper/.

From this point of view, a different weight to larger distances has also a well-grounded ecological meaning. In fact, larger distances account for the highest possible turnover in a species or spectral community and are therefore of valuable importance to describe the gradient of diversity (Rocchini 2007). Moreover, just adding a single category to the set of categories in the window of analysis can lead to a wide increase of diversity in case its distance from the others is higher than the (previous) mean distance (Shimatani 1999; Pavoine et al. 2009). Hence, focusing on maximum distances can help evaluating potential trends of β -diversity (spatial turnover) otherwise lost when only considering mean distances (Baselga 2013). Moreover, using different weights on distances can help discover all the potential facets of (Rao's Q index) spectral diversity on the entire cloud of pixels. In other words, weighting distances can help convey information on the lower and upper boundaries of diversity. This is not only true for diversity patterns measured at the ecosystem or species levels, but more generally for any model relating species to habitats. In these cases, different distance weighting leads to different patterns in the relationship between habitat cover and species abundance which is generally multi-scalar (Aue et al. 2012).

The relationship of species with habitats that rule their life can be explicitly estimated through remote sensing (Skidmore et al. 2021); applying proper measures like the Rao's Q index could enhance the power of remotely sensed data for species diversity estimate at different spatial scales and in a multivariate ecological space. This could be powered by linking species in the field with their spectral signatures, based on a concept known as "spectral species," which represent the particular spectral signal of every plant species on the ground (Féret and Asner 2014; Rocchini et al. 2022). Starting from this concept, maps of alpha- or beta-diversity could be derived by the Rao's Q index applied to hyperspectral data based on a high amount of different bands ensuring to capture of peaks related to each spectral (and ground) species.

Remote sensing data are particularly powerful in measuring diversity changes in space and time as they provide long-term images at constant intervals. That is why a plethora of studies has used them as ancillary variables for biodiversity in the field (see Gillespie et al. 2008 for a review). However, applying simplistic measures would definitively hide a wide part of the potential facets of diversity. From this point of view, the use of Rao's Q entropy catches a wider spectrum of the diversity pattern. Moreover, from a practical point of view, this measure is now available in different open source packages concerning both species (e.g., the R packages FD, Picante, SYNCASA, Rarefy) and spectral (e.g., the R packages rasterdiv) variability (Box 1).

Criticism arises about the real match between species and spectral diversity. In fact, in some cases, spectral heterogeneity does not necessarily correspond to species diversity in the field. In other words, heterogeneity patterns derived from the spectral signal could be related to land use classes or objects that do not reflect diversity patterns, e.g., wide urban areas (Rocchini et al. 2021) or seminatural areas with plantations mixed to natural forests (Fassnacht et al. 2022). Of course, in this view, remote sensing cannot be generally seen as a surrogate for species diversity measurement in the field but rather as a preliminary exploratory for first information about the spectral signatures of plant species.

Box 1 - Available R packages to calculate Rao's Q index

Species level

 adiv: analysis of community diversity - https://CRAN.Rproject.org/package=adiv.

- FD: functional diversity (FD) from multiple traits - https://CRAN.R-project.org/package=FD.
- picante: community analyses, null-models, traits and evolution https://CRAN.R-project.org/package=picante.
- Rarefy: spatially and non-spatially explicit rarefaction curves using different indices of taxonomic, functional and phylogenetic diversity - https://CRAN.R-project.org/package=Rarefy.
- SYNCASA: metacommunities analysis using functional traits and phylogeny of the community components. https://CRAN.R-project.org/package=SYNCSA.

Spectral level

rasterdiv: diversity indices for numerical matrices
 https://CRAN.R-project.org/package=rasterdiv.

Conclusion

Any index of diversity should account for differences among categories as well as the proportions of such categories (Pavoine 2012). From this point of view, the main lesson learned is that Rao's Q index satisfies these requirements from several points of view, guaranteeing not only to make use of relative abundances and distances but also to tune the index with a differential weighting of both categories (pixel values) and (spectral) distances.

Moreover, testing the interaction of different factors accounting for diversity is an important component of any measurement of diversity (Legendre and Anderson 1999). Using the Rao's Q index allows for the interpretation of results on diversity based on a set of different spatial layers interacting to shape biological diversity in the field.

Finally, a generalized version of Rao's Q index allows for the identification of interesting "regions" across the entire diversity spectrum in multivariate space, revealing hidden insights that may be lost when using point descriptors that overlook the diversity gradient (Rényi 1961, 1970; Nakamura et al. 2020). While this is a long-lasting theme in the functional diversity measurement of species communities, we present the first theoretical dissertation on the mathematical properties of the spatial version of Rao's Q index.

Acknowledgements We are grateful to the receiving Editor Alan Hastings and to an anonymous reviewer for precious insights on a previous version of the paper.

Author contribution Duccio Rocchini and Carlo Ricotta conceptualized and equally contributed to the writing of the manuscript. Michele Torresani provided writing, review, and editing support.

Funding Open access funding provided by Alma Mater Studiorum -Università di Bologna within the CRUI-CARE Agreement. This study has received funding from the project SHOWCASE (SHOWCASing synergies between agriculture, biodiversity and ecosystems services to help farmers capitalising on native biodiversity) within the European Union's Horizon 2020 Researcher and Innovation Programme under grant agreement No. 862480. DR was partially funded by a research project implemented under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 - Call for tender No. 3138 of 16 December 2021, rectified by Decree n.3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union - NextGenerationEU. Project code CN_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP J33C22001190001, Project title "National Biodiversity Future Center - NBFC". DR was also partially funded by the Horizon Europe projects Earthbridge (Grant agreement No 101079310) and B3 - Biodiversity Building Blocks for policy (Grant agreement No 101059592).

Data availability This is a theoretical paper, hence it does not contain data to be deposited.

Declarations

Conflict of interest The authors declare no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

- Aue B, Ekschmitt K, Hotes S, Wolters V (2012) Distance weighting avoids erroneous scale effects in species-habitat models. Methods Ecol Evol 3:102–111
- Baselga A (2013) Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. Ecography 36:124–128
- Bauman D, Drouet T, Fortin MJ, Dray S (2018) Optimizing the choice of a spatial weighting matrix in eigenvector-based methods. Ecology 99:2159–2166
- Botta-Dukát Z (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J Veg Sci 16:533–540
- Carranza L, Feoli E, Ganis P (1998) Analysis of vegetation structural diversity by Burnaby's similarity index. Plant Ecol 138:77–87
- Cervellini M, Zannini P, Di Musciano M, Fattorini S, Jiménez-Alfaro B, Rocchini D, Field R, Vetaas OR, Irl SDH, Beierkuhnlein C, Hoffmann S, Fischer J-C, Casella L, Angelini P, Genovesi P, Nascimbene J, Chiarucci A (2020) A grid-based map for the Biogeographical Regions of Europe. Biodivers Data J 8
- Champely S, Chessel D (2002) Measuring biological diversity using Euclidean metrics. Environ Ecol Stat 9:167–177
- Conti L, Malavasi M, Galland T, Komárek J, Lagner O, Carmona CP et al (2021) The relationship between species and spectral diversity in grassland communities is mediated by their vertical complexity. Appl Veg Sci 24:e12600
- Deák B, Kovács B, Rádai Z, Apostolova I, Kelemen A, Kiss R, Valkó O (2021) Linking environmental heterogeneity and plant diversity: the ecological role of small natural features in homogeneous landscapes. Sci Total Environ 763:144199
- Doxa A, Almpanidou V, Katsanevakis S, Queirós AM, Kaschner K, Garilao C et al (2022) 4D marine conservation networks: combining 3D prioritization of present and future biodiversity with climatic refugia. Glob Chang Biol 28:4577–4588
- Fassnacht FE, Müllerová J, Conti L, Malavasi M, Schmidtlein S (2022) About the link between biodiversity and spectral variation. Appl Veg Sci 25:e12643
- Féret JB, Asner GP (2014) Mapping tropical forest canopy diversity using high-fidelity imaging spectroscopy. Ecol Appl 24:1289–1296
- Gillespie TW, Foody GM, Rocchini D, Giorgi AP, Saatchi S (2008) Measuring and modelling biodiversity from space. Prog Phys Geogr 32:203–221

- Gower JC (1971) A general coefficient of similarity and some of its properties. Biometrics 27:857–871
- Graham LJ, Spake R, Gillings S, Watts K, Eigenbrod F (2019) Incorporating fine-scale environmental heterogeneity into broad-extent models. Methods Ecol Evol 10:767–778
- Guiasu RC, Guiasu S (2011) The weighted quadratic index of biodiversity for pairs of species: a generalization of Rao's index. Nat Sci 3:795
- Hardy G, Littlewood JE, Polya G (1952) Inequalities. Cambridge University Press, Cambridge, UK
- Hauser LT, Féret JB, Binh NA, van Der Windt N, Sil ÂF, Timmermans J et al (2021) Towards scalable estimation of plant functional diversity from Sentinel-2: in-situ validation in a heterogeneous (semi-) natural landscape. Remote Sens Environ 262:112505
- Kumar S, Stohlgren TJ, Chong GW (2006) Spatial heterogeneity influences native and nonnative plant species richness. Ecology 87:3186–3199
- Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecol Monogr 69:1–24
- Legendre P, Legendre L (2012) Numerical ecology. Elsevier, Amsterdam, NL
- Malavasi M, Bazzichetto M, Komárek J, Moudrý V, Rocchini D, Bagella S et al (2021) Unmanned aerial systems-based monitoring of the eco-geomorphology of coastal dunes through spectral Rao's Q. Appl Veg Sci 24:e12567
- Michele T, Duccio R, Marc Z, Ruth S, Giustino T (2018) Testing the spectral variation hypothesis by using the RAO-Q index to estimate forest biodiversity: effect of spatial resolution. IGARSS 2018–2018 IEEE International Geoscience and Remote Sensing Symposium. IEEE, pp 1183–1186
- Nakamura G, Gonçalves LO, Duarte LDS (2020) Revisiting the dimensionality of biological diversity. Ecography 43:539–548
- Pangtey D, Padalia H, Bodh R, Datt Rai I, Nandy S (2023) Application of remote sensing based spectral variability hypothesis to improve tree diversity estimation of seasonal tropical forest considering phenological variations. Geocarto International (in press)
- Pavoine S (2012) Clarifying and developing analyses of biodiversity: towards a generalization of current approaches. Methods Ecol Evol 3:509–518
- Pavoine S, Vallet J, Dufour AB, Gachet S, Daniel H (2009) On the challenge of treating various types of variables: application for improving the measurement of functional diversity. Oikos 118(3):391–402
- Podani J (1999) Extending Gower's general coefficient of similarity to ordinal characters. Taxon 48:331–340
- Randin CF, Ashcroft MB, Bolliger J, Cavender-Bares J, Coops NC, Dullinger S et al (2020) Monitoring biodiversity in the Anthropocene using remote sensing in species distribution models. Remote Sens Environ 239:111626
- Rao CR (1982) Diversity and dissimilarity coefficients: a unified approach. Theor Popul Biol 21:24–43
- Rényi A (1961) On measures of entropy and information. In Proceedings of the Fourth Berkeley Symposium on Mathematical

Statistics and Probability, Volume 1: Contributions to the Theory of Statistics, vol 4. University of California Press, pp 547–562

- Rényi A (1970) Probability theory. North Holland Publishing Company, Amsterdam
- Ricotta C, de Bello F, Moretti M, Caccianiga M, Cerabolini BE, Pavoine S (2016) Measuring the functional redundancy of biological communities: a quantitative guide. Methods Ecol Evol 7:1386–1395
- Rocchini D (2007) Distance decay in spectral space in analysing ecosystem β -diversity. Int J Remote Sens 28:2635–2644
- Rocchini D, Marcantonio M, Da Re D, Bacaro G, Feoli E, Foody GM et al (2021) From zero to infinity: minimum to maximum diversity of the planet by spatio-parametric Rao's quadratic entropy. Glob Ecol Biogeogr 30:1153–1162
- Rocchini D, Marcantonio M, Ricotta C (2017) Measuring Rao's Q diversity index from remote sensing: an open source solution. Ecol Ind 72:234–238
- Rocchini D, Balkenhol N, Carter GA, Foody GM, Gillespie TW, He KS, Neteler M (2010) Remotely sensed spectral heterogeneity as a proxy of species diversity: recent advances and open challenges. Eco Inform 5(5):318–329
- Rocchini D, Santos MJ, Ustin SL, Féret JB, Asner GP, Beierkuhnlein C et al (2022) The spectral species concept in living color. J Geophys Res Biogeosci 127:e2022JG007026
- Rossi C, Kneubühler M, Schütz M, Schaepman ME, Haller RM, Risch AC (2021) Remote sensing of spectral diversity: a new methodological approach to account for spatio-temporal dissimilarities between plant communities. Ecol Ind 130:108106
- Shannon CE (1948) A mathematical theory of communication. Bell Syst Tech J 27:379–423
- Shimatani K (1999) The appearance of a different DNA sequence may decrease nucleotide diversity. J Mol Evol 49:810–813
- Skidmore AK, Coops NC, Neinavaz E, Ali A, Schaepman ME, Paganini M et al (2021) Priority list of biodiversity metrics to observe from space. Nat Ecol Evol 5:896–906
- Torresani M, Rocchini D, Sonnenschein R, Zebisch M, Hauffe HC, Heym M, Tonon G (2020) Height variation hypothesis: a new approach for estimating forest species diversity with CHM LiDAR data. Ecol Ind 117:106520
- Torresani M, Rocchini D, Alberti A, Moudrý V, Heym M, Thouverai E, Tomelleri E (2023) LiDAR GEDI derived tree canopy height heterogeneity reveals patterns of biodiversity in forest ecosystems. Eco Inform 76:102082
- Turner MG, Donato DC, Romme WH (2013) Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. Landsc Ecol 28:1081–1097
- Wang D, Qiu P, Wan B, Cao Z, Zhang Q (2022) Mapping α and β -diversity of mangrove forests with multispectral and hyperspectral images. Remote Sens Environ 275:113021