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Spatio-temporal regression on compositional covariates: modeling vegetation in a gypsum outcrop

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1	SPATIO-TEMPORAL REGRESSION ON COMPOSITIONAL COVARIATES:
2	MODELING VEGETATION IN A GYPSUM OUTCROP
3	
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7	
8	SUMMARY
9	Investigating the relationship between vegetation cover and substrate typologies is important for habitat
10	conservation. To study these relationships, common practice in modern ecological surveys is to collect
11	information regarding vegetation cover and substrate typology over fine regular lattices, as derived from
12	digital ground photos. Information on substrate typologies is often available as compositional measures,
13	e.g., the area proportion occupied by a certain substrate. Two primary issues are of interest for ecologists:
14	first, how much substrate typologies differ in terms of relative suitability for vegetation cover and,
15	second, whether suitability varies over time. This paper develops a novel procedure for managing
16	compositional covariates within a Bayesian hierarchical framework to effectively address the
17	aforementioned issues. A spatio-temporal model is adopted to estimate the temporal pattern
18	characterizing substrate relative suitability for vegetation cover and, at the same time, to account for
19	spatio-temporal correlation. Relative suitability is modeled by time-varying regression coefficients, and
20	spatial, temporal and spatio-temporal random effects are modeled using Gaussian Markov Random Field
21	models.
22	
23	KEYWORDS: binomial data; compositional covariates; Intrinsic Gaussian Markov
24	Random Fields; hierarchical Bayesian model; vegetation cover; suitability
25	
26	

1 INTRODUCTION

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In ecological applications, over the past years, there has been an increasing interest in 29 collecting and analyzing datasets with both spatial and temporal dimensions. The 30 increasing use of imaging tools able to collect and process digital ground photos 31 managed by Geographic Information System (GIS) (Bennett et al. 2000; Richardson et 32 al. 2001; Booth et al. 2005) has introduced ecologists to a new framework in which the 33 analysis of ecological outcomes, such as species richness, abundance and vegetation 34 cover, is based on high-resolution spatially referenced data. Vegetation cover is one of 35 the most important indicators of rangeland condition and plays a key role in habitat 36 37 management and conservation policies (Booth and Tuller 2003).

In this paper, we investigate the relationship between vegetation cover and substrate typologies within a rupicolous basophilic habitat defined as priority by the European Commission (Council Directive 92/43/CEE). Available data consist of post-processed ground photos taken at several points throughout the study period, which provide information about vegetation cover and substrate typology in a fine regular lattice.

43 Modeling vegetation cover in terms of substrate typologies is crucial to evaluating 44 substrate suitability, i.e., substrates' natural ability to support vegetation. Knowledge 45 concerning substrate suitability is strategic in predicting future developments and 46 reactions to possible environmental changes in the considered habitat. The ecological 47 behavior of vegetation in arid and rocky environments has been investigated in several 48 studies (Kuntz and Larson 2006; Pueyo and Alados 2007).

Regression models, often including spatio-temporal components, have been largely
adopted in the ecological literature to investigate the relationships between ecological
outcomes and environmental factors (Guisan and Zimmermann 2000; Fortin et al. 2012;

52 Kneib et al. 2008). A flexible framework for ecological data is represented by 53 hierarchical Bayesian models (Wikle 2003). The hierarchical structure is useful for 54 accounting for multiple sources of uncertainty and allows for model complexity to be 55 handled in a suitable manner, namely by factorizing the joint distribution into simple 56 conditional models. The role of hierarchical modeling in ecological studies has been 57 discussed in Latimer et al. (2006).

In this paper, a hierarchical Bayesian approach is adopted to investigate the temporal pattern of substrate suitability for vegetation, considering four types of substrate that are found in the habitat under examination, namely moss, litter, soil and bare rock. To properly capture substrate suitability, spatio-temporal correlation must be taken into account: when handling lattice data, Gaussian Markov Random Fields (GMRFs, Rue and Held 2005) are popular tools for modeling structured effects in space and time or both.

A peculiar feature of the case study is that data concerning substrate typology are 65 compositional, i.e., at a given time, substrate data are expressed as the proportion of cell 66 grid occupied by each type of substrate. The compositional nature of substrate 67 information implies an additional challenge for statistical modeling: regression on 68 compositional covariates requires suitable techniques to obtain meaningful regression 69 coefficients indicating the effect of each single compositional part. Analyses involving 70 compositional data begin by mapping the compositional values belonging to the simplex 71 72 onto real space by any of several possible transformations (Aitchison 1986; Egozcue and Pawlowsky-Glahn 2006). A popular transformation for compositional data is the 73 isometric log-ratio (*ilr*) transformation (Egozcue et al. 2003), which has the advantage 74 75 of isolating the contribution of a given compositional part with respect to all others. In the context of linear regression on compositional covariates, ilr transformation was 76

adopted by Hron et al. (2012), who proposed an inferential procedure that requires the
estimation of as many models as the number of compositions.

In the present paper, starting from the proposal of Hron et al. (2012), a new approach for handling compositional covariates in regression models is developed within a Bayesian hierarchical framework. The proposed strategy provides regression coefficients that are easy to interpret as relative suitability values.

This paper is organized as follows. A motivating example describing the structure of the data concerning an ecological application is outlined in section 2. In section 3, the modeling approach is discussed, and the procedure for handling compositional covariates is proposed. The application results are discussed in section 4. The concluding remarks are provided in section 5.

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2 MOTIVATING EXAMPLE

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Our focus is on a study designed within the framework of the priority defined by the European Commission (Council Directive 92/43/CEE), with the aim of investigating habitat "6110* Rupicolous calcareous or basophilic grasslands of the *Alysso-Sedion albi*". A sampling campaign was performed on a gypsum outcrop within the Site of Community Importance "IT4050001 Gessi Bolognesi e Calanchi dell'Abbadessa" located in the Emilia Romagna Region, Italy. For a detailed description of the case study, see Velli (2014).

99 Data were collected over a study period going from April 2012 to late March 2013.
100 Sampling campaigns were adjourned during the dryness period of August and
101 September, when low vegetation cover is expected, and on January because of snow
102 cover. A total of nine sampling campaigns were conducted at unequally spaced times,

103 denoted as t = 1, ..., 9. The study area consists of a $1.5 \times 1.5m$ quadrat, structured as a regular lattice of dimension 30x30, containing 900 grid cells, indexed by $s = 1, \dots, 900$, 104 which are denoted as *plots* in the ecological literature . At each time, a ground-photo of 105 the study area was taken and then processed via GIS algorithms to produce a digital 106 image for vegetation cover and ground composition. Namely, ground composition 107 considers D = 4 substrates: moss, litter, soil and bare rock. Each grid cell (plot) in the 108 digital image provides information collected over n = 100 pixels. At time t and plot s, 109 the number of pixels covered by a plant is denoted as y_{st} , and the proportions of 110 substrate typologies are collected in the vector $\mathbf{z}_{st} = (z_{1st}, z_{2st}, z_{3st}, z_{4st})$. As an example, 111 z_{1st} is the count, or the proportion, of pixels covered by moss in plot s at time t; 112 analogously we obtain the substrate proportions for litter (z_{2st}) , soil (z_{3st}) and bare 113 rock (z_{4st}) . It is worth noticing that, at any time t and plot s, $z_{1st} + z_{2st} + z_{3st} + z_{4st} = n$ 114 , thus substrate typology z_{st} is a compositional variable. 115

Some descriptive statistics concerning pixel-specific vegetation cover (expressed as y_{st}/n) are summarized in Table 1, where means and quartiles over the study area are reported for each time.

119

Τ	1	2	3	4	5	6	7	8	9
Mean	0.158	0.127	0.102	0.046	0.195	0.258	0.338	0.340	0.393
Q1	0.010	0.000	0.000	0.000	0.000	0.000	0.040	0.060	0.110
Median	0.060	0.040	0.000	0.000	0.080	0.140	0.210	0.220	0.310
Q3	0.210	0.150	0.110	0.000	0.310	0.420	0.600	0.560	0.640
Moran's I	0.433	0.569	0.510	0.469	0.534	0.600	0.612	0.615	0.614

120 121

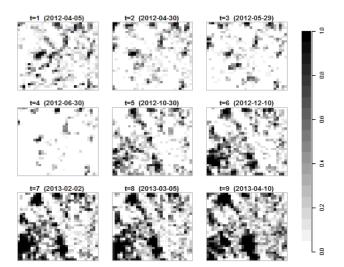
Table 1 Descriptive statistics of vegetation cover (y_{st}/n) over time

The average vegetation cover changes substantially across time. A decreasing trend is observed until t = 4; at the fourth time point, vegetation is almost absent, later it

increases in terms of both the number of pixels where vegetation is present (i.e., Q1 is 124 greater than zero only for $t \ge 7$) and average coverage. Last row in Table 1 reports the 125 126 Moran's I statistics measuring spatial correlation. Moran's I index (Moran 1948) measures the degree of correlation between observations at neighboring plots. This 127 128 index takes continuous values from -1 (maximum negative spatial correlation) to 1 129 (maximum positive spatial correlation) with 0 indicating absence of spatial correlation. A spatio-temporal representation of the vegetation cover is reported by maps in Figure 130 1. The spatial correlation characterizing the vegetation cover measured at the pixel level 131

is considerable throughout the entire study period and becomes more evident from the
fifth to the last time point, as evidenced by the Moran's *I* values in Table 1. Overall, the
data show both spatial and temporal correlation.

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Fig. 1 Maps of vegetation cover at each collection time (indicated within brackets)

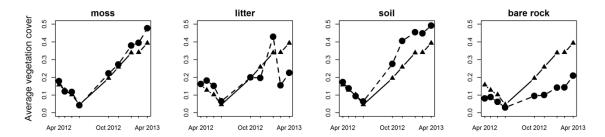
In Table 2, the pixel-specific shares z_{st} of substrate typologies are summarized, demonstrating the existence of temporal variability both within and between substrates.

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Т	1	2	3	4	5	6	7	8	9
Moss	0.46	0.30	0.35	0.35	0.42	0.50	0.57	0.54	0.49
Litter	0.29	0.15	0.14	0.19	0.06	0.01	0.03	0.01	0.01
Soil	0.09	0.30	0.26	0.14	0.22	0.23	0.17	0.20	0.18
Bare rock	0.16	0.25	0.25	0.32	0.30	0.26	0.23	0.25	0.32

143 144
 Table 2 Share of substrate typology averaged over the study region at each collection time

- 145 To investigate the effect of substrate typology on vegetation cover, the marginal average cover over time (see the first row of Table 1) is considered as a benchmark to be 146 147 compared to the substrate-specific conditional average. These syntheses are shown in 148 the four panels of Figure 2 as solid and dashed lines, respectively. Noisy behavior characterizes the pattern observed on litter substrates, particularly at the end of the study 149 period, when such a typology is scarcely represented in the region (see Table 2). 150 151 Vegetation cover on moss, soil and bare rock substrates shows a decreasing trend until summer, followed by an increasing trend; such a pattern reflects the general behavior of 152 vegetation over the study period due to the natural vegetation life cycle in dry 153 grasslands. 154
- 155



156 157 158 159

Fig. 2 Comparison of trends for average vegetation cover (solid line) and conditional vegetation cover (dashed lines) for each substrate

160 The aim of the model proposed in the following section is both to capture the marginal temporal trend for vegetation, basically due to climate, and to quantify the substrate-161 specific effect on vegetation, i.e., the ability of a substrate typology to favor/inhibit 162 163 vegetation cover . Because of the compositional nature of the substrate data, such an ability can only be evaluated comparatively among substrates. In fact, if a substrate 164 typology shows a higher-than-average vegetation cover, necessarily some other 165 substrates will show lower-than-average cover; for this reason, substrate effects will be 166 interpreted as "relative suitability" measures. Two main questions arise: How much do 167 substrate typologies differ in terms of relative suitability? Does this difference vary over 168 time? From a statistical point of view, substrate suitability estimates can be obtained as 169 170 regression coefficient estimates of a regression model where vegetation cover is the response variable and substrate typology is aa compositional covariate. A spatio-171 temporal modelling framework is seek in this work for two reasons. First, spatial and 172 temporal dependencies observed in the descriptive plots for vegetation cover need to be 173 modelled for reliable estimates of the regression coefficients to be obtained (ref?). 174 Second, it is of interest to model the temporal structure in the regression coefficients to 175 predict suitability of all substrates at unobserved times and investigate their temporal 176 variations across the study period. 177

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3 MODEL

182 The relationship between substrate typology and vegetation cover is modeled by the 183 hierarchical Bayesian model described in what follows; the strategy for handling 184 compositional covariates is discussed in the next subsection. Let y_{st} denote the count of pixels covered by vegetation at plot *s* and time *t*. Conditional on the vegetation occupancy probability π_{st} , counts are assumed to follow a Binomial distribution, i.e., the binary response at each pixel within a plot is considered as the realization of an independent trial. Spatio-temporal variability and dependence on covariates are managed at higher levels of the hierarchy. The likelihood is specified as follows:

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191
$$y_{st} | \pi_{st} \sim Binomial(\pi_{st}, n)$$
 $s = 1, ..., S; t = 1, ..., T$

192

where *n* denotes the constant number of pixels belonging to each plot. The model can be easily generalized to the case of a variable number of trials; nevertheless, having a constant number of trials simplifies the algebraic representation of the model presented in section 3.2 and in Appendix A. To model the vegetation occupancy probability as a function of covariates, we adopt the *probit* link; the linear predictor is specified as follows:

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200
$$\Phi^{-1}(\pi_{st}) = \eta_{st} = \mathbf{x}'_{st} \boldsymbol{\beta}_t + \alpha_t + \theta_s + \delta_{st}$$
 $s = 1, ..., S; t = 1, ..., T$ (0)

201

where \mathbf{x}_{st} is a *P*-dimensional covariate vector and $\boldsymbol{\beta}_t = (\beta_{1t},...,\beta_{pt},...,\beta_{Pt})$ denotes the vector of time-varying regression coefficients. Postulating time-varying coefficients implies that time is an effect modifier; checking this assumption in our case study is crucial because the aim is to evaluate the evolution (if any) of substrate suitability over time. Three sets of random effects are included to account for spatio-temporal variability not explained by the dependence on the covariates: $\boldsymbol{\alpha} = (\alpha_1,...,\alpha_t,...,\alpha_T)$ and 208 $\theta = (\theta_1, ..., \theta_s, ..., \theta_s)$ are vectors of temporal and spatial main effects, respectively,

209 whereas vector $\boldsymbol{\delta} = (\delta_{11}, ..., \delta_{st}, ..., \delta_{ST})$ contains space-time interactions.

Modeling of both regression coefficients and random effects is based on the theory 210 concerning Intrinsic Gaussian Markov Random Fields (IGMRFs, see Rue and Held 211 2005, for a comprehensive review), which are very popular tools for spatio-temporal 212 modeling of lattice data. Because of the Markov property, which implies the sparseness 213 214 of the precision matrix, IGMRFs allow for extremely fast computations. IGMRFs have also been extended to cope with irregularly spaced time locations by Lindgren and Rue 215 (2008); this is particularly useful in our case study, in which measurements have been 216 collected at unequally spaced times, as often occurs in ecological studies. 217

In the following, $IGMRF_J(\tau K)$ denotes the (multivariate normal) distribution of a Jdimensional random vector with $J \times J$ -dimensional structure matrix K and precision parameter τ ; the IGMRFs are improper, i.e., K is rank-deficient. Structure matrix Kdescribes conditional dependence relationships derived from assumptions concerning the spatial and temporal structure of the phenomenon.

Let $\boldsymbol{\beta}_{p} = (\beta_{p1}, ..., \beta_{pt}, ..., \beta_{pT})$ denote the *T*-dimensional vector of regression coefficients 223 referring to the p-th covariate obtained by re-arranging the p-th elements of vectors 224 $\boldsymbol{\beta}_t = (\beta_{1t}, \dots, \beta_{pt}, \dots, \beta_{Pt})$ for all $t = 1, \dots, T$. We introduce a temporal dependence among 225 these coefficients, assuming a smooth variation of the covariate effect over the study 226 period, by specifying the prior $\boldsymbol{\beta}_{p} \sim IGMRF_{T}(\tau_{\beta_{p}}\boldsymbol{K}_{\beta_{p}}); p = 1,...,P$. Following the 227 modeling strategy first proposed in Knorr-Held (2000) in the context of spatio-temporal 228 disease mapping, prior distributions for spatio-temporal random effects are specified as 229 follows: $\boldsymbol{\alpha} \sim IGMRF_T(\tau_{\alpha}\boldsymbol{K}_{\alpha}), \ \boldsymbol{\theta} \sim IGMRF_S(\tau_{\theta}\boldsymbol{K}_{\theta}) \text{ and } \boldsymbol{\delta} \sim IGMRF_{ST}(\tau_{\delta}\boldsymbol{K}_{\delta}).$ 230

Structure matrices \mathbf{K}_{β_p} and \mathbf{K}_{α} need to be specified to capture a smooth temporal behavior. In this context, Random Walk (RW) priors (i.e., IGMRFs on the line) of order 1 is a popular choice; we set common temporal structure matrices $\mathbf{K}_{\beta_p} = \mathbf{K}_{\alpha} = \mathbf{K}_{RW}$. It follows that $rank(\mathbf{K}_{RW}) = T - 1$. Because our data are irregularly spaced over time, the structure matrix typically used for this process must be adapted. To this aim, Rue and Held (2005) propose a solution by considering the integration of the Wiener process (Wahba, 1978).

Structure matrix \mathbf{K}_{θ} is specified as the $S \times S$ -dimensional Laplacian matrix of the graph induced by a first-order neighboring structure on the regular lattice formed by the plots. The *i*-th diagonal entry is equal to the number of neighbors of plot *i*, whereas the *ij*-th entry equals -1 *iff* plots *i* and *j* share a common boundary and zero otherwise. With this specification, $rank(\mathbf{K}_{\theta}) = S - 1$.

Regarding the spatio-temporal interaction term, four types of interactions are envisioned 243 in Knorr-Held (2000), leading to different structure matrices K_{δ} obtained as a 244 Kronecker product of temporal and spatial structure matrices $K_{\delta} = K_{time} \otimes K_{space}$. 245 Specifying $K_{\delta} = I_T \otimes I_S$ corresponds to a Type I interaction, in which independence 246 among δ s is postulated; a Type II interaction, obtained by specifying the structure 247 matrix as $K_{\delta} = K_{RW} \otimes I_{\delta}$, is suitable if plots show different temporal trends with no 248 structure in space; a Type III interaction, $K_{\delta} = I_T \otimes K_{\theta}$, assumes different spatial trends 249 with no structure in time. Finally, a Type IV interaction, $\mathbf{K}_{\delta} = \mathbf{K}_{RW} \otimes \mathbf{K}_{\theta}$, involves both 250 a spatial and a temporal structure. 251

To ensure model identifiability, appropriate linear constraints need to be imposed on the spatial (θ) and spatio-temporal (δ) random effects, whereas the temporal random 254 effects (α) are unconstrained and can be considered time-dependent random intercepts. The number of linear constraints needed to ensure identifiability corresponds to the rank 255 deficiency of the structure matrix of an IGMRF. As pointed out in Schrödle and Held 256 (2011), identifiability can be ensured by computing the null space of the structure 257 matrix and using the obtained eigenvectors as linear constraints. A simple sum-to-zero 258 constraint is required for the identifiability of the spatial effects because 259 $rank(\mathbf{K}_{\theta}) = S - 1$ (i.e., the null space of \mathbf{K}_{θ} is spanned by a constant vector). Because 260 of the properties of the Kronecker product, the rank deficiency of \boldsymbol{K}_{δ} depends on the 261 specified type of interaction: $rank(\mathbf{K}_{\delta}) = T \times S - rank(\mathbf{K}_{time}) \times rank(\mathbf{K}_{space})$; when a 262 Type IV interaction is considered, the number of required linear constraints becomes 263 extremely high when S and T are large. 264

Model hierarchy is completed by prior specification for precision parameters of the IGMRFs: we assume independent, small-parameter Gamma distributions both to preserve non-informativeness and to take advantage of the conjugacy between the Gaussian and the Gamma distribution in building the MCMC sampler.

269

270 *3.1 Managing compositional covariates*

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As discussed in section 2, the main aim of this study is to investigate the effect of substrate typology on vegetation cover. Because at each plot substrate typology is expressed as a proportion, these explanatory variables need to be managed coherently with compositional algebra. For the sake of simplicity, in this section, spatio-temporal subscripts are dropped, and the focus is on a simple linear regression model; nevertheless, the developed theory can be readily applied to model (1).

Consider a *D*-dimensional vector of compositional covariates, $z = (z_1, ..., z_d, ..., z_D)$, that 278 be represented with unit-sum 279 can constraint in the simplex $S^{D} = \left\{ \boldsymbol{z} = \left(z_{1}, \dots, z_{d}, \dots, z_{D} \right)^{'}, z_{d} > 0, \sum_{d=1}^{D} z_{d} = 1 \right\}.$ If untransformed compositional 280 281 covariates are used, the design matrix of the proportional representation of compositions is singular due to the sum-to-one constraint. This issue can be addressed by a 282 transformation that allows for a transition from the D-dimensional simplex to 283 unconstrained (D-1)-dimensional real space, \Re^{D-1} . In this paper, we adopt the *ilr* 284 transformation (Egozcue et al., 2003), which is an isometry between S^{D} and \Re^{D-1} , 285 leading to *ilr*-transformed covariates $\mathbf{x} = ilr(\mathbf{z}) = (x_1, \dots, x_i, \dots, x_{D-1})'$. Following Egoczue 286 et al. (2003), an orthonormal basis matrix B associated with the coordinate system 287 generated by ilr(z) can be obtained by sequential binary partitioning. The *i*-th row of 288 this matrix is 289

290

291
$$\boldsymbol{b}_{i} = \sqrt{\frac{D-i}{D-i+1}} \left[\underbrace{0,...,0}_{i-1 \text{ times}}, +1, \underbrace{-(D-i)^{-1},...,-(D-i)^{-1}}_{D-i \text{ times}} \right]; \quad \boldsymbol{b}_{i} \in \Re^{D}; i = 1,...,D-1. \quad (0)$$

292

293 The *i*-th component of the *i*lr coordinates vector x is defined as

294

295
$$x_i = i lr(z)_i = \sqrt{\frac{D-i}{D-i+1}} ln \frac{z_i}{\sqrt[D-i]{\prod_{j=i+1}^{D} z_j}} \text{ for } i = 1, ..., D-1.$$
 (0)

296

In the context of compositional data analysis, other widely used transformations include the centered log-ratio (*clr*) and the additive log-ratio (*alr*) transformations. The *alr* 299 transformation raises several issues in terms of interpretability because it is not an isometric transformation. According to Tolosana-Delgado and Van Den Boogaart 300 (2013), the *clr* representation of a composition is often convenient in a regression 301 302 framework because each coefficient can be related to an original component. Nonetheless, the *clr* is not expressed in terms of an orthogonal basis, neither of the 303 simplex nor of the real space and it generates a singular design matrix that requires a 304 sum-to-zero constraint for estimation of the regression coefficients. In a simple linear 305 regression framework, this does not raise particular issues, since estimation of the 306 regression coefficients is obtained by computing the Moore-Penrose inverse. This is not 307 practical in models where regression coefficients are modelled along time, as in our 308 309 application, since time-specific constraints would result in considerable computational 310 burden. Hence, our strategy for regression on compositional covariates consists in estimating the model with *ilr* coordinates and in obtaining the *clr* coefficients by 311 exploiting the relationship betwee *ilr* and *clr* coordinates. 312

313 The *ilr* transformation is directly associated with orthogonal coordinates in the simplex (Egozcue et al. 2003). The first component of the *ilr*-transformed vector is defined as a 314 function of the ratio between z_1 and the geometric mean of all of the remaining 315 components of z. Thus, when *ilr*-transformed covariates, X, are introduced into the 316 linear model $y = \alpha + X\beta + \varepsilon$, the first regression coefficient, β_1 , is directly interpreted 317 as the *relative* effect of part 1; namely, it is the expected increment of the response 318 319 variable when the first part increases its relative weight with respect to an average of all 320 the other parts. The other regression coefficients cannot be interpreted analogously, nonetheless, as will be discussed in the following, meaningful regression coefficients 321 for all parts can be obtained by switching from *ilr* to *clr* coefficients by a simple linear 322 transformation exploiting the relationship between *ilr* and *clr* coordinates. 323

The orthonormal basis B introduced in equation (XX) allows to switch from *ilr* to *clr* coordinates by the linear transformation $\tilde{x} = clr(z) = ilr(z)'B = x'B$.

The model fit is not sensitive to the chosen transformation, i.e., the models $y = \alpha + X\beta + \varepsilon$ and $y = \alpha + \tilde{X}\tilde{\beta} + \varepsilon$, based respectively on *ilr* and *clr* transformed covariates, deliver the same fit and the same estimate of the intercept, in fact the two models have the same hat matrix:

330

331
$$\tilde{X}(\tilde{X}'\tilde{X})^{-}\tilde{X} = XB(B'X'XB)^{-}B'X' = X(X'X)^{-1}X'$$

332

since $(\mathbf{B}'\mathbf{X}'\mathbf{X}\mathbf{B})^{-} = \mathbf{B}'(\mathbf{X}'\mathbf{X})^{-1}\mathbf{B}$ and $\mathbf{B}'\mathbf{B} = \mathbf{I}$, where \mathbf{A}^{-} denotes the Moore-penrose generalized inverse of \mathbf{A} . Eventually, *clr* coefficients can be obtained by means of the transformation $\tilde{\boldsymbol{\beta}} = \mathbf{B}\boldsymbol{\beta}$.

336

Vector $\tilde{\boldsymbol{\beta}}$ should be considered as the key parameter in the context of regression on compositional covariates. Indeed, the vector contains all the relevant information concerning the effect of each part on the response variable. A remarkable feature of $\tilde{\boldsymbol{\beta}}$ is that

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342
$$\boldsymbol{I}_{D}^{'} \boldsymbol{\tilde{\beta}} = \sum_{d=1}^{D} \boldsymbol{\tilde{\beta}}_{d} = 0$$
(0)

343

holds by construction. Relationship (0) demonstrates an intuitive dependence structure characterizing $\tilde{\beta}$ that is readily interpretable and particularly appealing in the context of regression on compositional covariates. For further illustration, consider an obvious feature of compositional data: if the proportion of part *d* increases, then the proportion of at least one of the other parts must decrease because of the sum-to-one constraint. Thus, if increasing the share of the *d*-th part does have a positive effect on the response variable, then increasing the share of some other part will necessarily have a negative effect. For this reason, we interpret $\tilde{\boldsymbol{\beta}}$ coefficients as "relative effects" of a part w.r.t. all of the others.

Referring to model (1), the set of compositional covariates z_{st} at plot s and time t is included in the linear predictor after *ilr* transformation as $\mathbf{x}_{st} = ilr(z_{st})$, i.e., $\Phi^{-1}(\pi_{st}) = \mathbf{x}_{st}' \boldsymbol{\beta}_t + \alpha_t + \theta_s + \delta_{st}$; hence, model (1) contains P = D - 1 regressors.

356

357 3.2 Computational details

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As is typical in complex hierarchical Bayesian models, the joint posterior distribution is 359 not available in closed form and needs to be approximated. The Markov property of 360 IGMRF models implies sparseness of the precision structure matrix, which allows fast 361 computations, making spatio-temporal modeling with a large amount of lattice data 362 feasible. Two alternative strategies are currently very popular for approximating the 363 joint posterior distribution: MCMC sampling and Integrated Nested Laplace 364 Approximations (INLA, Rue and Martino 2009). The latter is particularly suited for 365 latent GMRF models and provides very accurate approximations of the posterior 366 distribution. In addition, INLA definitely outperforms MCMC approaches in terms of 367 368 computational time and for more precise approximations to be obtained. Thus, such a method appears to be preferable and should be used whenever possible. INLA has been 369 made easily implementable by the R package INLA (Rue et al. 2013). The problem with 370

applying INLA to our case study is that, when a Type IV interaction is considered, the
large number of linear constraints required for model identifiability makes the approach
computationally unfeasible, causing computer crash.

For this reason, MCMC sampling is a necessary tool for the purpose of this paper. The MCMC algorithm has been implemented by adopting the popular auxiliary variable approach introduced in Albert and Chib (1993) and developed successively in several papers. This approach preserves full conditionals in GMRF form, which are lost in the case of non-normal likelihood: this is crucial for fast sampling. The approach based on data augmentation introduces, for each *Bernoulli* trial denoted by subscript *i*, in plot *s* at time *t*, the following auxiliary variables:

381

382
$$W_{ist} \sim N(\mathbf{x}'_{st}\boldsymbol{\beta}_t + \alpha_t + \theta_s + \delta_{st}, 1)$$
 $i = 1, ..., n; s = 1, ..., S; t = 1, ..., T$

383

384 The Binomial likelihood is retrieved by specifying

385

386
$$\tilde{y}_{ist} = \begin{cases} 1 \text{ if } w_{ist} > 0\\ 0 \text{ if } w_{ist} \le 0 \end{cases} \qquad \sum_{i} \tilde{y}_{ist} = y_{st}$$

387

where $\tilde{y}_{ist} = 1$ and $\tilde{y}_{ist} = 0$ appear y_{st} and $n - y_{st}$ times, respectively. It follows that the full conditional distributions of the auxiliary variables are truncated Normal:

390

391
$$w_{ist} \mid \dots \sim \begin{cases} N(\mathbf{x}_{st}' \boldsymbol{\beta}_{t} + \alpha_{t} + \theta_{s} + \delta_{st}, 1) I(w_{ist} > 0) \text{ if } \tilde{y}_{ist} = 1\\ N(\mathbf{x}_{st}' \boldsymbol{\beta}_{t} + \alpha_{t} + \theta_{s} + \delta_{st}, 1) I(w_{ist} \le 0) \text{ if } \tilde{y}_{ist} = 0 \end{cases}$$
(0)

Summing over the pixels, we obtain $w_{\bullet st} = \sum_{i=1}^{n} w_{ist}$. Conditionally on $w_{\bullet st}$, MCMC sampling can proceed as in a standard Bayesian linear model, where $w_{\bullet st}$ serves as

pseudo-data. The linear predictor can be written in compact form as follows:

396

395

397
$$\boldsymbol{w}_{\bullet} = \boldsymbol{X}'\boldsymbol{\beta} + \boldsymbol{\alpha} \otimes \boldsymbol{I}_{S} + \boldsymbol{I}_{T} \otimes \boldsymbol{\theta} + \boldsymbol{\delta}$$

398

where I_k denotes a k-dimensional unit vector, $X = diag(X_1, ..., X_t, ..., X_T)$ is the $ST \times T(D-1)$ -dimensional block-diagonal matrix with $S \times (D-1)$ -dimensional blocks X_t containing *ilr*-transformed covariates at time t and $\beta = (\beta_1, ..., \beta_t, ..., \beta_T)$ is the (D-1)T-dimensional vector of time-varying coefficients.

In the context of the Bayesian linear regression model, implementing a Gibbs sampler 403 involves standard MCMC tools; it is worth noting that sampling under linear constraints 404 405 for the interaction term, even for a Type IV interaction model, is not an hard task. In fact, it can be shown that the null space spanned by the eigenvectors associated with 406 null eigenvalues of the structure matrix K_{δ} is equivalent to the null space spanned by 407 the eigenvectors associated with null eigenvalues of the Kronecker product $C_{s} \otimes C_{T}$, 408 where C_k denotes the k-dimensional centering matrix. Therefore, samples from the full 409 conditional distribution of δ can be obtained by centering samples over space and time 410 on the fly at each MCMC iteration. Full conditional distributions for all of the 411 parameters are reported in Appendix A. 412

413 Several further refinements to the Gibbs sampler built for our case study can be adopted414 to improve the efficiency of the MCMC algorithm. Regarding the auxiliary variable

415	approach, Frühwirth-Schnatter et al. (2007) propose an augmented model with lower
416	dimensionality, where the number of required latent variables per observation becomes
417	independent of the number of trials. Furthermore, block-sampling has been shown to
418	considerably improve the mixing of Markov chains when some parameters show high
419	correlation. Nonetheless, we adopt a Gibbs sampler in our case study because it allows
420	for accurate results to be obtained within a fairly reasonable computational time.
421	
422	
423	4 APPLICATION
424	
425	4.1 Model selection
426	Starting from model (1), several specifications can be proposed, according to different
427	assumptions regarding the effect of substrate typology and the structured spatio-
428	temporal effects. Namely, we estimate and compare a total of 10 competing models: all
429	of them include a pure temporal effect (i.e., α_t) and a pure spatial effect (i.e., θ_s). The
430	models differ with respect to the spatio-temporal interaction type (I,II,III,IV); moreover
431	substrate effect is specified either as constant or time-varying. All temporal effects are
432	modeled as RW1 opportunely adapted for considering unequally spaced times.
433	The models are compared in terms of the Deviance Information Criterion (DIC,
434	Spiegelhalter et al. 2002) in Table 3.

			Interaction		
Substrate effect	Type 1	Type 2	Type 3	Type 4	No
Constant	33501	33518	33349	33510	188053
Time-varying	33496	33513	33343	33515	183137

436Table 3 Deviance Information Criterion (DIC) corresponding to different model specifications for spatio-437temporal interaction and substrate effect (time-constant or time-varying)

From the last column of this table, it can be observed that neglecting spatio-temporal 439 interactions produces very poor performance. The selected model (whose DIC is 440 reported in bold in the table) includes time-varying coefficients and a Type 3 441 interaction. The inclusion of a Type 4 interaction does not improve the model fit, 442 regardless of the assumption made about substrate effects. Despite the small differences 443 in terms of DIC exhibited by models with a Type 3 interaction, the results presented in 444 the following section provide evidence of a significant change in the covariate effect 445 over time, supporting the selection of the time-varying coefficient model. 446

- 447 Ultimately, the selected model is:
- 448

449
$$y_{st} | \pi_{st} \sim Binomial(\pi_{st}, n) \qquad s = 1, ..., S; \ t = 1, ..., T$$
450
$$\Phi^{-1}(\pi_{st}) = \mathbf{x}'_{st} \boldsymbol{\beta}_{t} + \alpha_{t} + \theta_{s} + \delta_{st} \qquad \text{where} \quad \boldsymbol{\beta}_{t} = \left(\beta_{1t}, ..., \beta_{dt}, ..., \beta_{(D-1)t}\right)$$
451
$$\boldsymbol{\beta}_{d} = \left(\beta_{d1}, ..., \beta_{dt}, ..., \beta_{dT}\right) \sim IGMRF_{T}\left(\tau_{\beta_{d}} \mathbf{K}_{RW}\right); \ d = 1, ..., D-1$$
452
$$\boldsymbol{\alpha} \sim IGMRF_{T}\left(\tau_{\alpha} \mathbf{K}_{RW}\right), \ \boldsymbol{\theta} \sim IGMRF_{S}\left(\tau_{\theta} \mathbf{K}_{\theta}\right); \ \boldsymbol{\delta} \sim IGMRF_{ST}\left(\tau_{\delta} \mathbf{K}_{\delta}\right)$$
453

where $K_{\delta} = I_T \otimes K_{\theta}$, in accordance with a Type III interaction. Because, as mentioned in section 3, vector α is unconstrained in model estimation, this purely temporal effect is devoted to capture, in the *probit* scale, the natural vegetation life cycle.

457

458

459 4.2 Results

Results are obtained from a post-convergence MCMC sample of size 10,000 obtained by thinning a 100,000 sample to reduce correlation while guaranteeing an adequate effective sample size.

463	In the upper panels (a1-a3) of Figure 3, posterior distributions ($\beta_t y$) of parameters
464	$\boldsymbol{\beta}_{t} = (\beta_{1t}, \dots, \beta_{dt}, \dots, \beta_{(D-1)t})$ are reported for $t = 9$ as an example. The lower panels (b1-
465	b4) report posterior distributions of <i>clr</i> -regression coefficients $\tilde{\beta}_t$; these posterior
466	distributions are obtained by transforming β_t at each MCMC iteration. Panels (a1) and
467	(b1) contain the same information, up to a scaling constant relating $\beta_{1,9}$ and $\tilde{\beta}_{1,9}$. The
468	positiveness of this coefficient implies that the first substrate typology (moss)
469	encourages vegetation cover when compared with other substrates typologies, i.e., moss
470	shows positive "relative suitability". Panels (a2) and (a3) contain, respectively, the
471	posterior distributions of $\beta_{2,9}$ and $\beta_{3,9}$: these parameters do not convey readily
472	interpretable information concerning substrate suitability because, as discussed in
473	section 3.1, they do not refer to any direct comparison between one compositional part
474	and all others. As a consequence, testing for the nullity of these coefficients is pointless
475	because a null coefficient does not directly imply a non-significant effect of some
476	compositional part on the response variable. As a matter of fact, no sound
477	considerations about the relative suitability of litter, soil and bare rock can be drawn
478	from panels (a2) and (a3). On the other hand, panels (b2)-(b4) convey direct
479	information about substrate relative suitability: the posterior distribution of regression
480	coefficient associated with litter (panel b2) is centered at zero, meaning that litter shows
481	average suitability, whereas soil (panel b3) and bare rock (panel b4) have positive and
482	negative relative suitability, respectively.

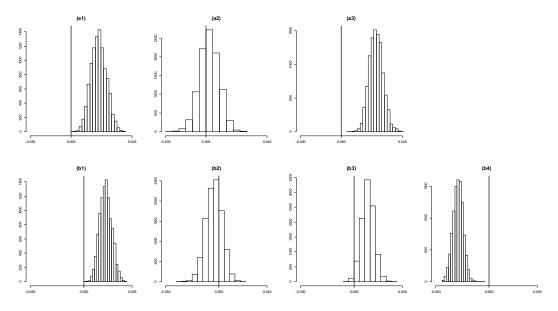


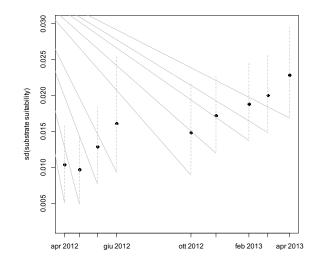
Fig 3 Po

Fig. 3 Posterior distributions of the regression coefficients for the last collection time (panels a1-a3).
 Posterior distributions of transformed regression coefficients expressing the relative suitability for moss
 (b1), litter (b2), soil (b3) and bare rock (b4). Vertical lines correspond to zero

Because transformed coefficients are directly comparable, we provide some suggestions 489 on how posterior estimates can be used to describe findings about substrate suitability. 490 Upon first glance, at a given time, the substrates can be ordered from the most to the 491 least suitable for vegetation cover based on the posterior means $E(\tilde{\beta}_{dt}|\mathbf{y})$: at time 9, 492 moss turns out to be the most suitable substrate typology, followed by soil, litter and 493 bare rock. Moreover, a rigorous comparison between the suitability of substrates d and 494 495 d' that takes account of the uncertainty about parameter estimates can be obtained by evaluating $Pr(\tilde{\beta}_{dt} > \tilde{\beta}_{d't} | \mathbf{y})$, i.e., the posterior probability that the suitability of 496 substrate d is higher than that of substrate d'. This task is easily addressed by 497 exploiting the MCMC sample. It is observed that, at time 9, the posterior probabilities 498 that moss is more suitable than litter, soil and bare rock are 0.98, 0.81 and 1, 499 respectively. 500

501 Furthermore, it is interesting to determine whether the heterogeneity characterizing 502 substrate suitability changes over time; it is worth noting that the more the estimated coefficients at time *t* are dispersed around zero, the more the substrates show differences in terms of suitability. Thus, the posterior distribution $sd(\tilde{\beta}_t)|y$, t=1,...,9, gives information about the heterogeneity of substrates in terms of the suitability at each time. Figure 4 shows that the heterogeneity increases over the study period.

507





509

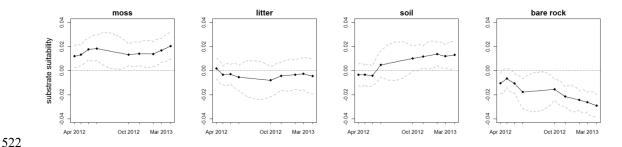
510

Fig. 4 Posterior distribution of $sd\left(\tilde{\boldsymbol{\beta}}_{t}\right)|\boldsymbol{y}$ over time

The biological motivation of this behavior can be found in the increase in vegetation cover, from October to the end of the study period, caused by a higher propensity of vegetation to occur in the substrates that exhibit greater availability of nutrient resources (i.e., moss and soil) than do the others (litter and bare rock).

Finally, we describe findings about the temporal evolution of substrate relative suitability that are helpful in addressing the ecological questions posed at the end of section 2. In each panel of Figure 5, the posterior mean of $\tilde{\beta}_t$ at the collection times (filled circles), the predictions at unobserved times (black solid line) and credible bands

(grey dashed lines) are reported. Predictions are obtained via MCMC sampling from the posterior predictive distribution of $\tilde{\beta}_t$.



523

524

Fig. 5 Substrate relative suitability over time

Moss is revealed to be the most suitable substrate at the beginning of the study period, and its relative suitability remains nearly constant over time. On the other hand, the relative suitability of soil is approximately zero (i.e., approximately average) at the beginning and increases over time, reaching a positive relative suitability level in winter. The opposite behavior is exhibited by bare rock, which is less suitable than average and shows a decreasing pattern over time. Finally, litter presents constant average suitability over time.

It is worth noting that, in contrast to the results shown in Figure 2, where the temporal pattern of substrate-specific effects is confounded with the marginal trend for vegetation, the results shown in Figure 5 provide direct information on the relative suitability level of each substrate and how these levels vary over the study period, after properly accounting for spatial and temporal correlation. These results are in agreement with the ecological literature on this type of habitat (Lundholm 2003, Otsus and Zobel 2002) as stated in Velli (2014).

539

In this work, a spatio-temporal model for ecological data derived from digital ground 543 544 photos is presented. The primary focus is on quantifying the relation between vegetation cover and substrate typology, expressed as compositional data, by accounting for spatial 545 and temporal correlation. The proposed models include spatial, temporal and spatio-546 temporal effects modeled as IGMRFs. A novel approach for estimating the relative 547 effect of compositional covariates on the response variable is developed within a 548 Bayesian framework, through a procedure based on appropriate transformations of the 549 550 regression coefficients. This procedure exploits the properties of the *ilr* transformation, 551 which admits an orthonormal basis representation; this transformation allows for a transition between different coordinate systems, providing meaningful regression 552 553 coefficients. In our opinion, the proposed approach constitutes a basis for future developments in such fields as non-linear and nonparametric regression for 554 compositional covariates. To the best of our knowledge, these topics have been scarcely 555 debated in the literature concerning both compositional data and Bayesian analysis. 556

The lattice structure of the data make GMRFs particularly suitable tools for modeling spatial and temporal dependence by specifying a conditional dependence structure. This ability allows for feasible computations that can be implemented both by the INLA approach and MCMC sampling; fast algorithms that allow for efficient sampling by exploiting the sparseness of the precision matrices are implemented within a Gibbs sampling scheme. Both the INLA and MCMC codes are available upon request from the corresponding author.

564 The model is applied to a dataset concerning a habitat included in the framework of the 565 priority defined by the European Commission, where investigating the relationship

between vegetation cover and substrate typology can be helpful in quantifying substrate 566 suitability. The case study demonstrates that the proposed modeling strategy produces 567 valuable outcomes for ecologists. First, in ecological studies, knowledge of substrate 568 suitability is strategic for habitat conservation, for instance, to predict future 569 developments and reactions to possible environmental changes. Second, a modeling 570 approach that is able to predict substrate suitability or other ecological responses over 571 un-monitored periods of time is extremely useful in many common situations in which 572 surveys cannot follow a regular plan, as in the case in which fieldwork activity is 573 impossible because of adverse environmental and weather conditions. 574

575 One interesting ecological finding of the paper is that substrate relative suitability varies 576 over time. A future line of research will focus on extending the proposed model to allow 577 for smooth, rather than simply linear, effects of compositional covariates on ecological 578 responses. Non-linear effects of substrate shares on ecological responses may often be 579 observed, especially when the response of interest is a biodiversity index, such as 580 species richness or evenness.

581

582 583

APPENDIX

584

585 The Gibbs sampler is implemented as follows:

586 1. Sample auxiliary variables from the truncated normal full conditionals (0).

Let \tilde{W} be the *nST*-dimensional vector of the auxiliary variables, full conditionals for the other parameters can be obtained as in the standard linear model with Gaussian likelihood, starting from the following expression of the linear predictor:

591
$$\tilde{\boldsymbol{\eta}} = (\boldsymbol{X} \otimes \boldsymbol{I}_n) \boldsymbol{\beta} + (\boldsymbol{I}_T \otimes \boldsymbol{I}_S \otimes \boldsymbol{I}_n) \boldsymbol{\alpha} + (\boldsymbol{I}_T \otimes \boldsymbol{I}_S \otimes \boldsymbol{I}_n) \boldsymbol{\theta} + (\boldsymbol{I}_T \otimes \boldsymbol{I}_S \otimes \boldsymbol{I}_n) \boldsymbol{\delta}$$
$$= \tilde{\boldsymbol{X}} \boldsymbol{\beta} + \tilde{\boldsymbol{A}}_1 \boldsymbol{\alpha} + \tilde{\boldsymbol{A}}_2 \boldsymbol{\theta} + \tilde{\boldsymbol{A}}_3 \boldsymbol{\delta}$$

593 In what follows, the multivariate normal distribution is expressed in the canonical form

- 594 (Rue and Held, 2005; page 27)
- 595 2. Sample the regression parameters from the distribution

596
$$\boldsymbol{\beta} | ... \sim N_C (\boldsymbol{b}_{\beta}, \boldsymbol{Q}_{\beta})$$

597 $\boldsymbol{b}_{\beta} = \tilde{\boldsymbol{X}}' (\tilde{\boldsymbol{W}} - \tilde{\boldsymbol{A}}_1 \boldsymbol{\alpha} - \tilde{\boldsymbol{A}}_2 \boldsymbol{\theta} - \tilde{\boldsymbol{A}}_3 \boldsymbol{\delta}) = n \tilde{\boldsymbol{X}}' (\boldsymbol{w}_{\bullet} / n - (\boldsymbol{I}_T \otimes \boldsymbol{I}_S) \boldsymbol{\alpha} - (\boldsymbol{I}_T \otimes \boldsymbol{I}_S) \boldsymbol{\theta} - \boldsymbol{\delta});$

598
$$\boldsymbol{Q}_{\beta} = \boldsymbol{P}_{0}\boldsymbol{\Gamma}_{\beta}\boldsymbol{P}_{0}^{'} + \tilde{\boldsymbol{X}}^{'}\tilde{\boldsymbol{X}} = \boldsymbol{P}_{0}\boldsymbol{\Gamma}_{\beta}\boldsymbol{P}_{0}^{'} + n\boldsymbol{X}^{'}\boldsymbol{X}$$

599 where $\Gamma_{\beta} = diag(\tau_{\beta_1}, ..., \tau_{\beta_{D-1}}) \otimes K_{RW}$ and P_0 is a permutation matrix with the following 600 structure:

601

602
$$\boldsymbol{P}_{0} = \begin{bmatrix} \boldsymbol{I}_{D-1} \otimes \boldsymbol{v}_{1}^{'} \\ \cdots \\ \boldsymbol{I}_{D-1} \otimes \boldsymbol{v}_{t}^{'} \\ \cdots \\ \boldsymbol{I}_{D-1} \otimes \boldsymbol{v}_{T}^{'} \end{bmatrix}$$

603 The *T*-dimensional vector v_t contains 1 at position *t* and zero elsewhere.

3. Sample the temporal effects, i.e., the time-varying intercepts, from the distribution

605
$$\boldsymbol{\alpha} | \dots \sim N_C \left(\boldsymbol{b}_{\alpha}, \boldsymbol{Q}_{\alpha} \right)$$

606
$$\boldsymbol{b}_{\alpha} = \tilde{\boldsymbol{A}}_{1}^{\prime} \left(\boldsymbol{\tilde{W}} - \boldsymbol{\tilde{X}}\boldsymbol{\beta} - \boldsymbol{\tilde{A}}_{2}\boldsymbol{\theta} - \boldsymbol{\tilde{A}}_{3}\boldsymbol{\delta} \right) = n\tilde{\boldsymbol{A}}_{1}^{\prime} \left(\boldsymbol{w}_{\bullet}/n - \boldsymbol{X}\boldsymbol{\beta} - (\boldsymbol{I}_{T} \otimes \boldsymbol{I}_{S})\boldsymbol{\theta} - \boldsymbol{\delta} \right);$$

- 607 $\boldsymbol{Q}_{\alpha} = \tau_{\alpha} \boldsymbol{K}_{RW} + \tilde{\boldsymbol{A}}_{1} \tilde{\boldsymbol{A}}_{1} = \tau_{\alpha} \boldsymbol{K}_{RW} + n \boldsymbol{S} \boldsymbol{I}_{T}$
- 608 4. Sample the spatial effect from the distribution

609
$$\boldsymbol{\theta} | \dots \sim N_C (\boldsymbol{b}_{\theta}, \boldsymbol{Q}_{\theta})$$

610
$$\boldsymbol{b}_{\theta} = \tilde{\boldsymbol{A}}_{2} \left(\tilde{\boldsymbol{W}} - \tilde{\boldsymbol{X}} \boldsymbol{\beta} - \tilde{\boldsymbol{A}}_{1} \boldsymbol{\alpha} - \tilde{\boldsymbol{A}}_{3} \boldsymbol{\delta} \right) = n \left(\boldsymbol{I}_{T} \otimes \boldsymbol{I}_{S} \right)^{\prime} \left(\boldsymbol{w}_{\bullet} / n - \boldsymbol{X} \boldsymbol{\beta} - \left(\boldsymbol{I}_{T} \otimes \boldsymbol{I}_{S} \right) \boldsymbol{\alpha} - \boldsymbol{\delta} \right);$$

611
$$\boldsymbol{Q}_{\theta} = \tau_{\theta} \boldsymbol{K}_{\theta} + \tilde{\boldsymbol{A}}_{2} \tilde{\boldsymbol{A}}_{2} = \tau_{\theta} \boldsymbol{K}_{\theta} + nT\boldsymbol{I}_{S}$$

612 Centre the sampled values.

613
$$\tilde{X}\beta + \tilde{A}_1\alpha + \tilde{A}_2\theta + \tilde{A}_3\delta$$

614 5. Sample the spatiotemporal random effects from the distribution 615 $\boldsymbol{\delta}|_{\dots} \sim N_C(\boldsymbol{b}_{\delta}, \boldsymbol{Q}_{\delta})$

616
$$\boldsymbol{b}_{\delta} = \left(\tilde{\boldsymbol{W}} - \tilde{\boldsymbol{X}}\boldsymbol{\beta} - \tilde{\boldsymbol{A}}_{1}\boldsymbol{\alpha} - \tilde{\boldsymbol{A}}_{2}\boldsymbol{\theta}\right) = n\left(\boldsymbol{w}_{\bullet}/n - \boldsymbol{X}\boldsymbol{\beta} - \left(\boldsymbol{I}_{T} \otimes \boldsymbol{I}_{S}\right)\boldsymbol{\alpha} - \left(\boldsymbol{I}_{T} \otimes \boldsymbol{I}_{S}\right)\boldsymbol{\theta}\right);$$

617
$$\boldsymbol{Q}_{\delta} = \tau_{\delta} \boldsymbol{K}_{\delta} + \tilde{\boldsymbol{A}}_{3} \tilde{\boldsymbol{A}}_{3} = \tau_{\delta} \boldsymbol{K}_{\delta} + n \boldsymbol{I}_{TS}$$

618 Centre the sampled values either row wise, column wise or both depending on the type

- 619 of interaction.
- 620 6. Sample the precision parameters $\tau_{\beta_1}, ..., \tau_{\beta_{D-1}}, \tau_{\alpha}, \tau_{\theta}, \tau_{\delta}$. The full conditionals for these

621 parameters are Gamma, for instance:

622
$$\tau_{\theta} | ... \sim G(a + .5 \times rank(\mathbf{K}_{\theta}), b + .5 \times \theta' \mathbf{K}_{\theta} \theta)$$

- 623
- 624

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640 641 642	Bennett LT, Judd TS, Adams MA (2000) Close-range vertical photography for measuring cover changes in perennial grasslands. J Range Manage 53:634–641
643 644 645 646	Booth DT, Cox SE, Fifield C, Phillips M, Williamson N (2005) Image analysis compared with other methods for measuring ground cover. Arid Land Res Manag 19:91–100
647 648	Booth DT, Tueller PT (2003) Rangeland monitoring using remote sensing. Arid Land Res Manag 17:455–478
649 650 651	Council Directive (92/43/CEE) on the conservation of natural habitats and of wild fauna and flora (http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm)
652 653 654	Egozcue JJ, Pawlowsky-Glahn V, Mateu-Figueras G, Barcelo-Vidal C (2003) Isometric logratio transformations for compositional data analysis. Math Geol 35: 279–300
655 656 657 658	Egozcue JJ, Pawlowsky-Glahn V (2006) Simplicial geometry for compositional data. In Buccianti et al. (eds) Compositional data analysis in the Geosciences: From theory to practice. Geological Society, London, Special Publications, 264, pp 145-159
659 660 661	Fortin MJ, James PMA, MacKenzie A, Melles SJ, Rayfield B (2012) Spatial statistics, spatial regression, and graph theory in ecology. Spatial Statistics 1:100-109
662 663 664	Frühwirth-Schnatter S, Frühwirth R, Held L, Rue H (2009) Improved auxiliary mixture sampling for hierarchical models of non-Gaussian data, Stat Comput 19:479-492
665 666 667	Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186
668 669 670	Hron K, Filzmoser P, Thompson K (2012) Linear regression with compositional explanatory variables. J Appl Stat 39:1115–1128
671 672 673	Kneib T, Muller J, Hothorn T (2008) Spatial smoothing techniques for the assessment of habitat suitability. Environ Ecol Stat 15: 343-364
674 675 676	Knorr-Held L (2000) Bayesian modelling of inseparable space-time variation in disease risk. Stat Med 19:2555–2567
677 678 679	Kuntz KL, Larson DW (2006) Microtopographic control of vascular plant, bryophyte and lichen communities on cliff faces. Plant Ecol 185:239–253
680 681 682	Latimer AM, Wu S, Gelfand AE, Silander JA Jr (2006) Building Statistical Models to Analyze Species Distributions. Ecol Appl 16:33-50
683 684 685	Lindgren F, Rue H (2008) On the Second-Order Random Walk Model for Irregular Locations. Scand J Stat 35:691–700
686 687 688 689	Lundholm JT, Larson DW (2003) Relationships between spatial environmental heterogeneity and plant species diversity on a limestone pavement. Ecography 6:715-722

- 690
- Pueyo Y, Alados CL (2007) Abiotic factors determining vegetation patterns in a semi arid Mediterranean landscape: Different responses on gypsum and non-gypsum
 substrates. J Arid Environ 69: 490–505
- Otsus M, Zobel M (2002) Small-scale turnover in a calcareous grassland, its pattern and
 components. J Veg Sci 13:199-206
- 697

- Richardson MD, Karcher DE, Purcell LC (2001) Quantifying turfgrass cover using
 digital image analysis. Crop Sci 41:1884–1888.
- 700
- Rue H, Held L (2005) Gaussian Markov random fields: theory and applications.
 Chapman & Hall/CRC Press, London.
- Rue H, Martino S (2009) Approximate Bayesian inference for latent Gaussian models
 by using integrated nested Laplace approximations (with discussion). J Roy Stat Soc B
 706 71:319-392
- Rue H, Martino S, Lindgren F, Simpson D, Riebler A (2013) INLA: Functions which
 allow to perform full Bayesian analysis of latent Gaussian models using Integrated
 Nested Laplace Approximaxion. R package version 0.0-1383402327
- Schrödle B, Held L (2011) Spatio-temporal disease mapping using INLA.
 Environmetrics 22:725–734
- 714

717

711

- Spiegelhalter DJ, Best NG, Carlin BP, Van der Linde A (2002) Bayesian Measures of
 Model Complexity and Fit (with Discussion). J Roy Stat Soc B 64:583-616
- Velli A. (2014) Relationships between plant diversity and environmental heterogeneity
 in rupicolous grasslands on gypsum. The case study of Alysso-Sedion albi (Habitat
 6110). Dissertation, University of Bologna
- Wahba G (1978) Improper priors, spline smoothing and the problem of guarding against
 model errors in regression. J Roy Stat Soc B 40:364–372
- 724
- Wikle CK (2003) Hierarchical Bayesian models for predicting the spread of ecological
 processes. Ecology 84:1382-1394.