The ternary diagram of functional diversity

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PERSPECTIVE

The ternary diagram of functional diversity

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Abstract

1. Among the many diversity indices in the ecologist toolbox, measures that can be partitioned into additive terms are particularly useful as the different components can be related to different ecological processes shaping community structure.
2. In this paper, an additive diversity decomposition is proposed to partition the diversity structure of a given community into three complementary fractions: functional diversity, functional redundancy and species dominance. These three components sum up to one. Therefore, they can be used to portray the community structure in a ternary diagram.
3. Since the identification of community-level patterns is an essential step to investigate the main drivers of species coexistence, the ternary diagram of functional diversity can be used to relate different facets of diversity to community assembly processes more exhaustively than looking only at one index at a time.
4. The value of the proposed diversity decomposition is demonstrated by the analysis of actual abundance data on plant assemblages sampled in grazed and ungrazed grasslands in Tuscany (Central Italy).

KEYWORDS
diversity decomposition, functional homogeneity, functional redundancy, functional uniqueness, Simpson dominance

1 | INTRODUCTION

Community ecologists typically use diversity measures to explore the complex mechanisms that drive compositional heterogeneity within sampling units (plots, quadrats, etc.). Classical diversity measures, such as the Shannon entropy or the Simpson index, generally quantify community diversity based solely on species abundances, thus assuming that all species are equally and maximally distinct from each other while neglecting information on their functional differences. More recently, several 'functional diversity measures' have been proposed to summarize different aspects of functional differences between species (Champely & Chessel, 2002; Chao et al., 2014; Laliberté & Legendre, 2010; Leinster & Cobbold, 2012; Rao, 1982; Ricotta & Szeidl, 2006).

According to Gregorius and Kosman (2017), classical diversity and functional diversity address 'intrinsically disparate aspects' of the notion of biological variation: the first focuses on the assessment of richness and abundance of distinct species, while the second emphasizes ecological differences between species. As such, the information content of functional diversity is ecologically much richer compared to classical diversity. However, no conceptual framework has been suggested to handle these two different facets of diversity simultaneously.

The aim of this paper is thus to fill this gap by proposing a method to summarize different facets of the species functional differences within sites. The essence of the new approach is the decomposition of the classical Simpson diversity into two additive fractions: Rao's functional diversity and functional redundancy. The two components, together with the complement of Simpson's diversity (i.e. Simpson's dominance), can then be used to display the functional structure of a given site on a ternary diagram. If diversity decomposition is performed for all sites sampled in a given region, we obtain a graphical tool for displaying the functional structure of the whole set of sites, similarly to the beta-diversity/similarity partitioning of Podani and Schmera (2011) and Podani et al. (2013).

2 | METHODS

Imagine a sample site containing N species with relative abundances $p_i (i = 1, 2, \ldots, N)$ with $0 < p_i \leq 1$ and $\sum_{i=1}^{N} p_i = 1$. Information on the functional organization of species is usually represented by a matrix of $N \times N$ pairwise dissimilarities d_{ij} which represent the multivariate functional differences between species i and j such that $d_{ij} = d_{ji}$ and $d_{ii} = 0$. A synthetic table with all mathematical symbols and equations used in this paper can be found in Appendix S1.

Among the many measures of functional diversity available in the ecologist toolbox, Rao's quadratic diversity Q is defined as the expected (i.e. mean) dissimilarity between two individuals chosen at random with replacement from the site (Rao, 1982):

$$Q = \sum_{i,j=1}^{N} p_i p_j d_{ij}. \quad (1)$$

A relevant aspect of this index is that if the functional dissimilarities d_{ij} are in the range [0,1], a condition maintained throughout this paper, quadratic diversity is less than or equal to the classical Simpson diversity:

$$S = \sum_{i=1}^{N} p_i (1 - p_i) = 1 - \sum_{i=1}^{N} p_i^2, \quad (2)$$

which is usually interpreted as the probability that two individuals selected at random with replacement from a given site belong to different species. In terms of functional differences, the Simpson diversity can also be interpreted as the expected dissimilarity between two individuals chosen at random with replacement from the site if all N species are equally and maximally distinct from each other. Consequently, $Q \leq S$ where the equality holds if $d_{ii} = 0$ and $d_{ij} = 1$ for all $i \neq j$. Compared to the Simpson index, Rao's Q can thus integrate the observation that species are not maximally dissimilar from each other, but differ to a variable extent in their functional traits (Pavoine, 2012).

Similarly, if the interspecies dissimilarities d_{ij} are bounded in the unit range, the complement of Rao's quadratic diversity $1 - Q$ becomes a measure of 'functional homogeneity' expressed as the mean *similarity* between two individuals chosen at random with replacement from the site (Ricotta et al., 2016):

$$1 - Q = \sum_{i,j=1}^{N} p_i p_j s_{ij}, \quad (3)$$

where $s_{ij} = 1 - d_{ij}$ is the functional similarity between species i and j.

Since $Q \leq S$, we can also define a measure of functional redundancy as the amount of species diversity not expressed by functional diversity:

$$R = S - Q. \quad (4)$$

Since $d_{ii} = 0$ and $\sum_{i=1}^{N} p_i (1 - p_i) = \sum_{i \neq j}^{N} p_i p_j$, combining Equation 1 and 2, we have: $S - Q = \sum_{i \neq j}^{N} p_i p_j (1 - d_{ij}) = \sum_{i \neq j}^{N} p_i p_j s_{ij}$. Functional redundancy is, therefore, the mean functional similarity between two randomly selected individuals of different species. The measurement of functional redundancy as the difference between the Simpson diversity and Rao's quadratic diversity was first proposed by de Bello et al. (2007). Redundancy is zero when all species in the assemblage are maximally dissimilar from each other such that $Q = S$ and is maximum if the assemblage is composed of functionally identical species (i.e. if $d_{ij} = 0$ for all $i \neq j$ such that $Q = 0$). In this case $R = S$.

From a biological point of view, when several species perform similar functions but differ in their responses to disturbances, the loss of a given species will have relatively little impact on ecosystem functioning (Pillar et al., 2013). Accordingly, functional redundancy is generally assumed to provide insurance against the loss of ecosystem processes due to local species extinctions, thus enhancing community stability under ongoing perturbations (Naeem, 1998; Yachi & Loreau, 1999).

In addition to Q and R, the third component of the proposed diversity decomposition is the complement of the Simpson diversity:

$$D = 1 - S = \sum_{i=1}^{N} p_i^2. \quad (5)$$

D is a measure of species dominance, calculated as the probability that two individuals selected at random with replacement from a given plot belong to the same species. In terms of functional similarity, the Simpson dominance is the contribution to the mean species similarity obtained if both randomly selected individuals belong to the same species.

From Equation 4 and 5 it follows that Rao's functional diversity (Q), functional redundancy (R) and the Simpson dominance (D) always sum to one

$$D + R + Q = 1. \quad (6)$$

This offers the opportunity to use a triangular plot, which we will call the ternary diagram of functional diversity (or DRQ ternary diagram), to express the relationship among D, R, and Q in graphical form. As such, the DRQ ternary diagram is similar to the ternary plot suggested by Podani and Schmera (2011) to visualize the relationship between similarity, richness difference and species replacement in the decomposition of Jaccard similarity and dissimilarity. In the DRQ plot, the vertices of the triangle correspond to the three components D, R and Q and each site is represented by a point with its position determined by the actual values of the three additive components. Each corner of the triangle refers to a situation where the value of one component equals 1, and the other two values are zero. The value of each component decreases linearly with increasing distance from the corresponding corner. For example, for large values of D, the point falls close to the D corner reflecting a situation where the study site shows high species dominance and low functional diversity and redundancy (Figure 1). Similarly, if a point falls close to the R corner, the corresponding site is characterized by a very high functional redundancy. Finally, if a point falls close to the Q corner, the site shows high functional diversity and low redundancy and dominance. Remarkably, the three diversity components of the ternary diagram differ in the type of variation they capture. While Q focuses on individual-level functional variation, R considers only interspecific functional variation and D variation in species abundances.

Starting from the two-dimensional DRQ ternary diagram, we can define three one-dimensional functional gradients by adding two components at a time and using the third one as contrast. These gradients are shown as line segments running from a vertex through the centroid to the opposite edge of the triangle. The contrast between a vertex and its opposite edge may therefore reflect three different facets of the functional structure of a given community:

a. D versus $R + Q$, that is, the classical (abundance-based) contrast between the Simpson dominance D and the Simpson diversity $S = R + Q$ (see Figure 1). $D = 1$ if the sample site contains only one species and tends to zero for increasing species richness and evenness (i.e. if there are many species with similar abundances). Note that the level of species dominance is rarely considered in real study situations. What is usually considered is the Simpson diversity. However, since $D = 1 - S$, both quantities are fully equivalent to summarize this facet of community structure.
b. Functional diversity Q versus functional homogeneity $D + R$. That is, the contrast between individual-level functional dissimilarity Q and individual-level functional similarity $D + R$. If Q is low, then the point will fall close to the left edge of the triangle, and its position is mainly determined by the values of between-species similarity R and within-species similarity D. Rao's Q tends to 1 if species diversity is very high and all species are maximally dissimilar from each other (i.e. if $d_{ij} = 1$ for all $i \neq j$), whereas $Q = 0$ if all species are functionally identical.
c. R versus $D + Q$, that is, the contrast between functional redundancy and the sum of dominance and functional diversity. The component $D + Q$ is a new facet of community structure, for

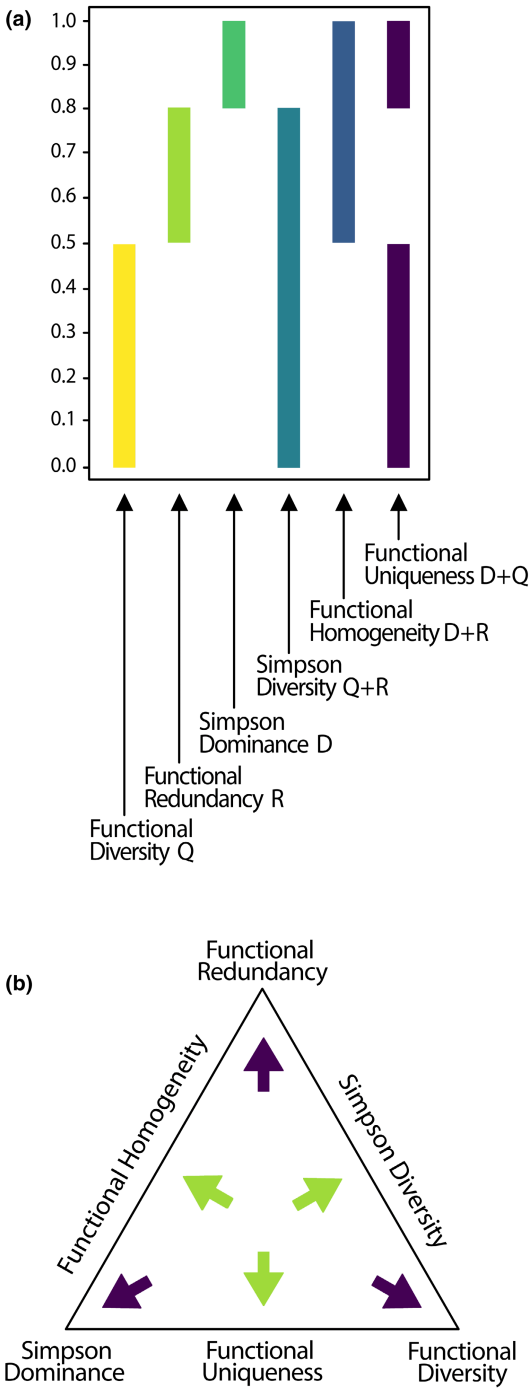

FIGURE 1 Schematic illustration of the proposed additive diversity decomposition. Vertical bars in (a) illustrate the different fractions of functional diversity. The DRQ ternary diagram in (b) represents the same diversity components in graphical form, with species dominance, functional redundancy and functional diversity corresponding to the three corners of the ternary diagram.

which we suggest the name 'functional uniqueness'. This term was first used by Ricotta et al. (2016) to define the opposite of redundancy. From an ecological point of view, high uniqueness (i.e. low interspecific functional similarity) is related to the lack of insurance against the loss of ecosystem processes due to local species extinctions. $R = 0$ if all species are maximally dissimilar. On the contrary, R tends to 1 if species diversity is very high and all species are functionally identical to each other. In this case $Q = 0$ with the Simpson diversity approaching 1, and hence $S - Q \approx 1$. Note that in this paper the term functional uniqueness is used differently from Violle et al. (2017). Here, functional uniqueness is measured as $D + Q$, while for Violle et al. (2017) functional uniqueness refers to the functional distance of a focal species to the nearest neighbour within the regional species pool.

If we have a dataset for many sample sites, then the corresponding point cloud in the DRQ triangle will graphically represent the compositional structure of those sites in terms of functional diversity, functional redundancy and species dominance. Therefore, the DRQ ternary diagram can be used to interpret the ecological processes that shape different facets of community diversity and to compare two or more groups of plots more exhaustively than looking only at differences in functional diversity.

3 | CASE STUDY

The proposed diversity decomposition is illustrated by the analysis of functional changes in plant community structure following grazing exclusion on a dry calcareous grassland in Tuscany (Italy). For eight grazed plots and seven ungrazed plots, we calculated Rao's functional diversity (Q), functional redundancy (R) and Simpson's dominance (D) based on four functional traits that include specific leaf area (SLA, mm^2/mg), leaf dry matter content (LDMC, mg/g) and nitrogen and carbon content (N% and C%). For details on the study site, data and methods, see Appendix S2 and Ricotta et al. (2023). Here, we provide the main findings of the study.

The ternary diagram in Figure 2 shows that testing for differences in the functional diversity structure of grazed and ungrazed plots with permutational distance-based multivariate ANOVA and Bray–Curtis dissimilarity (see Appendix S2), both treatments differ significantly in their DRQ composition at $p < 0.001$. Standard univariate ANOVA on the single D, R and Q ternary components further shows that the grazed plots have significantly higher values of Rao's functional diversity and lower values of Simpson's dominance (Table 1). The increased functional diversity of grazed plots is mainly determined by selective grazing and the patchy distribution of nutrients due to animal manure. This produces a heterogeneous pattern of contrasting microsites with reduced species dominance and a high turnover of functionally diverse species (Maccherini, 2006; Pierce et al., 2007). In contrast, the lower species and functional diversity of ungrazed plots is mainly due to the progressive expansion of *Bromus erectus* and the colonization of pastures by functionally

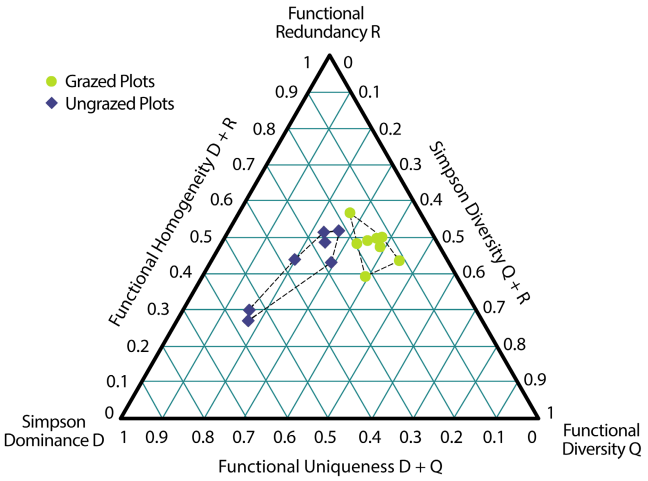

FIGURE 2 DRQ ternary diagram for the grazed and ungrazed plots of the dry calcareous grassland in Tuscany. Convex hulls delimit groups of grazed and ungrazed plots. According to distance-based multivariate ANOVA, the two groups of plots occupy significantly different positions of the ternary diagram at $p < 0.001$ ($F = 12.84$; Bray–Curtis dissimilarity and 10,000 randomizations).

similar shrubs, which give rise to an increasing homogenization of the vegetation along the succession. The redundancy values in both treatments do not show significant differences. Therefore, the higher functional homogeneity of the ungrazed plots is mainly due to their higher species dominance (i.e. the higher probability of picking up two individuals of the same species), whereas the mean functional similarity between individuals of different species is almost the same in both treatments.

These results confirm the findings of Ricotta et al. (2022), who analysed the same data set. Herbivory acts as a filter, selecting for many perennial and annual forbs such as *Teucrium chamaedrys*, *Orlaya grandiflora* and *Xeranthemum cylindraceum* with ruderal fast-growing strategies that confer them a competitive advantage in grazing conditions. On the contrary, ungrazed communities are less rich and diverse and are mainly composed of species with more conservative growth strategies (Busch et al., 2019; Herrero-Jáuregui & Oesterheld, 2018). Grazed plots host on average species that are located on the acquisitive side of the leaf economics spectrum with higher SLA and lower LDMC. This strategy allows grazed species to minimize leaf construction and maintenance costs while maximizing the ability to acquire resources more rapidly and regrow after disturbance (Díaz et al., 2016). Ungrazed plots host more conservative slow-growing species, which invest more resources in durable leaves (higher LDMC) and are also more resistant to drought stress. At the same time, the high nitrogen input from livestock in grazed plots results in higher N% values than in ungrazed plots.

4 | DISCUSSION

Ternary diagrams have long been used in geosciences to display the proportions of three components that are constrained to

TABLE 1 Mean (SD) values of individual plots within each treatment (grazed and ungrazed) for Rao's quadratic diversity *Q*, functional redundancy *R* and Simpson's dominance *D*. Pairwise comparisons of index differences between the two treatments were performed with standard univariate ANOVA. *p*-values were obtained by randomly permuting individual plots between the treatments (10,000 permutations). Asterisks show significant differences at $p < 0.001$; NS, not significant at $p < 0.05$.

	Grazed plots (eight plots)	Ungrazed plots (seven plots)
Rao's quadratic diversity Q^*	0.355 (0.051)	0.215 (0.044)
Functional redundancy R^{NS}	0.494 (0.048)	0.435 (0.095)
Simpson's dominance D^*	0.151 (0.033)	0.349 (0.131)

sum to 1 or 100% (see e.g. Pawlowsky-Glahn & Buccianti, 2011; Verma, 2015). In ecology, ternary diagrams have been introduced by Grime (1974, 1977) for the classification of plants based on their main adaptive strategies into competitor, stress tolerator and ruderal (CSR) species. In the same way, in this paper we proposed a triangular representation of community diversity based on three complementary components: Rao's functional diversity (*Q*), functional redundancy (*R*) and Simpson's dominance (*D*). Since all three diversity components can be interpreted in terms of functional similarities/differences, the representation of a given community in terms of its fractions *D*, *R* and *Q* mirrors the resemblance structure between all species in the community. In classical (abundance based) diversity theory, where all species are considered equally and maximally dissimilar from each other, this dissimilarity-based representation of community diversity would not have been possible.

A relevant aspect of the idea that different species possess different degrees of functional (dis)similarity is represented by the decomposition of the Simpson diversity into two distinct additive terms, such as functional diversity (*Q*) and redundancy (*R*). This could prove particularly useful because functional diversity and redundancy are among the primary concepts of community ecology (Biggs et al., 2020; Fonseca & Ganade, 2001; Micheli & Halpern, 2005; Mouillot et al., 2013, 2014; Pavoine & Ricotta, 2021; Ricotta et al., 2016; Rosenfeld, 2002). However, both terms have considerably different implications for the functioning and stability of the ecosystem. On the one hand, the ecosystem ability to persist after disturbance requires that different individuals perform similar functions. Therefore, high values of functional redundancy and the Simpson dominance (i.e. a high amount of between-species and within-species similarity) ensure the maintenance of immediate ecosystem processes sensu Grime (1998), such as productivity, carbon sequestration or nutrient cycling. In this context, if functionally similar species differ in their responses to disturbances, high functional redundancy limits the potential loss of ecosystem processes due to nonrandom individual mortality and local species extinctions, thus enhancing ecosystem stability (Naeem, 1998). For example, as recently shown by Cantwell-Jones et al. (2022), the level of functional overlap among species affects the robustness to perturbations of a plant–bumblebee interaction network in a montane Arctic ecosystem.

On the other hand, over the longer term, the availability of many functionally different species (i.e. high values of functional diversity) increases the probability that, in the event of major perturbations, some of them may be able of exploiting the new conditions, thus contributing to the ecosystem reassembly (Grime, 1998). Functional differences between species may also have relevant effects in buffering oscillations in immediate ecosystem functioning, particularly over periods of climatic instability or fluctuating disturbance regimes (Grime, 1998).

According to Hill (1973): "There is little point in merely confirming the obvious: the purpose of determining diversity by a numerical index is rather to provide a means of comparison between less clear-cut cases". However, being composed of two additive terms with different ecological meanings, the classical Simpson diversity is generally unsuitable for going much further than confirming the obvious. Therefore, Hurlbert (1971) defined classical diversity measures as a 'nonconcept', whereas in recent years dozens of articles have been published that relate functional diversity to various aspects of ecosystem functioning.

Note that, as suggested among others by Cianciaruso et al. (2009) or de Bello et al. (2011), if we want to replace species with individuals as the fundamental ecological accounting unit to explore trait differentiation (i.e. if we have trait estimates for all individuals in the sample site), as the number of individuals increases, *D* rapidly approaches zero leaving *R* as $\approx 1 - Q$. Therefore, ignoring species, the functional structure of the community intuitively reduces to two main components: mean individual dissimilarity *Q* and its similarity counterpart $R \approx 1 - Q$. Note also that, while high functional diversity is generally considered a desirable ecological attribute, a highly diverse community is typically a highly vulnerable community with many rare and functionally dissimilar species (Ricotta et al., 2016). Therefore, to ensure short-term and long-term community stability, an appropriate balance of functional diversity and redundancy is needed.

In addition, the fractions *D*, *R* and *Q* can be further decomposed into their species-level contributions. For example, Rao's quadratic diversity (the mean functional dissimilarity between pairs of individuals of different species) can be formulated as:

$$Q = \sum_{i=1}^{N} p_i \left(\sum_{j=1}^{N} p_j d_{ij} \right), \tag{7}$$

where

$$q_i = \left(\sum_{j=1}^{N} p_j d_{ij} \right), \tag{8}$$

is the unweighted contribution of species *i* to functional diversity.

Similarly, functional redundancy (the mean functional similarity between pairs of individuals of different species) is equal to:

$$R = \sum_{i=1}^{N} p_i \left(\sum_{j=1, j \neq i}^{N} p_j s_{ij} \right), \tag{9}$$

where

$$r_i = \left(\sum_{j=1, j \neq i}^{N} p_j s_{ij} \right), \quad (10)$$

is the unweighted contribution of species i to R. Since $D = \sum_{i=1}^{N} p_i^2$ we thus have:

$$D + R + Q = \sum_{i=1}^{N} p_i (p_i + r_i + q_i) = 1, \quad (11)$$

and

$$p_i + r_i + q_i = 1. \quad (12)$$

Therefore, according to Equation 12, we can also use a ternary diagram to characterize each species in terms of its unweighted contribution to D, R and Q.

In conclusion, data on community composition are surprisingly rich in ecological information (Podani & Schmera, 2011). The additive decomposition of functional diversity into its basic constituents helps us to extract part of this information, to graphically represent it, and to analyse it with appropriate quantitative methods. The different diversity components can then be related to different ecological processes that contribute to shaping community organization to varying degrees under different environmental conditions. Therefore, we hope that the proposed framework will help shed light on the intricate processes that drive the organization and functioning of communities.

AUTHOR CONTRIBUTIONS

Carlo Ricotta formulated the research problem; JánosPodani, Dénes Schmera and Sandrine Pavoine provided important feedback which helped shape the research; Giovanni Bacaro and Simona Maccherini sampled the data; Carlo Ricotta, Giovanni Bacaro and Simona Maccherini analysed the data; Carlo Ricotta took the lead in writing the manuscript. All authors critically reviewed the manuscript and approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

Data on species abundances and functional traits used in this study are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.7pvmcvdzc (Ricotta et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Synthetic table with all mathematical symbols and equations used in this paper.

Appendix S2. Case study: data and methods.

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