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Methodological Advances

Functional ecology of rare and common epigeic lichens in alvar grasslands

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ABSTRACT

The autecology of rare species can be derived using similarities among functional traits and environmental conditions observed for common species, i.e. we employed the ‘matching analogy approach’ with the analytical scheme ‘common species → driver → trait → driver → rare species’. We addressed the driver–trait relationship for common epigeic lichens of thin-soil calcareous grasslands, which are endangered by cessation of traditional land use. Common lichens were suppressed by encroaching herbs and shrubs, and were supported by ground disturbances. The lichens of open low-productivity alvars are predominantly calciphilous, epibryic, crustose-squamulose, sexually reproducing and contain UV-protective pigments. Lichens of encroached alvars are soil-type generalists, fruticose, reproduce vegetatively and contain herbivore-deterring compounds. Rare lichens resemble the species of open low-productivity alvars, except their more limited niche space, i.e. they are restricted to arctic-alpine habitats. The conservation practices on alvars should support the formation of crust-forming communities by suppressing the growth of shrubs and herbs, and by promoting recurrent small-scale soil disturbances.

Introduction

The conservation of rare species is often problematic due to their poorly known ecology (Brown et al., 1994). Species' autecology can be learned on the basis of their life history or functional traits (Rogers, 1990; Cornelissen et al., 2007; Ellis, 2012), but such information can only be reliably quantified for frequently occurring species. Therefore, we suggest a ‘matching analogy approach’ for low-occurrence species. For this, we assume that the pattern of relationships between an environmental driver and a responding trait (a ‘driver–trait relationship’) has a uniform meaning regardless of species frequency, i.e. a link which was revealed for frequently occurring (common) species, can be extrapolated to rare species. When a number of drivers and traits are involved, leading to a set of extracted driver–trait complexes of common species, statistically supported functional response groups can be formed. Further, these response groups of common species can be used to explain the autecology of rare species by matching to the response group with the highest similarity in

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trait composition (Fig 1). To recap, the approach can be defined as the 'common species → driver → trait → driver → rare species' algorithm.

To apply this approach in practice, we investigated epigeic/terricolous lichens from shallow soil calcareous grasslands called alvars (Rosén, 1982). Alvars came into existence as a consequence of livestock grazing over centuries or even millennia (Rosén, 1982). The shallow soil on monolithic rock is susceptible to extreme droughts in summer, frost-induced soil movements in winter and small-scale flooding in spring (Rosén, 1995; Ott et al., 1996, 1997). Environmental stress and grazing disturbance have created a sparse sward but species-rich plant community (Rosén, 1982; Poschlod and WallisDeVries, 2002; Pärtel et al., 2007) where cryptogams also flourish (Fröberg, 1988; Dengler et al., 2006; Leppik et al., 2013). In the last century, however, traditional land use practices of alvars ceased, and abandonment and/or afforestation initiated the degradation of semi-natural grasslands, the consequence of which is encroachment with *Juniperus communis* and *Pinus sylvestris* (Laasimer, 1975; Kaar, 1986; Rosén and van der Maarel, 2000). As a result, a unique biodiversity accumulated in these grasslands has become endangered (WallisDeVries et al., 2002; Helm et al., 2006), including lichens (Ott et al., 1996; Löbel et al., 2006; Leppik et al., 2013). In terms of biodiversity loss, the semi-natural grasslands are a central issue in contemporary nature conservation policy in Europe (Poschlod and WallisDeVries, 2002).

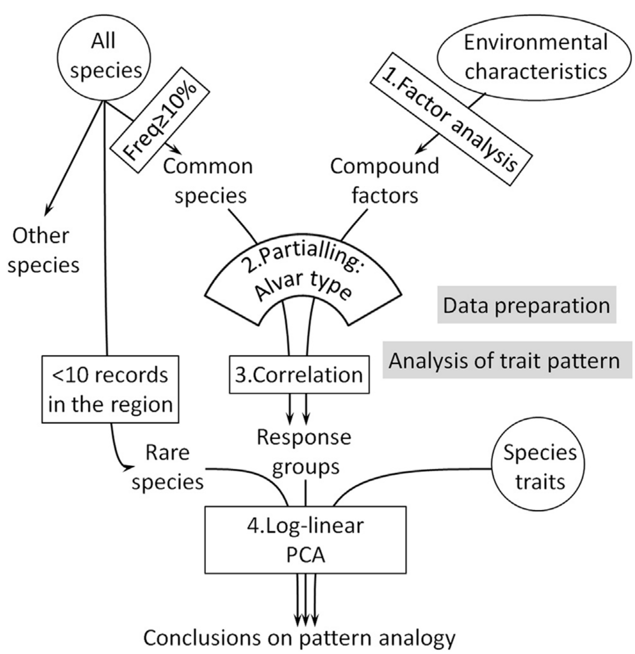

Fig 1 – The scheme of the analytical algorithm applied. Data entry units are species list (All species), matrix of environmental data (Environmental characteristics) and matrix of species traits (Species traits). The upper half comprises steps of data preparation: simplification of environmental data by extracting compound factors; partialling out the variation caused by differences in habitat type. The lower half comprises steps of analysis of driver–trait correlations, combination of species into response groups, and trait-pattern comparisons between response groups of common and nationally rare species using log-linear analysis and PCA.

Conservation strategy should rely on the knowledge of limiting ecological processes. Therefore, identification of the environmental factors driving the composition and richness of ground layer lichens, particularly rare species, should be a first priority. Recently, we have found that herb and shrub encroachment can impoverish epigeic lichen communities causing extinction, and species with a conservation value are the first to react (Leppik et al., 2013). Species' response to a changing environment depends on the composition of their functional or life-history traits (Rogers, 1990; Cornelissen et al., 2007; Ellis, 2012).

In this study we address drivers that potentially affect lichen species on alvar grassland and nationally rare species by applying driver-trait responses. The first task was to estimate a correlation between frequently observed (common) ground layer lichen species and their potential drivers in alvars and alvar-like habitats and to extract the response groups of common species (also termed 'functional types'). The second step was to draw parallels between the trait composition of nationally rare species and the response groups of common species.

Materials and methods

Study area and study sites

Estonian alvars are mainly distributed on the islands of the eastern coast of the Baltic Sea (57.3–59.5°N, 21.5–28.1°E), in regions where the dominant soil types on limestone are rendzinas (Laasimer, 1965; Kõlli and Lemetti, 1999). The area of alvars has diminished dramatically over the last century; only 30 % (ca 15 000 ha) of the former territory (ca 50 000 ha, Kukk and Sammul, 2006) has remained, while even this is mostly overgrown by junipers (*J. communis*) or Scots pine (*P. sylvestris*). The region has a mild maritime climate with a mean annual temperature of 6.2 °C and a precipitation of 600 mm (http://www.emhi.ee).

In 2009, 2010, we selected 76 study sites throughout the main alvar distribution in western Estonia (Leppik et al., 2013). The study sites were selected on the basis of information on land cover type, soil type, soil layer depth (max 10 cm) and the history of grasslands. Information was obtained from the grassland database of the Estonian Seminatural Community Conservation Association and from various maps provided by the Web Map Server of the Estonian Land Board (http://xgis.maaamet.ee: land cover maps, soil maps, historical maps dated back to 1894 and orthophotos). Maps and orthophotos were also used to detect former large-scale disturbances (Supplementary Appendix 1). The sample sites were distributed evenly over various factor combinations.

The study sites were classified into one of the four alvar grassland types, based on the exposure of bedrock or the type of deposits, i.e. plate, ryhk, shingle or heath alvar, as defined by Zobel (1987). The fifth type is a novel (newly formed) community – alvar-like grassland on old limestone quarry floor. A more detailed characterization of these habitats and a relevant floristic analysis are presented in Leppik et al. (2013).