



Modelling pin-point cover data of complementary vegetation classes



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ARTICLE INFO

Article history:

Received 5 April 2015

Received in revised form 5 October 2015

Accepted 7 October 2015

Available online 22 October 2015

Keywords:

Joint distribution of plant abundance

Plant cover

Hierarchical models

Plant ecology

Point-intercept

Structural equation modelling

ABSTRACT

It is often ecologically meaningful to divide the vegetation into a number of complementary vegetation classes or functional types. Here, a method for modelling pin-point plant cover data for such complementary classes is presented. The joint distribution of pin-point cover data of complementary vegetation classes is modelled using a mixture distribution of the multinomial distribution and the Dirichlet distribution, where the Dirichlet distribution is used to model the effect of spatial aggregation. In order to demonstrate the method, the variation in cover with space or time is modelled using a hierarchical Bayesian approach, where the mean cover of each site at a specific time is modelled by a latent variable. The statistical modelling procedure is exemplified in a case-study of pin-point cover data of the two dominating species *Calluna vulgaris* and *Deschampsia flexuosa*, and the abundance of the complement species class of all other higher plants on Danish dry heathlands. The cover of *C. vulgaris* increased significantly with annual precipitation and the cover of *D. flexuosa* decreased significantly with annual precipitation. Furthermore, the mean cover of *C. vulgaris* and *D. flexuosa* within-sites was negatively correlated. There were no significant changes in the cover of the three complementary dry heathland vegetation classes from 2007 to 2012. The presented model allows information of complementarity to be incorporated and whereby increasing the statistical power. Furthermore, the spatial aggregation of the vegetation is modelled so that statistical inference tests will not be deflated due to pseudo-replication.

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1. Introduction

In the study of plant community dynamics, it is often convenient and ecologically meaningful to divide the vegetation into a number of complementary vegetation classes or functional types. For example, the herbaceous plant species in grassland plant communities may be divided into three complementary vegetation classes; grasses, sedges and rushes, and forbs, where forbs is defined as the complementary class of herbaceous plant species that is not a graminoid. Likewise, North-European dry heathland vegetation may be described by the abundance of the two dominating species *Calluna vulgaris* and *Deschampsia flexuosa* and the abundance of the complement species class of all other higher plants. Furthermore, the vegetation at a habitat may be divided into complementary plant functional types, or life history strategies, e.g. according to the CSR strategy classification scheme (Grime, 2001).

Typically, the abundance of complementary vegetation classes is modelled as if they were independent. This is unfortunate, because clearly the abundance of the different vegetation classes will be expected to covary negatively within sampling plots. However, the statistical modelling of the joint abundance of complementary vegetation classes or functional types has not received much attention in the ecological literature (Clark et al., 2013; Valle et al., 2014).

Plant abundance may be described by the cover, i.e. the relative projected area covered by a species. Plant cover takes the size of individuals into account and is an important and often measured characteristic of the composition of plant communities (Kent and Coker, 1992). A common way to measure plant cover in herbal plant communities is to make a visual assessment of the relative area covered by the different species in a small circle or quadrat (Kent and Coker, 1992). However, an alternative more objective methodology, called the pin-point method (or point-intercept method), has been widely employed (Kent and Coker, 1992; Levy and Madden, 1933; Lindquist, 1931). In a pin-point analysis, a frame with a fixed grid pattern is placed on top of the vegetation and a thin pin is inserted vertically through each of the grid points, and the cover is defined as the relative number of pins that hit a specific species.

It has been demonstrated that it is critical to model the effect of spatial aggregation (spatial auto-correlation) in plant cover data in order to prevent incorrect inflation of the statistical power (Damgaard, 2013). This is an important point to consider, since the cover of many plant species has been shown to have an aggregated spatial pattern due to the size of the plant, clonal growth, and limited seed dispersal (Chen et al., 2006, 2008; Herben et al., 2000; Pacala and Levin, 1997; Stoll and Weiner, 2000), and pin-point plant cover data at the local scale will, consequently, typically be over-dispersed relative to the binomial distribution (Damgaard, 2008, 2009, 2012, 2013). Furthermore, if plant cover data are sampled using a hierarchical sampling procedure with several sites, and where several plots are sampled within each

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site, then the possible among-site variation in plant cover need to be modelled as well (Damgaard, 2013). The among-site variation in mean cover is thought to arise from two different plant ecological processes: 1) plant species do not occur everywhere they may occur, i.e. in some sites a plant species may be absent due to random extinction events and/or limited possibility of the plant to colonise the habitat (Cordonnier et al., 2006; Leibold et al., 2004; MacArthur and Wilson, 1967; Rees et al., 2001), or 2) the mean plant cover at a site may vary due to an underlying variation in abiotic and biotic factors or due to random stochastic perturbations of species cover (e.g. Adler et al., 2007; Hubbell, 2001).

The aim of this study is to introduce a procedure for the statistical modelling of the plant cover of complementary vegetation classes or functional types using a mixture distribution of the multinomial

distribution and the Dirichlet distribution, where the Dirichlet distribution is used to model the effect of spatial aggregation. The variation in cover with space or time is modelled using a hierarchical Bayesian approach, where the mean vegetation class cover of each site at a specific time is modelled by a latent variable. The statistical modelling procedure will be exemplified in a case-study of pin-point cover data of the two dominating species *C. vulgaris* and *D. flexuosa* and the abundance of the complement species class of all other higher plants on Danish dry heathlands. Using the outlined statistical procedure, two questions that are central in the understanding of the plant community dynamics of dry heathlands will be asked in the study: i) Does the cover of the complementary vegetation classes covary with an abiotic driver that possibly may explain observed spatial variation in plant community structure? ii) Does the cover of the vegetation classes change over time?

2. Materials and methods

2.1. Case study

In order to illustrate the developed method, it was applied on dry heathland vegetation by modelling the cover of the two dominating species *C. vulgaris* and *D. flexuosa* (Rodwell, 1991) and the cover of the complement species class of all other higher plants. Dry heathlands are found throughout northwestern Europe on free draining acid soils with low nutrient availability (Britton et al., 2001; Grime et al., 1988). *C. vulgaris* has an Oceanic distribution (Loidi et al., 2010), whereas *D. flexuosa* has a wider geographical distribution (Jowett and Scurfield, 1949). Both species are well studied and known to frequently interact and to compete in nature (Damgaard et al., 2009, submitted for publication; Ransijn et al., 2015).

Hierarchical pin-point cover data from sites that included several plots that were classified as dry heathlands (habitat type 4030) according to the habitat classification system used for the European Habitat Directive (EU, 2003) was used in the analyses. The pin-point cover data was sampled using a square frame of 16 grid points that were equally spaced by 10 cm (Nielsen et al., 2012) in the period from 2007 to 2012. The used cover data is a small subset of the ecological data that is collected within the Danish terrestrial habitat monitoring programme NOVANA (Nielsen et al., 2012).

The pin-point cover data from 179 sites with a total of 2526 randomly placed plots was used in an analysis of the spatial variation of the complementary vegetation classes at dry heathlands sites (Fig. 1). In 29 of the 179 sites (Fig. 1), the plots were resampled with GPS-certainty (< 10 m) and in the time series analysis all 1928 observations from the 29 sites where the plots were resampled several years in the period from 2007 to 2012 (108 combinations of sites and years) were used in the analysis. However, in the analysis of the spatial variation only the first observation of these resampled plots from the 29 sites were included in the 2526 randomly placed plots.

The possible effect of precipitation, as an example of an abiotic driver, on the spatial distribution of the three dry heathland vegetation classes was investigated using the average annual precipitation in the period 2001 to 2010 with a spatial resolution of 10 km (DMI, 2014) as abiotic driver. The annual precipitation among the 179 dry heathland sites varied between 604 mm and 987 mm (mean = 820 mm, std. = 89 mm).

2.2. The distribution of pin-point plant cover data of complementary vegetation classes within a site

The measurement of pin-point cover data is a binary event where a pin in the pin-point frame either hits or does not hit a specific plant species. A discrete stochastic vector $Y = (y_1, \dots, y_n)$ may be defined as the number of pins in the pin-point frame that hit a plant species that belongs to one of n complementary vegetation classes. Typically, a pin will hit more than one species and the sum of the stochastic vector Y may be larger than the number of pins in a frame. Since the individual plant species are spatially aggregated (Damgaard, 2013), the stochastic vector Y is assumed to be Dirichlet-multinomial mixture distributed, i.e.

$$Y \sim Mn\left(\sum_n Y_i, (p_1, \dots, p_{n-1}, 1-p_1-\dots-p_{n-1})\right) \Lambda(p_1, \dots, p_{n-1}) \sim Dir\left(\frac{q_1-q_1\delta}{\delta}, \dots, \frac{q_{n-1}-q_{n-1}\delta}{\delta}, \frac{1-\delta}{\delta} - \frac{q_1-q_1\delta}{\delta} - \dots - \frac{q_{n-1}-q_{n-1}\delta}{\delta}\right). \quad (1)$$

The used parameters are explained in Table 1. The rationale for using the above parameterisation of the Dirichlet distribution (1) is that it has the useful property that the mean cover of the vegetation classes is parameterized, $E(p_1, \dots, p_{n-1}) = (q_1, \dots, q_{n-1})$, where E denotes the mean. Furthermore, the covariance matrix of the probabilities is simple functions of q_i and δ , and thus δ is a simple measure of the intra-plot correlation due to spatial aggregation of the complementary vegetation classes. For example, in the case of three complementary vegetation classes,

$$\text{Covar}(p_1, p_2) = \begin{bmatrix} \delta q_1(1-q_1) & -\delta q_1 q_2 \\ -\delta q_1 q_2 & \delta q_2(1-q_2) \end{bmatrix} \quad (2)$$

where Covar is the covariance matrix.

In the case of three complementary vegetation classes, the probability density function of the Dirichlet-multinomial mixture distribution (1) is,

$$f(y_1, y_2, y_3; q_1, q_2, \delta) = \frac{\binom{y_2}{y_1+y_2} \binom{y_3}{y_1+y_2+y_3} \Gamma\left(y_1 + q_1 \left(\frac{1}{\delta} - 1\right)\right) \Gamma\left(y_2 + q_2 \left(\frac{1}{\delta} - 1\right)\right) \Gamma\left(y_3 + \left(1 - q_1 - q_2\right) \left(\frac{1}{\delta} - 1\right)\right) \Gamma\left(\frac{1}{\delta} - 1\right)}{\Gamma\left(q_1 \left(\frac{1}{\delta} - 1\right)\right) \Gamma\left(q_2 \left(\frac{1}{\delta} - 1\right)\right) \Gamma\left(\left(1 - q_1 - q_2\right) \left(\frac{1}{\delta} - 1\right)\right) \Gamma\left(y_1 + y_2 + y_3 - 1 + \frac{1}{\delta}\right)}. \quad (3)$$

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