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Measuring Them all: Individual-Based Functional Spatial Patterns in Mountain Grasslands

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ABSTRACT

Questions: Spatial patterns of plant traits have rarely been studied at distances below 10 cm. Is it possible to detect nonrandom functional patterns at a very fine scale in mountain secondary grasslands? An analysis in terms of trait similarity, magnitude and density correlation can highlight the importance of different biotic and abiotic processes at these scales. We expect species identity to be of secondary importance if all individuals are identified by their measured traits, resulting in consistent patterns whether it is considered or not, especially if ITV (intraspecific trait variability) and functional overlap are high.

Location: Natural reserve "Montagna di Torricchio," a strict reserve in the Marche region, central Apennines, Italy.

Methods: Plant height, leaf area, and specific leaf area have been measured for each individual (1094 ramets) in 10 quadrats, divided into two grasslands differing in canopy cover. Functional redundancy and ITV were evaluated with overlap measures and variance partitioning. Marked point pattern statistics have been used to test for non-randomness of trait patterns either by considering all individuals at once or by excluding conspecific pairs.

Results: At distances below 8 cm, we found evidence of trait convergence, pairs smaller than expected and negative density correlation. Above 8 cm, we found trait divergence and larger than expected pairs. We suggest biotic and abiotic causes for this, linked to physical packing or similarity in soil depth, respectively. The results differed between traits and between grasslands. The results were consistent whether conspecific pairs were excluded or not. There is a high functional overlap among species, and ITV has a large contribution to variability.

Conclusions: We found nonrandom functional patterns in grasslands below 10 cm, an almost unexplored scale range in any vegetation. The approach used showed that taxonomic identity is less important than the functional setting of individuals at this scale.

1 | Introduction

The search for processes shaping communities has been a focus of plant ecology since its early days (Clements 1916), often through the procedure of investigating the underlying mechanisms through observation of spatial and temporal patterns (Watt 1947). Since then, the role of pattern and process in community assembly, dynamics, and functioning has been increasingly investigated (Brown et al. 2011; Detto and Muller-Landau 2013; Velázquez et al. 2015), highlighting the need to study ecological processes in a spatially explicit way (Levin 1992). Stochastic and deterministic processes co-participate in various proportions to realize the observed community (Götzenberger et al. 2012), with different processes hierarchically being more important at different scales (Chase 2014).

Traditionally, the focus has been on species coexistence, with the term "assembly rules" originally referring to nonrandom co-occurrence patterns (Cody and Diamond 1975), that is, the restriction on the pattern by the process (Wilson 1999). Trait-based approaches are now often used, which allow to investigate patterns of resource use and adaptation to the environment, resulting in functional divergence or convergence: these approaches are "analogous to the comparison of observed versus expected functional diversity" (Götzenberger et al. 2012). Functional diversity (Tilman 2001) measures trait differences within a community (Petchey and Gaston 2002), usually considering species as the fundamental unit (Petchey and Gaston 2006) and often neglecting the variability within species, that is, intraspecific trait variability (ITV) (Leps et al. 2006). So, even in functional analyses, the focus is often on taxonomic information: functional traits are a way to measure functional dissimilarity among *species*, that is to say, they are an additional detail on top of a fundamentally taxonomic framework, which can be used to infer trait distributions (Carmona et al. 2016), or just species means. Having traits data at the individual level, instead, opens the door to a primarily functional analysis: the focus is on the functional pattern itself, and not on how the taxonomic pattern is influenced by the functional structure.

The focus on ITV (Siefert et al. 2015; Des Roches et al. 2018; Puglielli et al. 2024) brings attention to the individual, not just as representing a certain species, but as capable of having its own response to the environment. Functional diversity can be extended to include ITV (Cianciaruso et al. 2009), but since collecting samples and measuring traits is time consuming, research on spatial trait patterns has so far made use of a limited amount of trait data, either from a representative few individuals (de Bello et al. 2013a; Scherrer et al. 2019), or from databases (Carboni et al. 2014; Kattge et al. 2020). Not considering ITV can lead to very different conclusions about patterns at the community level (Carmona et al. 2019a). Measuring traits for each individual would allow not just estimation of ITV but also consider the spatial pattern of functional individuals in their own right, since "ecologists interested in community assembly have much to gain by shifting their focus from species to traits" (Messier et al. 2010). Competition and environmental factors are a source of ITV, and especially the one caused by the former can even exceed interspecific variability for closely related species (Janíková et al. 2024). Studies of community assembly in which these processes are expected to be important should not neglect this source of variability (Kraft et al. 2014).

Deviations of trait patterns from randomness can have different biotic and abiotic causes, which can point toward either convergence or divergence. It should be mentioned that multiple processes can act at the same time at different scales (de Bello et al. 2009; Kraft and Ackerly 2010), and the detection of convergence or divergence may be strongly scale-dependent (Götzenberger et al. 2012); furthermore, contrasting patterns can co-occur for different traits (Grime 2006), even if related to similar strategies (Mason et al. 2011). At smaller scales, limiting similarity (Macarthur and Levins 1967) can result in trait divergence, while the exclusion of weaker competitors in hierarchical competition results in convergence (Mayfield and Levine 2010; Kraft et al. 2014). At intermediate (within patch) and landscape scales, abiotic factors are thought to be the main cause of assembly patterns (de Bello et al. 2013a), with habitat filtering resulting in convergence (Cornwell et al. 2006; Mason et al. 2011), and environmental heterogeneity resulting in divergence, although dispersal limitation can result in random patterns (Götzenberger et al. 2012; de Bello et al. 2013a). Additionally, abiotic effects of microhabitat heterogeneity can reach down to smaller scales, for example fine-scale soil depth, a proxy of water holding capacity (Andreetta et al. 2016), resulting in functional convergence (Mudrák et al. 2016) (Conti et al. 2017), and plants can themselves influence the environmental filter at these scales (Pillar et al. 2023; Pillar 2024).

Given this scale dependence, the a priori choice of the range of interest influences the results that can be obtained and the possible conclusions (de Bello et al. 2013a; Carboni et al. 2014; Scherrer et al. 2019). Small scales are relatively unexplored in studies of spatial patterns of functional traits in any vegetation, with a lower limit of $0.01\,\mathrm{m}^2$ reached in grassland (Wellstein et al. 2014; Carboni et al. 2014). Little is known about whether convergence or divergence is more likely to be detected at scales below $0.04\,\mathrm{m}^2$ and whether the results are context-dependent or more general. Very small scales are particularly interesting if one expects biotic interactions to get stronger the shorter the distance between individuals (Stoll and Weiner 2000).

The reason for this lower limit is the widespread use of quadrat-based sampling at these scales; this kind of sampling establishes an a priori grain size that will be the resolution limit of the study. Therefore, quadrat-based sampling can only look at properties of a neighbourhood, for how small it is chosen to be; conversely, point pattern analysis can consider individuals themselves and is only limited by the resolution of the measurement tools used. In the case of noncumulative measures, specific distances of interest between pairs can be analysed, allowing for the separation of contrasting processes acting at different scales.

Point pattern statistics study the arrangement of points in space as a result of a random point process (Baddeley et al. 2015 p. 127). They have been used in many fields, including plant ecology, but they have been most often applied to trees (Velázquez et al. 2016), owing also to the existence of fully mapped forest dynamics plots, such as those in the CTFS-ForestGEO network (Anderson-Teixeira et al. 2015); still, there are some notable exceptions (Escudero et al. 2005; Fajardo et al. 2008; Benot et al. 2013; Chacón-Labella et al. 2016; Losapio et al. 2018). Of special interest here are the so-called second-order statistics, which measure the properties of pairs of points at or within a given distance (Ripley 1977; Stoyan and Stoyan 1995; Wiegand and Moloney 2004). The minimum requirement for point pattern methods is to fully map the coordinates of individuals (points) inside a window, which is usually rectangular. Additional data about each point are called marks, which in plant ecology can most naturally be traits (Wiegand and Moloney 2014 p. 212), and an additional suite of statistics is available to analyse the patterns of qualitative or quantitative marks. Although spatial patterns of functional or phylogenetic similarity have been studied with point pattern methods (Shen et al. 2013; Parmentier et al. 2014), fully mapping individuals does not necessarily mean measuring traits for each, so those measures have been based on a dissimilarity matrix between species, constructed from mean species data in the functional case. The only previous point pattern grassland study with traits measured for each individual (Losapio et al. 2018) has not analysed their spatial patterns by using them as marks.

The present study aims to investigate the spatial patterns of functional traits at very small scales, following an individual-based approach using the tools of point pattern analysis. Among the large number of plant functional traits (Kattge et al. 2020), we selected vegetative height, specific leaf area (SLA), and leaf area (LA). They are three aboveground traits of recognized ecological importance, which represent different functions and trade-offs: height corresponds to competitive ability to preempt light and disperse diaspores, LA is important for energy and water balance, and SLA represents a trade-off for carbon gain strategies (Díaz et al. 2016). Together, these traits are sufficient to define the two main independent dimensions of variation in the global spectrum of plant form and function, those referring to plant size and to leaf economics (Díaz et al. 2016).

We expect the fine-scale spatial pattern of traits to depend on the specific values at those coordinates, so the traits have been measured at the individual level. This allows the estimation of ITV in terms of its relative importance, functional space overlap and redundancy, and conversely, the importance of species identity for the observed patterns. A high degree of functional overlap between species and high community redundancy would give support to the consideration of individuals as a fundamental unit, regardless of species, each with the potential of covering a large proportion of the community trait distribution.

For the selected traits, we ask whether there is a nonrandom functional pattern at scales smaller than usually considered, and which are the scales of interest. Since functional divergence, as evidence of limiting similarity, has been the most common result in studies focusing on the smallest scales (0.01–$0.04\,\mathrm{m}^2$) (Stubbs and Wilson 2004; de Bello et al. 2013a; Wellstein et al. 2014; Carboni et al. 2014; Scherrer et al. 2019; Pescador et al. 2021), as a working hypothesis we expect the same effect to carry over to smaller scales. However, given the lack of previous evidence, we do not exclude deviations in the direction of convergence. In fact, the opposite result of competitive interactions to niche differentiation is the determination of trait-based hierarchies; such mechanisms have been shown for height (Carmona et al. 2019a) by which taller plants are favored in the competition for light (Mason et al. 2011), so we can expect trait convergence for height, driven by the exclusion of weaker competitors.

The statistics used can highlight patterns of traits, deviations in terms of similarity, directionality, and correlations with neighborhood density as a function of distance. The explicit consideration of space allows the identification of patterns with multiple characteristic scales: for example, the existence of functional patches would show convergence at smaller scales and divergence at larger scales, without the trait at those distances being necessarily larger or smaller than average. The presence of trait hierarchies is expected to cause, within the radius of biotic interactions, deviations in the direction of the most competitive value, together with convergence.

2 | Methods

2.1 | Sampling

Sampling was conducted between June and July 2018 in the natural reserve "Montagna di Torricchio," a strict reserve since 1970 in the Marche region, central Apennines, Italy. Ten quadrats of size 50 × 50 cm have been placed randomly in two distinct mountain secondary grasslands (*Festuco-Brometea* class) at about 1100 m a.s.l., one with a dense and closed vegetation cover (from now on "closed"), and one which is more open and eroded (from now on "open"), with five replicates in each. For a more detailed description of the physiognomy, see Wellstein et al. (2014). The five plots in a group are at a short distance from each other and considered representative of an internally homogeneous grassland, justifying their use as replicates. In each plot, all fully grown functional rooting units (ramets), considered as plant individuals, have been marked with a stick and the cartesian coordinates of each have been measured with respect to a corner of the plot taken as origin, with a resolution of 0.1 cm (Appendix S1); an individual was considered inside the plot if the base of the stem is within the plot; tufts, given the difficulty of distinguishing individuals, were considered as a single individual if they were clearly connected and the distance between units was less than 5 cm.

For each individual in a plot, aside from the coordinates, the species was determined, together with the measurement of vegetative height, LA, and SLA according to standard procedures (Perez-Harguindeguy et al. 2016). Additionally, soil depth and horizontal spread have been measured: soil depth is a proxy of water availability and represents the distance of the bedrock from the surface, measured by inserting a stick as far as possible in the soil at those coordinates; horizontal spread is a proxy of horizontal plant space occupation defined as the maximum distance between two leaves parallel to the soil.

In total, 1094 individuals were identified and measured, of which 64 had a missing value for LA and SLA because the leaves were damaged. Given the small proportion of missing values, those individuals were simply omitted from the respective analyses.

2.2 | Trait Space Analysis

A preliminary step analysed the functional traits in a nonspatial way to show the degree of overlap and redundancy between species and with the respective communities, relationships between traits and the functional space of the two grasslands, and to quantify ITV. At the level of traits, after testing for normality with the Shapiro–Wilk test, the Spearman rank correlation was used to test the independence of the measured traits. Because the trait distributions were asymmetric, they have been $\log_{10}$-transformed for the nonspatial analyses and point pattern statistics based on principal component analysis (PCA); for point pattern statistics on single traits, the original trait values have been used because we wanted to study their patterns as observed. PCA was applied to reduce the three traits considered into orthogonal dimensions, allowing the construction of a trait space in which to locate individuals, compare species and the two grasslands. The 'funspace' package (Carmona et al. 2024) was used to check the number of principal components to keep and to make a functional space plot.

Similarity (1-dissimilarity, for these measures), calculated from the overlap of trait probability distributions (TPD), was used to compare the two grasslands, each species with its grassland, and species within a grassland; the mean of the species-grassland overlaps has been calculated, weighted by abundance, and the specific pairwise similarities were used to calculate the abundance-weighted pairwise overlap between species in a grassland (Mason et al. 2011). Shared trait space, functional richness, and redundancy were also calculated for the grasslands. Overlap measures at the species level were calculated for single traits and for the functional space determined by PCA. The overlap-based dissimilarities were calculated with the 'TPD' package (Carmona et al. 2019b).

Trait variability has been partitioned into nested levels of grassland, quadrat, species, and individual, to show the relative contribution of each (Messier et al. 2010; Kraft et al. 2014; Carmona et al. 2015). This has been done by fitting a linear mixed effects model with the function 'lme' from package 'nlme' (Pinheiro et al. 2024), followed by variance partitioning with the function 'varcomp' from package 'ape' (Paradis and Schliep 2019).

2.3 | Point Pattern Analysis

The summary statistics used belong to the family of mark correlation functions for quantitatively marked patterns. In their general form, they represent the conditional mean of a test function $t(m_1, m_2)$ calculated for the marks (i.e., traits) of a pair of points at a distance r from each other, over all pairs at that distance (Illian et al. 2008 p. 343; Wiegand and Moloney 2014 p. 65; Baddeley et al. 2015 p. 645):

$$c_t(r) = \mathbb{E}\left[t\left(m_1, m_2\right)\right]$$

In which m_1 and m_2 are the marks of two individuals belonging to the pattern at distance r. The statistic is calculated for a range of distances $r_{\max} \geq r > 0$, for a chosen maximum distance $r_{\max}$. Since, in the absence of spatial structure, $c_t(r)$ yields the average of the test function over all pairs of individuals c_t, it is often normalized by dividing it by this nonspatial expectation:

$$k_t(r) = \frac{c_t(r)}{c_t}$$

Different test functions t result in different mark correlation statistics; the ones used here are:

- $t(m_1, m_2) = m_1 \times m_2$: mark correlation *sensu stricto* $k_{mm}(r)$, the product of the marks
- $t(m_1, m_2) = (m_1 - m_2)^2/2$: mark variogram $\gamma(r)$, half the squared difference of the marks
- $t(m_1, m_2) = m_2$: r-mark correlation $k_{\cdot m}(r)$, the value of the mark of the second individual

The choice of complementing $k_{mm}(r)$ with $\gamma(r)$ allows for the decomposition of deviations into directionality and magnitude. Being based on the product of the pairs of marks, $k_{mm}(r)$ can estimate the directionality of the relationship; it can show if the pair of marks is bigger or smaller than average by comparison with the expected value (i.e., 1 for the normalised function), but the effects can be masked by opposing deviations (a product of a mark which is bigger and one which is smaller than the mean μ can result in the same product μ^2). Being based on the squared difference of the marks, $\gamma(r)$ can instead measure differences between marks regardless of sign and relation to the mean value, but by itself does not show if more similar marks are larger or smaller than average.

Additionally, a related measure, the cumulative density correlation function $C_{mK}(r)$, estimates the Pearson correlation between the mark of a focal individual m_1 and the density of neighbours within distance r (Fedriani et al. 2015). A noncumulative version of this measure exists, but we found it more meaningful to relate the trait of an individual to the number of neighbours *within* a certain distance, instead of *at* that distance.

To extend the concept of the variogram to the trait space, a multivariate version of $\gamma(r)$ is proposed, calculated on the values obtained by PCA. Since the PCA axes are orthonormal, it is sufficient to sum the (not normalized) variograms of the different axes to obtain a measure that represents the average squared Euclidean distance in the trait space (Bourgault and Marcotte 1991; Wagner 2003).

Mark correlation functions require a kernel function to identify which individuals belong to a certain distance class. 'Programita' (Wiegand and Moloney 2014) uses a box kernel, whose bandwidth has been chosen based on pattern intensity, following the equation $0.2/\lambda^{0.5}$ (Illian et al. 2008, p. 236). Because it is preferable to restrict r to ¼ of the side length of the window (Ripley 1977; Ripley 1988; Diggle and Cox 1983), the summary functions have been evaluated in the distance range 0.1–12.5 cm, which encompasses the scales of interest.

Two kinds of analyses have been performed: in the "univariate" analysis, all individuals have been treated in the same way, using $k_{mm}(r)$, $\gamma(r)$ and $C_{mK}(r)$; in the "bivariate" analysis, individuals of a focal species have been considered part of the first pattern, from which m_1 is taken, and heterospecific individuals have been considered part of the second pattern that yields m_2, using $k_{mm}(r)$, $\gamma(r)$, and $k_{\cdot m}(r)$. Those two complementary analyses allow considering all individuals as functionally independent with the former, but also to exclude possibly confounding pairs belonging to the same species or clonal colony (genet) with the latter.

To assess the significance of the detected patterns, they were compared against randomizations according to the independent random marking null model: for the univariate tests, the randomizations consisted of 999 permutations of the traits among all individuals of a plot; for the bivariate tests, for each species and for each plot, the traits of all individuals of other species were permuted 999 times, while keeping the traits of the focal species fixed. The choice of $C_{mK}(r)$ for the univariate analysis and $k_{\cdot m}(r)$ for the bivariate relates to the choice of null model: the former is the density correlation of the traits of the focal individuals, so it is not randomised in the second model; there it is replaced by the latter, which corresponds to the ecological question "what is the average trait of an heterospecific at distance *r*" and correctly calculates this without including the values of conspecifics.

Since the plots of each grassland are considered independent homogeneous samples of the same pattern, the results are presented as averages over each grassland, according to the aggregation formulas for point pattern statistics (Wiegand and Moloney 2014 p. 248; Baddeley et al. 2015 p. 680), achieving higher statistical power by having a sufficient number of individuals and lower variance of the estimators (Illian et al. 2008 p. 267). By randomizing only within each plot, and assuming that conditions within each are homogeneous, we are considering a valid null model that is not accidentally liberal by bringing in the characters of an individual from a different plot (Götzenberger et al. 2012). In the case of the bivariate analysis, the test statistic is the weighted average of all the specific patterns in all plots of that grassland, which is valid because each individual is the focal point once and only once, and combining replicates can be done not just for different samples of the same process, but also for different species (Wiegand and Moloney 2014 p. 254).

Traditionally, the comparison between observed point pattern statistics and the null model has been performed with a *pointwise* envelope that shows the observed function and critical bounds built from the kth highest and lowest ranked of the s simulation functions at each distance r, for a given significance level $2k/(s+1)$ for a two-tailed test. Despite the popularity of this approach, it has long been known that it suffers from type I error inflation because as many hypotheses are being tested as the evaluated distances (Loosmore and Ford 2006), unless a specific distance r has been chosen a priori (Baddeley et al. 2014). Among the proposed solutions, the global envelope tests presented in Myllymäki et al. (2017) combine a test with correct type I error probability with the intuitive graphical representation of envelopes, which can be inspected to find the reason for the rejection of the null hypothesis; besides having this biunivocal correspondence, these tests have been shown to have higher power than unscaled global tests (Myllymäki et al. 2015; Myllymäki et al. 2017). Global envelope tests have been applied using the package 'GET' (Myllymäki and Mrkvička 2023); the "area" rank measure was chosen because it performs well both in the case of maximum and integral extremeness (Myllymäki and Mrkvička 2020).

Since the application of marked point pattern statistics assumes the pattern to be stationary (Gelfand et al. 2010, chap. 21; Baddeley et al. 2015, p. 644), we checked first-order homogeneity of the patterns using a quadrat test based on a 4 × 4 grid and 1999 simulations, with the function 'quadrat.test' from the package 'spatstat' (Baddeley et al. 2015). One plot of open grassland was found to be inhomogeneous and has been excluded from point pattern analysis; its collected traits have still been used in the nonspatial analysis.

Calculation of marked point pattern statistics has been performed with the software 'Programita' (Wiegand and Moloney 2004; Wiegand and Moloney 2014). All other analyses and data handling have been done with R, version 4.3.3 (R Core Team 2024).

3 | Results

3.1 | Trait Space Analysis

Spearman correlations between the three traits are significant but weak (Appendix S2). The first two components of PCA explain 91.9% of the variance, so the trait space has been reduced to two dimensions. Plotting the kernel-based trait probability densities (TPD) in this space (Figure 1) shows that LA and SLA contribute most to the first principal component, whereas the second corresponds mostly to height (Appendix S3). The TPDs in the two grasslands seem very

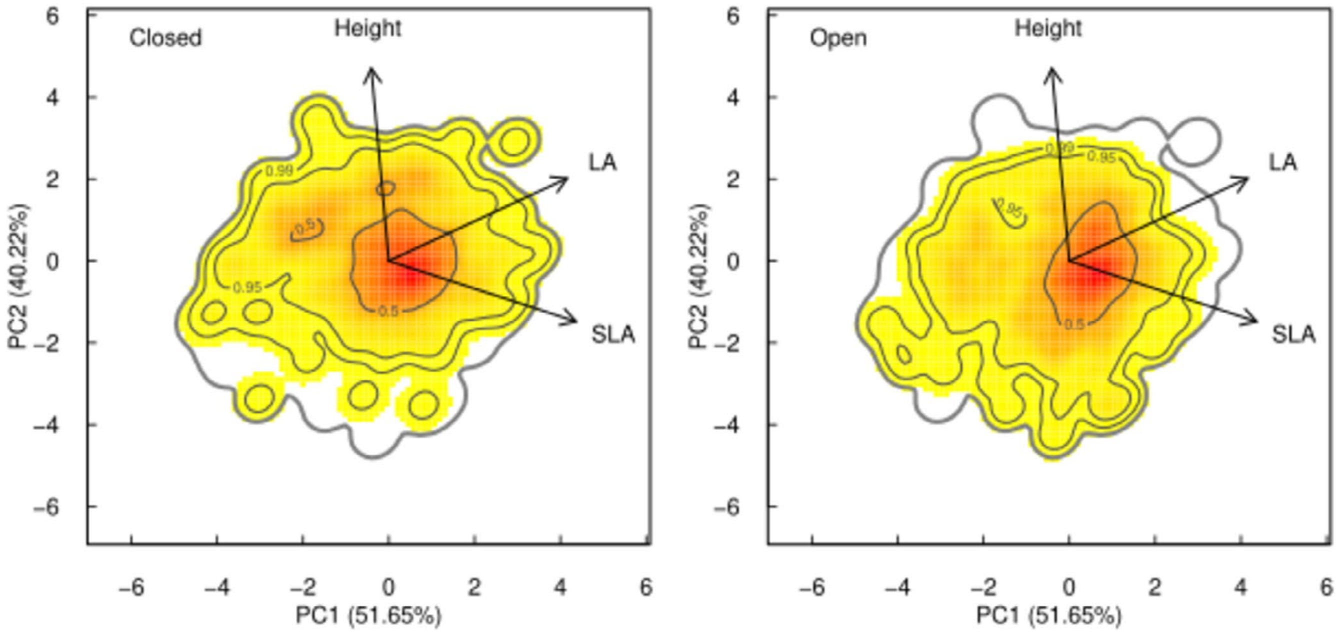

FIGURE 1 | Representation in the two-dimensional trait space of the trait probability density in the two grasslands. Loadings of the measured traits in this space are shown. The gray contour represents the global distribution with a threshold of 0.999.

similar, with almost overlapping 95% quantile contours, but a slight tendency toward lower height and SLA for the open grassland. The measured dissimilarity (Table 1) is correspondingly low, being 22%, of which 98% is due to different probability densities in the shared part of the trait space. Since the purpose of this study is not comparative, with the two grasslands being analysed separately because they represent two possibly different environments, the differences would not be formally tested; rather, this comparison is presented to show that a nonspatial analysis does not suggest different functional patterns in the two grasslands.

Functional redundancy is high in both grasslands: at the community level, they can each lose half of their species while keeping the same functional richness (Table 1). This is further confirmed by the overlap-based similarity measures between each species and the respective grassland, which are often above 40% and, in some cases, reach 60% (Table 2).

Variance partitioning for the three traits shows almost equal contributions from the interspecific and intraspecific levels, with almost none from the grassland and quadrat levels (Table 3). This does not only indicate large functional differences between the two grasslands, but also supports the assumption of homogeneity among replicate plots. Intraspecific variation is especially large for height and LA, and less for SLA. It must be stated that the intraspecific level contains both ITV and measurement errors.

3.2 | Point Pattern Analysis

Without considering traits, analysis of the distribution of individuals using the pair correlation function is consistent with the CSR null model, the homogeneous Poisson process (Appendix S4). While mark correlation functions factor out this aspect of the spatial pattern, it is interesting to note that individuals, without considering their traits, show neither aggregation nor dispersion in the considered range.

TABLE 1 | Functional dissimilarity between closed and open grassland, decomposed into dissimilarity within and outside the shared trait space, and functional redundancy of the two grasslands.

Dissimilarity	0.219	
Shared component	0.984	
Nonshared component	0.016	
	Closed	**Open**
Redundancy	9.149154	11.434499
Relative redundancy	0.435674	0.571725

Note: “shared” and “nonshared” components partition dissimilarity into differences in density within the shared and unique portions of the functional space. Relative redundancy is divided by species richness minus 1.

For the “univariate” mark correlation analysis, which considers all individuals as the same, most of the significant results are found in the closed grassland. For height, there is moderate evidence of convergence, as indicated by lower than expected $\gamma(r)$ at distances around 6 cm, and strong evidence of negative density correlation below 8 cm (Figure 2I[b,c]). LA shows a similar negative density correlation, but no evidence of convergence, instead featuring a trait product higher than expected at distances above 12 cm (Figure 3I[a,c]). No or weak evidence of a nonrandom pattern was found for SLA (Figure 4I[a–c]). The multivariate variogram highlights, instead, convergence in the two-dimensional trait space in the open grassland above 8 cm (Figure 5IIa).

Repeating the analysis only considering pairs of heterospecifics shows patterns consistent with the univariate analysis. For height, there is still evidence of convergence in the closed grassland, and additionally, the trait product is smaller than expected at shorter distances and higher at larger distances (Figure 2I[d–f]). For LA in the closed grassland, $k_{mm}(r)$ is again larger than expected above 12 cm, but divergence around 10 cm is also revealed, and $k_{\cdot m}(r)$, the average trait of the heterospecific at distance r, is smaller than expected at short distances, larger than expected around 10 cm (Figure 3I[d–f]). Differently from the “univariate” model, excluding conspecifics for SLA provides strong evidence for higher $k_{mm}(r)$ at intermediate distances in closed grassland, but smaller at very small or large distances in the open grassland; $\gamma(r)$ shows divergence in closed grassland around 10 cm, with $k_{\cdot m}(r)$ higher than expected at those same distances (Figure 4I[d–f],II[d–f]), as with LA. The multivariate variogram in this case indicates convergence in the closed grassland (Figure 5Ib).

4 | Discussion

We have found nonrandom patterns of aboveground functional traits at distances smaller than 12.5 cm, a range of distances rarely considered in this kind of study (but see Wellstein et al. 2014; Carboni et al. 2014). The specific results depended on the scale, the trait considered, and the grassland, but in general, convergence has been detected at smaller distances and divergence at

TABLE 2 | Two measures of species-community functional overlap, both representing abundance-weighted means.

	Trait space	Height	LA	SLA
Closed grassland				
Species pairwise overlap	0.429522	0.446154	0.444157	0.378024
Species to grassland overlap	0.403805	0.577496	0.66037	0.459328
Open grassland				
Species pairwise overlap	0.43753	0.45965	0.456959	0.409174
Species to grassland overlap	0.379165	0.64595	0.60328	0.474806

TABLE 3 | Variance partitioning of traits across the four levels of the study.

	Grassland	Quadrat	Species	Within species and error
Height	0.128	0.018	0.49	0.364
LA	0	0	0.511	0.489
SLA	0	0	0.753	0.247

larger distances. The strongest evidence was found in the closed grassland, where the distance of 8 cm seems to divide those contrasting patterns, consistent with the hypothesis of a patchy distribution of traits, with convergence within patches and divergence between them. In detail, for size-related traits (height, LA), we found lower values within patches, together with convergence, and higher values between patches. Patterns at this scale are consistent with both the average horizontal spread of individuals (Appendix S5) and the range in which the soil depth is more similar than expected by the overall variance (Appendix S6),

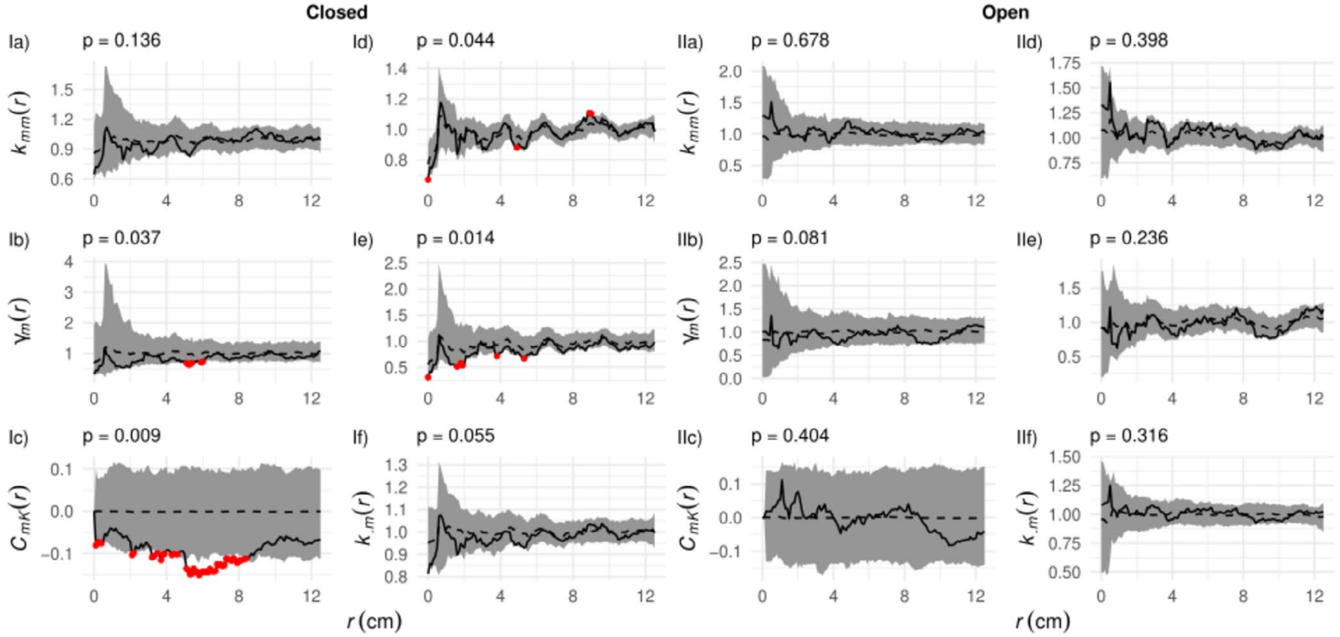

FIGURE 2 | Summary statistics and global envelope for plant height, for closed (Ia–f) and open (IIa–f) grassland. Plots a–c are the results with the "univariate" model, d–f with the "bivariate." In this figure and the following, the red colour highlights the distances that lead to rejection of the null hypothesis.

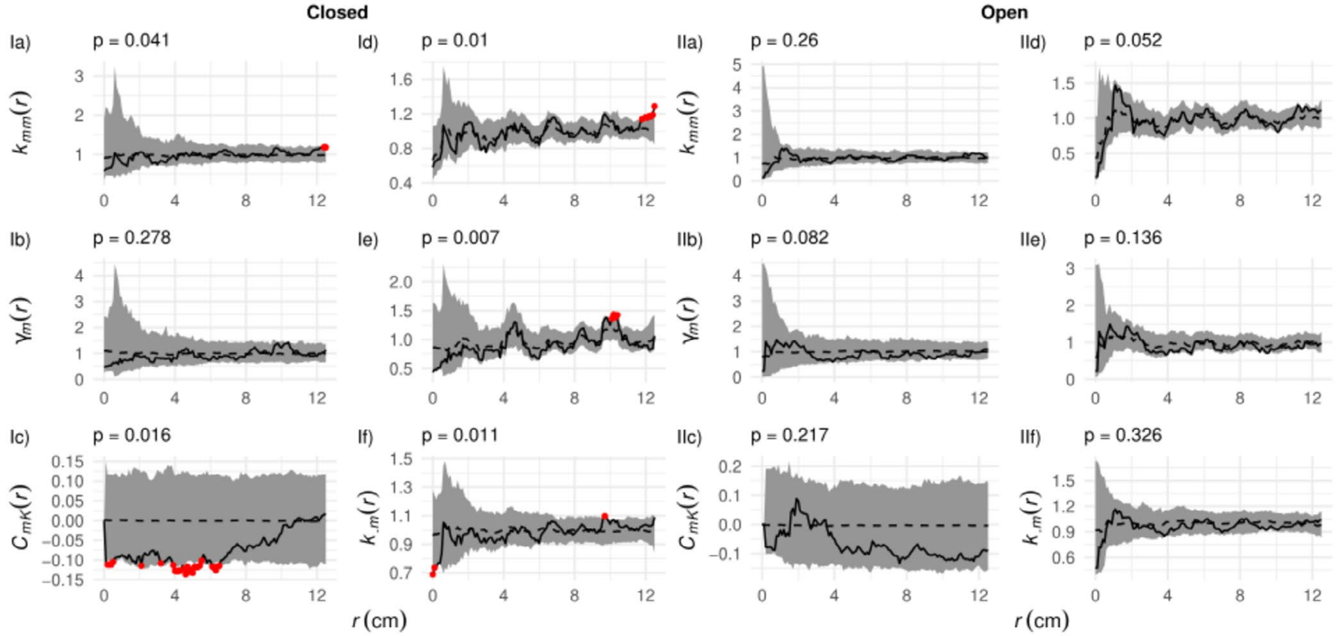

FIGURE 3 | Summary statistics and global envelope for LA, for closed (Ia–f) and open (IIa–f) grassland. Plots a–c are the results with the "univariate" model, d–f with the "bivariate."

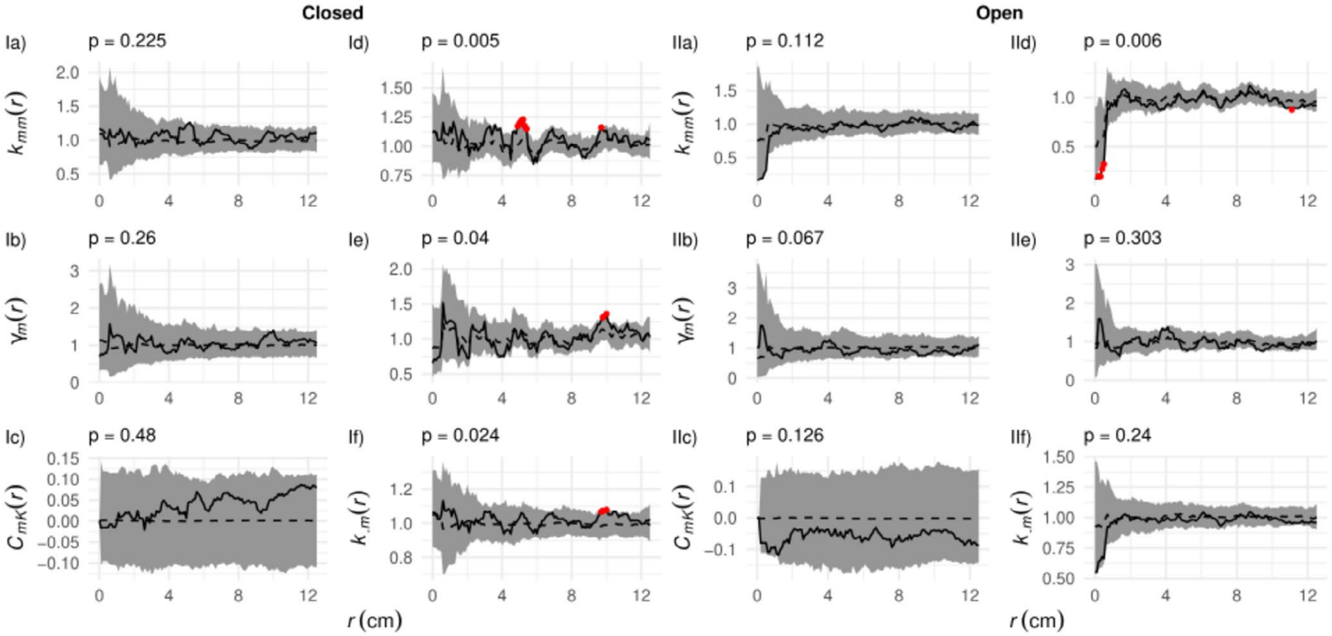

FIGURE 4 | Summary statistics and global envelope for SLA, for closed (Ia–f) and open (IIa–f) grassland. Plots a–c are the results with the "univariate" model, d–f with the "bivariate."

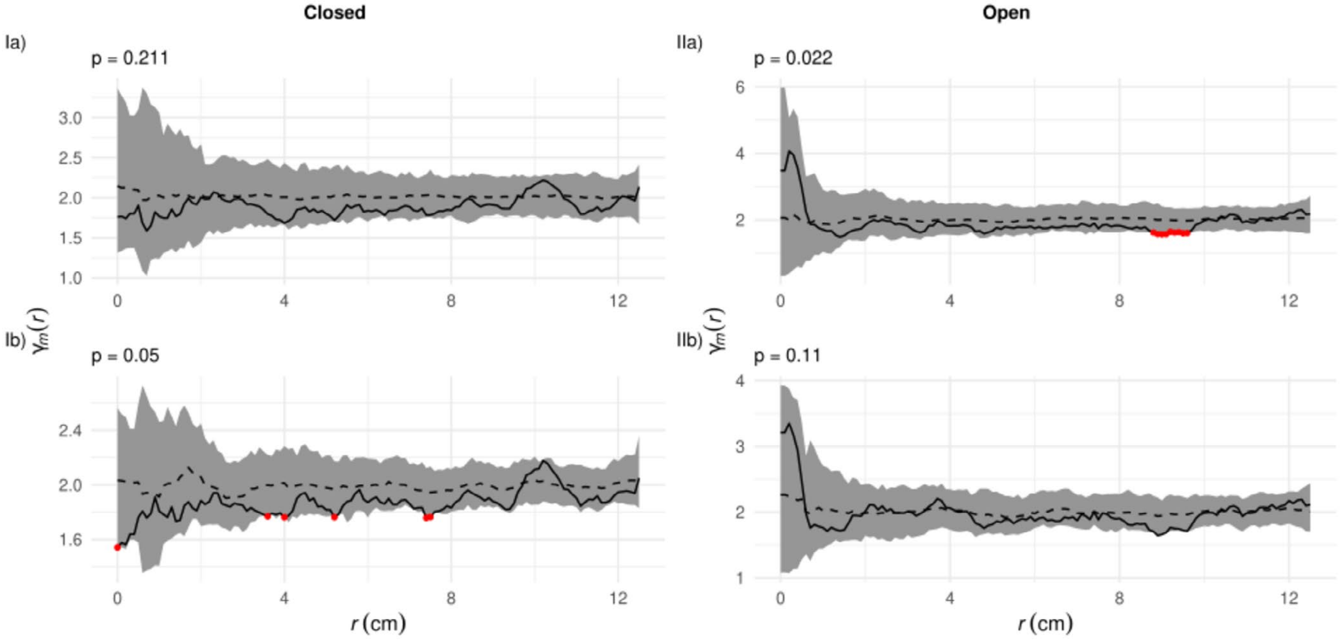

FIGURE 5 | Multivariate variogram based on the first two PCA components and global envelope, for closed (Ia, b) and open (IIa, b) grassland. Plots Ia and IIa are the results with the "univariate" model, Ib and IIb with the "bivariate."

pointing to biotic (i.e., competition) or abiotic (i.e., water availability) causes, respectively. On the contrary, SLA of heterospecifics showed a different pattern, with the pairwise product being larger than expected at distances both above and below 8 cm, and a larger trait at a distance of 10 cm. These different patterns could be related to light availability, as SLA is expected to respond faster to this resource than LA and height. The results for the squared trait space distance of heterospecifics are consistent with the patch interpretation and similar to those of height and LA because those two traits contribute to each of the principal components kept.

Few pieces of evidence of nonrandom patterns were detected in the open grassland, either because the patterns are truly mostly random or because this analysis could not detect them. The trait space distance showed convergence at scales that are larger than those in which it was found in closed grassland, so it is also possible that other nonrandom patterns were not found because the characteristic scales are overall larger, outside the range considered in this study. A possible explanation may be related to the features of the open grassland, characterized by constant soil erosion, which might prevent the formation of a structured pattern by reducing the strength of biotic interactions.

Together, those results suggest that the closed grassland, with a higher density of individuals and a higher possibility of biotic interactions, is a competitive environment where the functioning of individuals is limited by the presence of others at small distances (Janíková et al. 2024). This is consistent with the negative density correlation within patches for height and LA, which would point in the direction of biotic interactions. However, since the correlation between pattern intensity and soil depth, or other measurable microenvironmental factors, is unknown, abiotic effects cannot be excluded. We suggest that negative density correlations are an effect of space occupancy, with overall larger individuals having a lower number of neighbors within their average radius as height and LA are both positively correlated with horizontal spread (Appendix S2). To better examine the relationship of this feature and soil depth with the trait space, a GAM model on the two principal components was fit and visualized on the functional space (Appendix S7), showing a particularly strong positive relationship of horizontal spread with height. Both are measures of physical size that show similar patterns (Appendix S8), in particular negative density correlation. In fact, given that the scales considered are very small, comparable to the size of the individuals, competition for space might be the main mechanism of biotic interactions at these scales, as observed for size-related traits not only in the negative density correlation but also in the combination of convergence, lower than average trait product, and trait value: physical packing makes larger values of height and LA less likely at shorter distances.

Considering all pairs of individuals or only those of different species never resulted in contrasting results. Convergence in the "univariate" model could be caused by conspecific individuals being more similar than heterospecifics, but aside from trait space distance in the open grassland, when convergence was detected with the "univariate" model it also was with the "bivariate" one; in the case of squared trait space distance for closed grassland, it was even shown only by the "bivariate" model. Considering species and excluding conspecific pairs allowed the detection of functional divergence, which was perhaps concealed in the "univariate" model, but consistent results between the two kinds of analysis show that, when functional individuals are identified solely by their measured traits, it is still possible to detect nonrandom patterns without involving taxonomy and possible determination errors. As dispersal limitation is a mechanism acting on species, we speculate that this approach can lessen its influence.

The parallel quantification of functional overlap and redundancy gives support to considering functional individuals regardless of their species. Using overlap measures allowed the consideration of ITV, which could be quantified from the collected values. Compared to Gower distance measures of dissimilarity, overlap measures have been found to be less sensitive to trait ranges and distributions and to result in higher dissimilarity values (de Bello et al. 2013b); despite this, we found that, on average, species have a high degree of functional overlap and each can cover a good proportion of the overall trait distribution when considering either individual traits or the trait space. Variance partitioning has shown that ITV is a likely contributor to functional overlap, being comparable to interspecific variability, with the highest explained proportion for the traits with the highest functional overlap (height, LA). Interestingly, repeating some of the point pattern analyses after replacing the measured traits with species means led to completely different results (Appendix S9). In this system, in which ITV has been found to be high, it is not sufficient to use species mean traits to describe patterns at fine scales.

Heterogeneity can be the cause of the observed patterns, especially for the $k_{mm}(r)$ and $k_{\cdot m}(r)$ functions. By checking the kernel-weighted spatial smoothed distribution of traits, some plots appear to have a heterogeneous distribution of traits (Appendix S10). By repeating the analyses featuring $p \leq 0.05$ with the local independent marking null model, there was weak or no evidence of deviation from a random pattern (Appendix S11). This could point to larger within-plot scale heterogeneity in the trait distribution causing the deviations from randomness, but the lack of evidence could also result from the sample size becoming too small to generate a sufficient number of unique permutations, or the assumption of separation of scales being violated (Wiegand and Moloney 2014 p. 308). Either way, inhomogeneity and interaction cannot be distinguished based just on an observed realization of a point process (Gelfand et al. 2010 p. 345). Since equalizing mechanisms, such as those indicated by functional convergence, cannot, according to niche theory, support coexistence, environmental heterogeneity can represent the necessary stabilizing mechanism through the spatial storage effect (Chesson 2000). That within-plot functional heterogeneity can still be detected at these scales should be considered when sampling individuals, especially if the goal is to study convergence or divergence.

5 | Conclusions

This study has shown the potential of fully mapping and applying point pattern statistics to grassland field studies, the considerable sampling effort required notwithstanding. Furthermore, the analyses conducted here do not exhaust the possibilities of one such fully mapped data set, but instead represent just a small selection chosen to answer a specific question. Another extension of point pattern theory is multivariate point patterns, in which multiple classes of points are distinguished a priori; a natural application in ecology is considering different species (Wiegand and Moloney 2014 s. 4.3). Indeed, spatially explicit, point pattern versions of classical diversity indices have been developed for multivariate patterns (Shimatani 2001).

Sampling functional traits on an individual basis is labour intensive and not always possible, but doing so has allowed us to estimate trait variability, functional overlap, and redundancy without the biases that could result from assuming a species' trait distribution instead of measuring it (Carmona et al. 2019b). Furthermore, by describing functional individuals by their own measured traits in a spatially explicit analysis, we were able to investigate how the functional features of each are related to those of its neighbours at specific scales. Our tests using species means, calculated from the collected data (Appendix S9), revealed them to be insufficient in approximating our results.

This study has presented evidence in support of nonrandom patterns in grassland at scales smaller than those previously considered: this is possibly another merit of fully mapping individuals, allowing sufficient sample size and resolution to show significant deviations from the null model. When contrasting patterns have been found at different scales, they could have cancelled out in a traditional quadrat-based approach, given that the maximum scale considered is similar to the common quadrat size used in grassland. Previous studies predominantly identified divergence as the emerging pattern at small scales (Stubbs and Wilson 2004; de Bello et al. 2013a; Wellstein et al. 2014; Carboni et al. 2014; Scherrer et al. 2019; Pescador et al. 2021), but further increasing the resolution showed evidence of convergence for some of the traits considered. In addition to the spatial storage effect, other mechanisms can allow coexistence, like divergence for other traits, temporal storage (Chesson 2000b) in the form of clonal growth and phenology, or disturbance.

Given these considerations, we think our approach is well suited to analyse and compare community patterns affected by fine-scale biotic and abiotic factors (microhabitat filtering, competition, facilitation). Although point pattern analysis could be applied without such an extensive trait sampling, focusing just on the coordinates, even for functional diversity (Shen et al. 2013), it would require assuming that ITV is irrelevant or estimating it in other ways. Knowledge about ITV is still limited, but it has been found to be context, trait, and scale dependent (Puglielli et al. 2024); our results show that it should be considered in mountain grasslands at fine scales. Still, point pattern analysis by itself can be a powerful preliminary approach to find the scales of interest in a system, and more efficient sampling methods have been proposed for less densely populated grasslands (Wang et al. 2020).

Considering the lack of previous knowledge, the approach used is necessarily explorative, and further studies are necessary to identify the causes of the patterns found, whether they are biotic or abiotic. Still, ecological understanding of the system is the first step to develop precise hypotheses, which can later be tested to understand the process from the pattern (McIntire and Fajardo 2009), and we believe the analysis techniques used here are suitable. Additional studies can show if the patterns found here are context-dependent or not, whether they would differ at different levels of stress and competitive intensity. Repeated sampling could reveal eventual shifts in the case of nonequilibrium dynamics, for example during different phases of natural disturbance regimes. Finally, point pattern statistics usually express a mean value of a typical point, but, as in general in ecology, there is much to be gained also from the study of variance, and summary functions of this kind (Schlather et al. 2004) are expected to give a more complete understanding of patterns.

Author Contributions

L.L.M.D.B., S.C., R.C., and G.C. conceived the research idea; S.C. and G.C. collected data; L.L.M.D.B. set up and performed the statistical analyses; L.L.M.D.B. wrote the paper; and L.L.M.D.B., S.C., and G.C. discussed the results and commented on the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and settings for reproducibility are available at https://doi.org/10.5281/zenodo.13990541. All the R scripts used are available at https://doi.org/10.5281/zenodo.13969411.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.