Preslia 87: 87–108, 2015

Habitats and ecological niches of root-hemiparasitic plants: an assessment based on a large database of vegetation plots

Biotopy a ekologické niky kořenových poloparazitů: zhodnocení na základě velké fytocenologické databáze

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Těšitel J., Fibich P., de Bello F., Chytrý M. & Lepš J. (2015): Habitats and ecological niches of root-hemiparasitic plants: an assessment based on a large database of vegetation plots. – Preslia 87: 87–108.

Root hemiparasites are a specialized group of green photosynthetic plants that obtain resources from the roots of other plants. Some root hemiparasites are considered to be important keystone species in temperate grasslands while others are listed as endangered. In this study, we used vegetation-plot data from the Czech National Phytosociological Database to construct habitat suitability models for root hemiparasites occurring in the Czech Republic. These models were based on a formalized vegetation classification, species co-occurrence patterns in vegetation units and actual presence of hemiparasitic species in the database. The resulting habitat models defined as sets of suitable plots for each species were further described by a climatic gradient, community Ellenberg indicator values and the leaf-height-seed (LHS) plant ecology strategy scheme values characterizing the associated vegetation. Using the properties of each vegetation unit, descriptors of the habitat suitability models and information from experimental studies, we interpreted the habitat suitability models as axes and shapes of ecological niches of individual root-hemiparasitic species. The individual hemiparasites differed in their favoured type of vegetation but almost all types of vegetation in the Czech Republic could host some of them. Semi-natural and natural grasslands with moderate availability of mineral macronutrients and water were identified as types of vegetation with a high incidence of hemiparasites and the highest number of species of hemiparasites. High incidence but low species richness of hemiparasites was recorded in forests and scrub. In contrast, most species of root hemiparasites did not occur in extreme habitats with a high level of stress or disturbance and at nutrient-rich and moist sites dominated by fast-growing species, i.e. at sites with intense above-ground competition. This reflects the ecophysiological fundamentals of the hemiparasitic strategy, which provides efficient yet low-cost access to below-ground abiotic resources. On the one hand, this advantage diminishes at sites where primary macronutrients and soil moisture are abundant but on the other hand, exploitation of this advantage, however, requires non-extreme environmental conditions. Apart from this common pattern, individual species of hemiparasites differ in their ecological requirements, which frequently underlie their possible use as ecosystem engineers in grassland restoration or their conservation status.

Keywords: *Bartsia*, Beals index, *Euphrasia*, habitat suitability model, hemiparasite, *Melampyrum*, *Odontites*, *Pedicularis*, phytosociology, *Rhinanthus*, *Thesium*

Introduction

Identification and description of the habitats of individual species is one of the important goals of ecology. A model of habitat suitability can serve as the first step in identifying the ecological niche of a species (Kearney 2006). In addition, it is an invaluable tool in conservation management as it can identify habitat requirements of endangered species and suitable sites for its reintroduction (Hirzel & Le Lay 2008). The habitat of a plant species is defined in terms of the abiotic and biotic conditions of sites where a species grows (Kearney 2006). A number of stochastic factors such as fecundity, dispersal limitation and demographic stochasticity (Hirzel & Le Lay 2008, Chase & Myers 2011) cause that species may not occur at all sites with favourable conditions (Ozinga et al. 2005). Therefore, analysing the habitats of the species involves considering not only its observed but also potential distribution. This idea is summarized by the concepts of species pool (Eriksson 1993) and dark diversity (Pärtel et al. 2011), respectively, referring to the pool of species that can potentially grow at a given site and the set of species that are missing but have ecological requirements compatible with site conditions. The habitat definition and analysis should take this into account and consider differences in conditions between sites, which are suitable for species occurrence and sites where species cannot occur.

Exploring large sets of vegetation plots is one approach to habitat analysis, which can cover also the local and community aspects. Such vegetation plot data are increasingly available as extensive databases (Schaminée et al. 2009, Dengler et al. 2011) that are representative of vegetation across a defined territory. The data available for each plot usually consist of species composition and cover-abundance, location of the site and a few additional observations or measurements. Vegetation recorded in the plots can be classified and individual plots assigned to one of the vegetation units based on the species composition. Thus, co-occurrence of a given species with others and its incidence in vegetation units can be explored. Species co-occurrence patterns are crucial for definitions of species pools (Ewald 2002) and dark diversity (Pärtel et al. 2011). However, they can also be used to define a set of suitable but unoccupied sites based on species composition of plots where the species actually occurs (Münzbergová & Herben 2004). Three classes of vegetation plots can thus be defined for each of the species included in a database: occupied, suitable but unoccupied (hereafter referred to as suitable), and unsuitable and unoccupied (hereafter referred to as unsuitable; Fig. 1). The habitat of a species is then defined in terms of the set of plots comprised in the first two groups. The contrast of occupied and suitable vs unsuitable is crucial for exploring abiotic and biotic conditions defining the limits of a species habitat, since it filters out the stochastic effects of dispersal limitation and sampling (each vegetation plot is a spatial subsample of a stand and cannot contain all species present in a habitat). As a result, it should provide a more realistic picture of species habitats in comparison to the contrast between occupied vs unoccupied (= suitable + unsuitable) plots.

The vegetation databases can be used to model habitats in terms of a set of plots suitable for a given species. A habitat model defined in this way is, however, of limited informative value and predictive power. Its properties cannot be described in a straightforward manner and more importantly, habitats of individual species can hardly be compared or located on environmental gradients. Comparison of the habitats of the same species based on two different databases is also very complicated. Therefore, habitats need to be

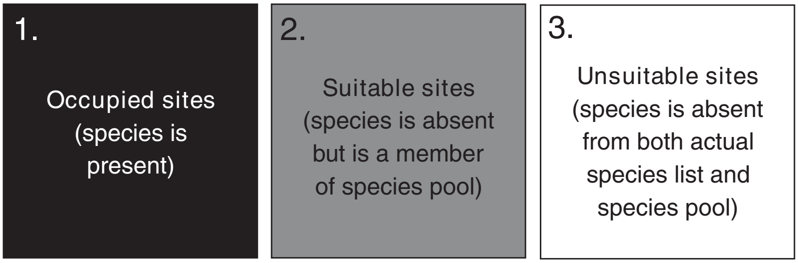

Fig. 1. – Three classes of sites: occupied, suitable (but unoccupied) and unsuitable based on the occurrence of individual species and their patterns of co-occurrence with other species in the vegetation-plot database.

described in terms of a few descriptors, which are biologically meaningful in relation to the environmental gradients at a given site. Description of climatic conditions is generally possible based on plot location (together with plot aspect and slope, a characteristic generally available in the vegetation-plot databases; Chytrý & Rafajová 2003). Expert-based systems of species environmental preferences (such as Ellenberg indicator values, EIVs; Ellenberg et al. 1991) can be used to estimate environmental conditions of plots on the basis of species composition. Functional traits of species (available from trait databases) can be used to identify ecological strategies of species occurring in individual plots. Such a two-step approach of model construction and consequent description is required by the fact that the EIVs cannot be used as predictors in models where the response contains information derived from species composition. This is because of an intrinsic interdependence of the predictors and the response in such a model resulting in biased outcomes as demonstrated by Zelený & Schaffers (2012). Due to the similar way of computation, the same issue applies for community weighted mean of functional trait values. Both EIVs and traits can, however, be used in descriptions to indicate the positions of suitable plots on environmental gradients and availability of resources. These descriptions consequently allow mechanistic (yet informal) interpretations of habitat models in relation to individual axes of species ecological niches (Fig. 2). Thus the correlative nature of the habitat models can be connected with mechanistic principles underlying the shape of a species' ecological niche, a concept proposed by Kearney (2006)

In this paper, we explore the habitats of species of root hemiparasites in the Czech Republic. Root hemiparasites form a distinct functional group of plants. They are green, photosynthetic species, which, however, use specialized root organs called haustoria to attach to the roots of other plants and withdraw resources from the host's xylem (Irving & Cameron 2009). Mineral nutrients, water and a limited amount of organic assimilates are thus acquired from their hosts (Irving & Cameron 2009, Těšitel et al. 2010a). Nevertheless, root hemiparasites tend to be dependent on their own photosynthesis for most organic carbon and are thus affected by above-ground competition (Matthies 1995, Mudrák & Lepš 2010, Těšitel et al. 2013, 2015). Several species of root hemiparasites are keystone species in some ecosystems due to their ability to suppress their hosts (Press & Phoenix 2005), thus affecting competitive relations in communities (Cameron et al. 2005) and altering nutrient cycling (Quested et al. 2003, Spasojevic & Suding 2011, Demey et al. 2014). Thus, it is suggested they play the role of ecosystem engineers in semi-natural grassland communities where they can reduce asymmetric competition,

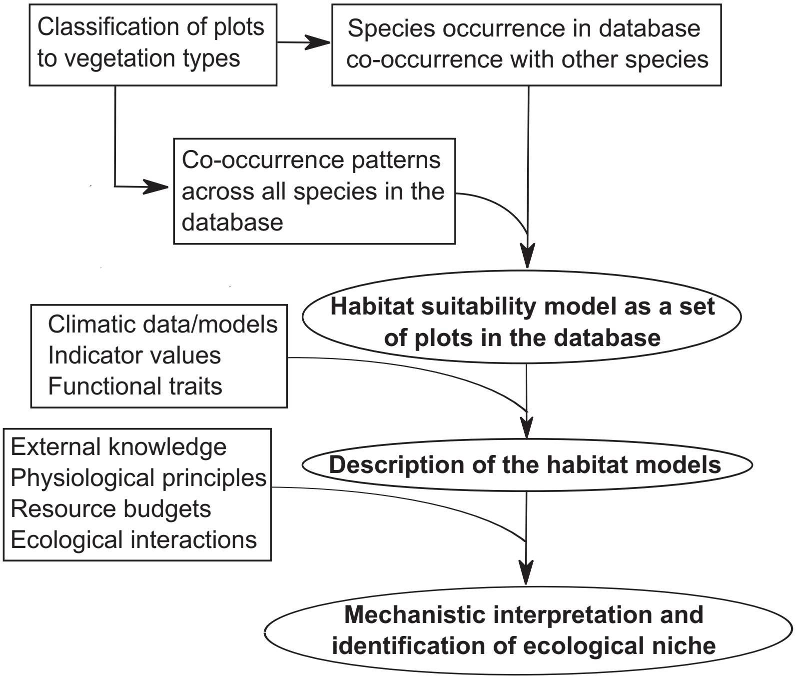

Fig. 2. – Conceptual scheme of the steps and data sources needed to construct a habitat suitability model, and describe and interpret it in terms of niche axes and shape.

facilitating species coexistence and increasing diversity (Westbury et al. 2006). The hemiparasites, in particular those of the genus *Rhinanthus*, are therefore currently used in grassland restoration (Westbury et al. 2006, Pywell et al. 2007, Westbury & Dunnett 2007, Hellström et al. 2011, Mudrák et al. 2014). In contrast, many other hemiparasitic species are considered threatened from the nature conservation perspective (Svensson & Carlsson 2005, Ramsay & Fotherby 2007, Schmalholz & Kiviniemi 2007, Grulich 2012). Knowledge of the favourable habitats and factors shaping the ecological niches of species of root hemiparasites is thus crucial for the development of both appropriate restoration strategies (identification of potentially suitable sites for introduction) and conservation.

In total, 42 species and subspecies of root hemiparasites belonging to the families *Orobanchaceae* and *Santalaceae* have been reported from the Czech Republic (Electronic Appendix 1; Danihelka et al. 2012). Their habitats and ecology are indicated in regional floras but this is based on various observations and has never been studied in a formal way based on the features of occupied or suitable sites. Using the data available in the Czech National Phytosociological Database (for 18 species of root hemiparasites, the others being rare or extinct), a climatic model (Tolasz et al. 2007), Ellenberg indicator values (EIVs; Ellenberg et al. 1991) and a set of functional traits (leaf-height-seed traits; Westoby 1998) we aim to (i) identify the types of vegetation in which individual species of root hemiparasites occur, (ii) construct habitat suitability models for each species of hemiparasites and (iii) interpret the habitat suitability models using knowledge of the biology of root hemiparasites revealed by experimental studies.

Methods

Data sources

Czech National Phytosociological Database containing records of vegetation plots (relevés) in the Czech Republic (Chytrý & Rafajová 2003) is the principal source of data for this study. For each plot there is a list of species of vascular plants with their cover-abundances and basic information on geographic location, habitat and vegetation structure. We used a stratified subsample of the database following the resampling criteria used by Chytrý et al. (2005; see also Knollová et al. 2005) in order to reduce local oversampling of some areas or habitats. This resulted in a set of 31,512 plots covering all the different types of vegetation in the country, which was used in this analysis. Ellenberg indicator values (EIVs) for each plot were calculated as unweighted means of the indicator values (from Ellenberg et al. 1991) for species present in the plots using the JUICE 6.5 program (Tichý 2002). Phytosociological class was determined for each relevé using an automated classification and an expert system based on the Cocktail method (Bruelheide 2000, Kočí et al. 2003) developed for the Czech national vegetation classification (Chytrý 2007–2013). The expert system can be downloaded and the database obtained upon request following instructions at www.sci.muni.cz/botany/vegsci. Climatic data were obtained from the national climatic atlas (Tolasz 2007), which includes spatial models of individual climatic variables based on interpolated values for climate stations.

We used the leaf-height-seed (LHS) plant ecology strategy scheme (Westoby 1998) to characterize the ecological strategies of species occurring in vegetation plots using functional traits. In addition, we considered the life spans of plants (proportion of annuals in the community). Most of the root hemiparasites studied are annuals and, remarkably, they are often the only annuals present in an otherwise perennial community (Strykstra et al. 2002). Here we want to explore the extent to which this applies to multiple species systems at a broad spatial scale. Values of specific leaf area (SLA) and shoot canopy height (Height) were acquired from the LEDA database (Kleyer et al. 2008). Data on seed weight and life span were obtained from the BiolFlor database (Klotz et al. 2002). Community weighted means (CWM) of traits were computed for each vegetation plot on the basis of species abundances and their trait values. Only herb-layer species were considered in computations of CWMs for all vegetation plots including forest plots since all root hemiparasites in the Czech Republic are herbaceous plants, and consequently, they potentially compete with other species in the herb layer, but not those in the shrub and tree layers.

We included in our study all the root hemiparasites occurring in the Czech Republic (see Electronic Appendix 1 for a list of taxa, their Red-List status and habitat descriptions in the Flora of the Czech Republic). Only species with more than 10 occurrences in the database were analysed (n = 18). Of these, all species with 10–30 occurrences (n = 4) were considered rare and the informative power of their habitat analyses should be interpreted with caution. Occurrences in phytosociological classes were also listed for species with at least one occurrence in the database (n = 8; Appendix 2). Eleven species were not recorded in the database. The nomenclature of plant taxa and syntaxa follows Danihelka et al. (2012) and Chytrý (2007–2013), respectively.

Taxonomy and nomenclature of the root hemiparasites studied

Most species studied are well defined taxonomically. Hybrids between them occur with rather low frequency (e.g. between *Rhinanthus major* and *R. minor*; Ducarme & Wesselingh 2005). Many species display ecotypic seasonal variation typical of annual hemiparasitic *Orobanchaceae* (Wettstein 1895), which could not be included in our analyses since it was not recorded in vegetation-plot records. In most cases, however, this variation is more or less continuous and there are no distinct ecotypes (e.g. in *Melampyrum pratense* and *M. sylvaticum*; Štech 1998), or the ecotypes share similar habitats (e.g. *Rhinanthus major*; Skála & Štech 2000). An exception to this is *M. nemorosum*, a species with very distinct ecotypes one of which grows in open habitats and the other at the edges and in forests (Štech 2000). The most complicated taxon studied is the *Odontites vernus* group, which consists of two cytotypes, diploids and tetraploids, and the cytotypic variation furthermore interacts with seasonal variation (Koutecký et al. 2012). However, the novel taxonomic concept based on the recognition of these patterns could not be used in our study because we used older data. Therefore, we only report results for the *Odontites vernus* group as an aggregate taxon. *Melampyrum sylvaticum* might be another taxonomically complicated species. *Melampyrum herbichii*, its closely related congener, was, however, rejected from a taxonomic perspective and all Czech populations previously referred to this taxon were assigned to *M. sylvaticum* (Těšitel et al. 2009)

Habitat modelling

Habitats of individual species consist of occupied and suitable sites. While the former group is directly available, suitable sites have to be identified using a probabilistic approach based on species co-occurrence patterns in the database. We adopted approach used by Münzbergová & Herben (2004), based on Beals' index of sociological favourability (Beals 1984, see also Ewald 2002), which measures the threshold for the suitability of unoccupied sites. The threshold is defined as a minimum of Beals' index values of occupied sites. Unoccupied sites with Beals' index higher than the threshold are considered to be suitable. This method computes thresholds of habitat suitability for individual species because the threshold depends on the frequency of occurrence (rare species should have lower thresholds than common species).

We made two modifications to the method of Münzbergová & Herben (2004): (i) the threshold for suitable sites was defined as the 10th percentile of the Beals' index distribution for occupied sites (this reduces the effect of outliers; see Botta-Dukát 2012); (ii) the threshold for a given species was computed separately for each of the phytosociological classes in which it occurs (i.e. for one species, there are multiple thresholds of suitability, one for each of the phytosociological classes in which it occurs). This is based on the fact that Beals' indices are frequency-dependent and species occurring in multiple phytosociological classes are not present with the same frequency in each of them. The suitable and occupied plots in individual phytosociological classes were finally pooled to specify a single set of plots defining the habitat of each species. For rare or moderately rare hemiparasitic species that occur in fewer than 50 vegetation plots in the database, we included phytosociological classes with more than one occupied plot in the niche computation. For the common hemiparasites, which occur in more than 50 plots, we included only vegetation classes with more than four plots. These restrictions reduce the effects of outliers caused by the transitional random occurrence of species at unsuitable sites or possible misidentification of species.

Habitat model descriptors

The habitat model descriptors are the positions of occupied and suitable sites on gradients of climate, EIVs and functional traits (disregarding other variables). Such habitat models for the root hemiparasites and the whole of the vegetation in the Czech Republic (represented by the complete data set of the stratified database) were compared. Thus, we plotted the positions of occupied and suitable sites of each of the root hemiparasites against the site scores for the whole database (or their interquartile range in the case of boxplots).

In addition, we quantified the proportions of the variation in the habitat models explained by individual groups of descriptors (climate, EIVs, LHS traits). This was done by fitting sets of generalized binomial models, separately for each species of root hemiparasites, using the classical variation partitioning approach (Borcard et al. 1992). Models contain suitability of habitats as a response (unsuitable = 0; occupied or suitable = 1) and groups of descriptors (both linear and quadratic trends of each descriptor were included) as predictors. Partial proportion of variability in a habitat suitability model accounted by a descriptor group was computed as deviance explained by a model containing climate+ EIVs+traits minus deviance explained by a model containing all the other descriptor groups (e.g. for climate, this model contained EIVs+traits). For example R^2(climate) = R^2(climate+EIVs+traits) – marginal R^2(EIVs+traits). For partial shared effects of two predictor groups (overlap of effects), we subtracted the deviance explained by the third predictor group and partial explained deviance of each of the predictor groups for which the shared effect is computed from the deviance explained by the full model. For example partial R^2(climate+traits) = R^2(climate+EIVs+traits) – partial R^2(climate) – marginal R^2(EIVs) – partial R^2(traits). The proportion of deviance explained not attributable to any individual descriptor or shared effects of pairs of descriptors was considered to be accounted for by the combination of all three descriptors. The proportions of explained deviance in variation partitioning do not sum up to 100% as there is always a certain amount of residual variance not attributable to any of the descriptors or their combinations. R software (version 3.1.1; R Core Team 2014) was used for all computations.

Despite their correlative nature, the habitat suitability models present a basis for identifying the ecological niches of species. This is based on the biological meaning of the habitat suitability model descriptors, which indicate the principal factors limiting plant performance in natural communities including below-ground resources (soil nutrients and water), disturbance and competition for light (Grime et al. 1997). The below-ground resources can be indicated by the EIVs in a straightforward manner, while intensity of disturbance and competition can be estimated from the LHS traits, EIVs and proportion of annual species. Disturbance can be indicated by annual species with small seeds and low canopy height not attributable to scarcity of below-ground resources (Westoby 1998). In contrast intense above-ground competition can be indicated by high canopy height coupled with high SLA, high nutrient and moisture EIVs (Grime et al. 1997, Westoby 1998) and in some cases (competition from the tree layer) also by low EIV for light. In addition, proportions of variation in suitability accounted for by individual habitat descriptor groups are key parameters indicating their significance for defining the niches of individual species.

Results

Habitats of species of root hemiparasites and their phytosociological classification

The occurrence of root hemiparasites in different types of vegetation differed for the different species (Electronic Appendix 2). Nevertheless, some general trends are evident. High or moderately high incidence of hemiparasitic species (13.7–30.1% plots with hemiparasites) combined with high species numbers was recorded in open semi-natural and natural types of vegetation, many of them with limited availability of primary macronutrients (*Molinio-Arrhenatheretea*, *Festuco-Brometea*, *Calluno-Ulicetea*, *Scheuchzerio palustris-Caricetea nigrae*). The *Mulgedio-Aconitetea* and *Elyno-Seslerietea* vegetation classes probably also belong here but they are rare types of vegetation for which there are few plots in the database, which prevents drawing a definitive conclusion. High incidence of hemiparasites (9.3–48.7% plots with hemiparasites) underlain, however, by the occurrence of only one or two species is typical of forest/scrub, often also on macronutrient-poor soils (*Carpino-Fagetea*, *Quercetea robori-petraeae*, *Quercetea pubescentis*, *Vaccinio-Piceetea*, *Erico-Pinetea*, *Roso pendulinae-Pinetea mugo*), which host various *Melampyrum* species (*M. pratense*, *M. sylvaticum*, *M. nemorosum*). A similar pattern of occurrence of hemiparasites (14.3–38.5% plots with hemiparasites) is present in habitats stressed by low macronutrient availability combined with high water level (*Oxycocco-Sphagnetea*), extreme climatic conditions (*Loiseleurio-Vaccinietea*; low number of plots) or high concentrations of salts (*Festuco-Puccinellietea*). The first two are habitats of *Melampyrum pratense* and *Odontites vernus* occurs in the latter. Despite the very low percentage of occupied plots (4.0% plots with hemiparasites) in annual vegetation of arable fields and heavily disturbed sites (*Stellarietea mediae*), this habitat hosts *Odontites vernus*, *Rhinanthus alectorolophus* and *Melampyrum arvense*, and is even the most common type of habitat for the first two. Rarely (less than 5% of plots with hemiparasites) do the hemiparasitic species occur in vegetation in wet mesotrophic to eutrophic places (*Phragmito-Magno-Caricetea*, *Montio-Cardaminetea*, *Bidentetea tripartitae*), disturbed eutrophic habitats (*Galio-Urticetea*, *Epilobietea angustifolii*, *Artemisietea vulgaris*), periodically flooded habitats (*Isoëto-Nano-Juncetea*, *Littorelletea uniflorae*), extremely dry and stressed (*Asplenietea trichomanis*), dry and disturbed (*Koelerio-Corynephoretea*), cold and stressed (*Juncetea trifidi*) or strongly disturbed habitats (*Polygono arenastri-Poëtea annuae*). Similarly, the incidence of species of hemiparasites in eutrophic wet forests and scrub with intense competition in the understory (*Alnetea glutinosae*, *Rhamno-Prunetea*) is very low. Hemiparasites are absent from aquatic habitats (*Lemnetea*, *Potametea*, *Charetea*) and some of saline (*Crypsietea aculeatae*, *Thero-Salicornietea strictae*) and stressed and disturbed habitats (*Cymbalario muralis-Parietarietea judaicae*, *Festucetea vaginatae*, *Thlaspietea rotundifolii*).

Habitat models

Positions of occupied and suitable plots along gradients of annual precipitation and mean annual temperature describe the habitat models in relation to climate. The two climate parameters are closely correlated in the Czech Republic (Fig. 3). Due to the intrinsic dependence of climate on altitude, the habitat models for species can also be described by their ranges in terms of altitude (Electronic Appendix 3). Most of the models for hemiparasitic species indicate relationships with climate (Fig. 3). The habitats of *Euphrasia stricta*, *Melampyrum arvense*, *M. cristatum*, *M. nemorosum*, *Odontites luteus* and *Thesium linophyllon* are located at the dry and warm end of the gradient. The habitats of the *Odontites vernus* group, *Rhinanthus alectorolophus* and *R. major* occupy similar positions but the pattern is less distinct. In contrast, the habitats of *Bartsia alpina*, *Rhinanthus riphaeus* and to some extent also *Thesium alpinum* appear to be associated with a cold and wet climate. All of these three species, however, are rare. The habitats of *Euphrasia officinalis*, *Melampyrum pratense*, *M. sylvaticum*, *Pedicularis palustris*, *P. sylvatica* and *Rhinanthus minor* extend along the whole climatic gradient; although there are higher densities of some species at certain positions on the gradient (e.g. *Melampyrum sylvaticum* grows mostly but not exclusively in cold and wet areas).

The gradients in soil moisture and primary macronutrient availability indicated by the Ellenberg indicator values show a more complex, two dimensional picture of the habitats (Fig. 4). The root hemiparasites are generally absent at sites with high values of both EIVs (except the *Odontites vernus* group and in part also *Pedicularis palustris*). Apart from this rule, it is also possible to distinguish the typical habitats of several groups of species. *Euphrasia officinalis*, *Melampyrum pratense*, *Rhinanthus major* and *R. minor* share a niche which extends from moderately dry to moderately moist macronutrient-poor conditions (extending further towards mesotrophic in the drier part of the gradient). *Euphrasia stricta*, *Melampyrum arvense*, *M. cristatum*, *M. nemorosum*, *Odontites luteus*, *Rhinanthus alectorolophus* and *Thesium linophyllon* occur in dry (to moderately dry) places with low to moderate macronutrient availability. In contrast, *Bartsia alpina* and both *Pedicularis* species prefer wet sites with generally low macronutrient availability. Sites included in the habitats predicted for almost all hemiparasitic species have high EIVs for light (Fig. 5). Exceptions to this are *Melampyrum* species, the predicted habitats of which are located in slightly to heavily shaded areas. EIVs for soil reaction identified four species restricted to alkaline soils (*Melampyrum arvense*, *M. cristatum*, *Odontites luteus*, *Thesium linophyllon*). In contrast, habitats of *Melampyrum sylvaticum*, *Pedicularis sylvatica* and *Rhinanthus riphaeus* are mostly characterized by acidic soils.

The habitat models descriptions obtained using LHS and lifespan traits are summarized by comparing the gradients of community weighted means of the sites included in the models with the median and interquartile range of the whole database (Fig. 6). All of the species of root hemiparasites occur at sites with a low mean canopy height with *Euphrasia stricta*, *Odontites luteus*, *Pedicularis sylvatica* and *Rhinanthus pulcher* displaying the strongest trend in this direction. Similarly, most of the species occur in vegetation with a low mean SLA. *Bartsia alpina*, *Euphrasia stricta*, *Odontites luteus*, *Pedicularis palustris* and *Thesium linophyllon* display the strongest trend in this direction. In contrast, *Melampyrum nemorosum* and to some extent also *M. pratense* show the opposite trend. There is no clear trend in relation to CWM of seed weight across the whole

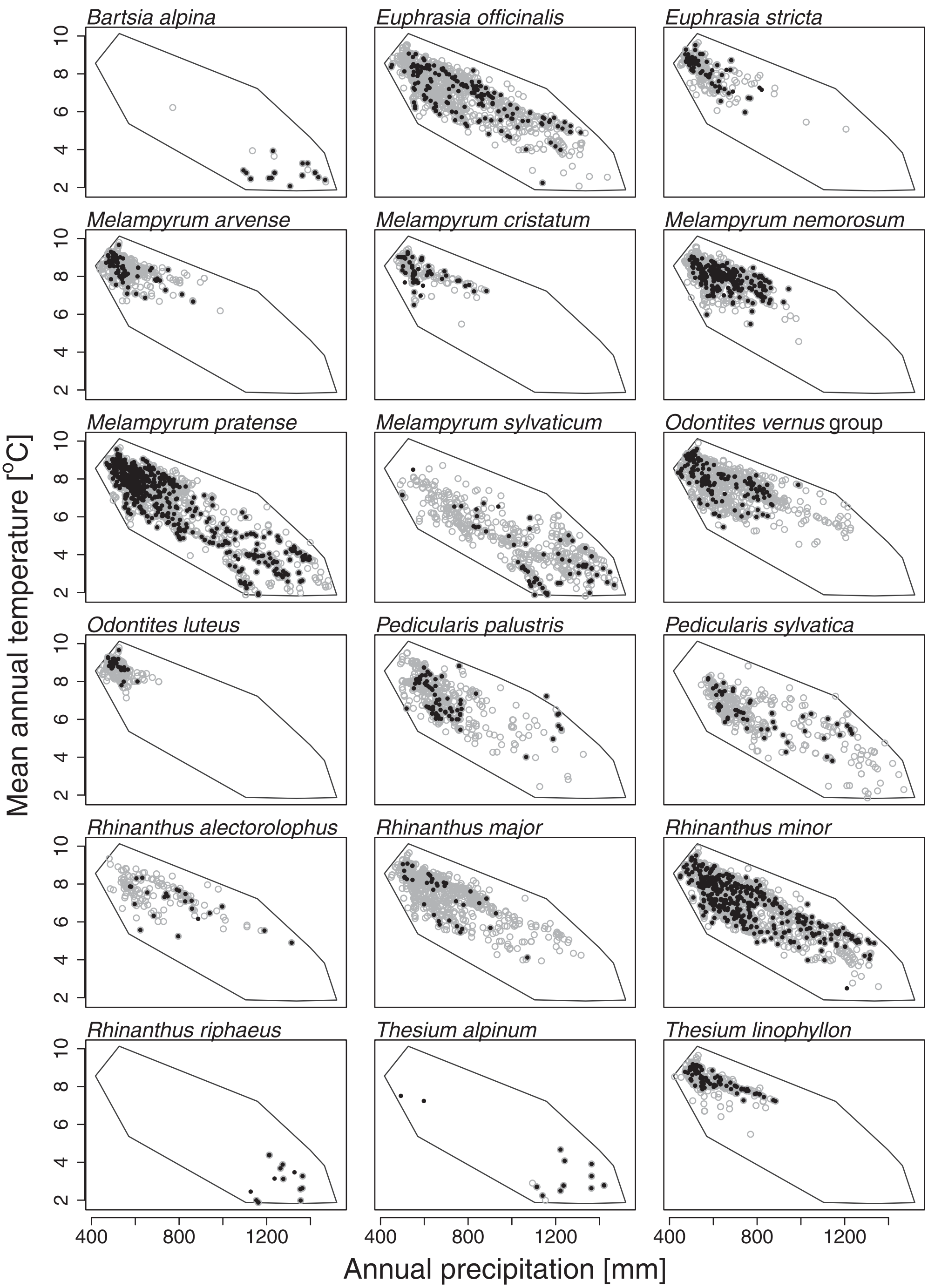

Fig. 3. – Scatterplots of mean annual precipitation and temperature based on data from all the vegetation plots in the database (displayed by the envelope). Suitable sites are displayed for each species of hemiparasite by grey circles. Occupied sites are indicated by black dots.

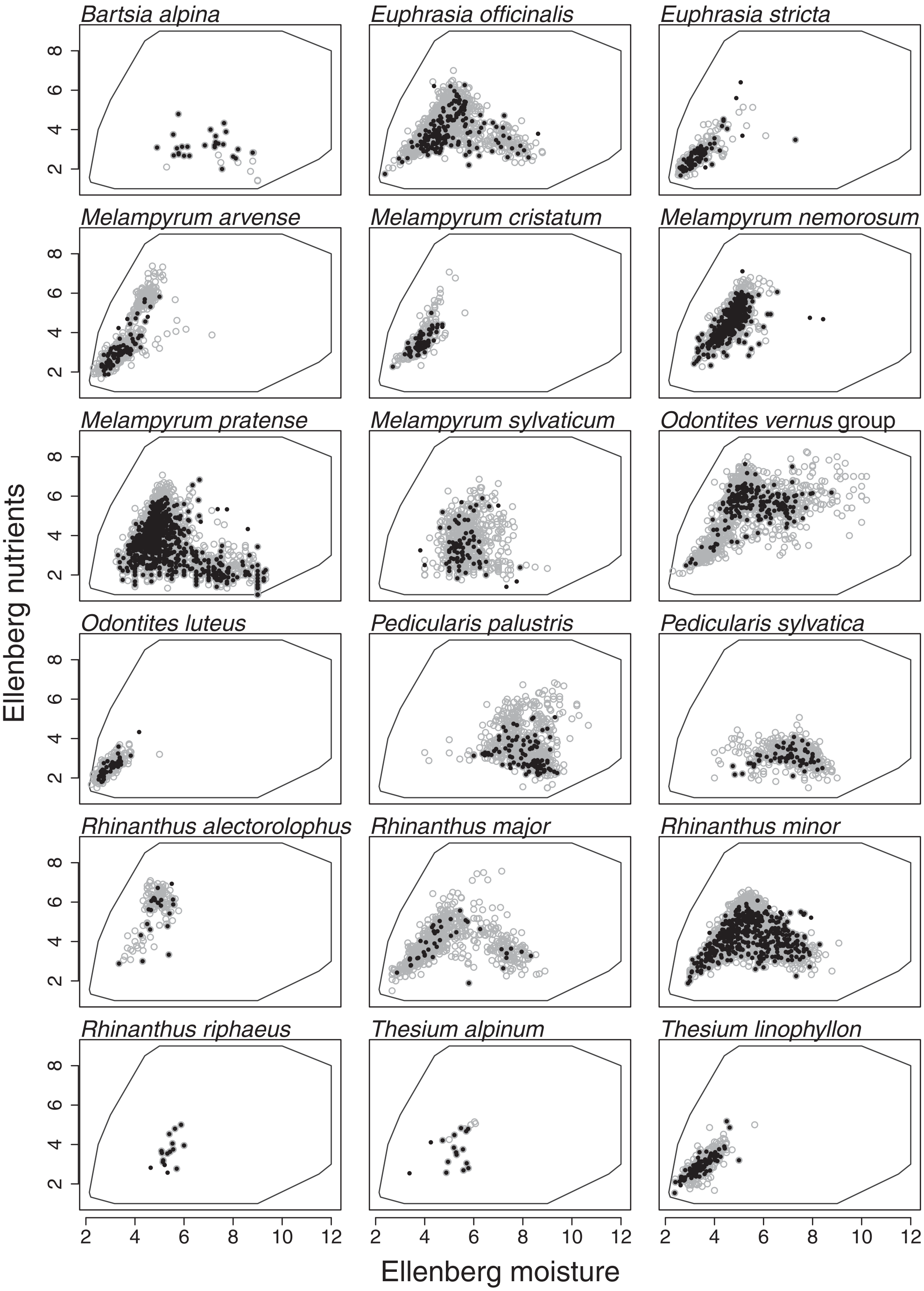

Fig. 4. – Scatterplots of mean Ellenberg indicator values for mineral nutrients and soil moisture based on data from all the vegetation plots in the database (displayed by the envelope). Suitable sites are displayed for each species of hemiparasite by grey circles. Occupied sites are indicated by black dots.

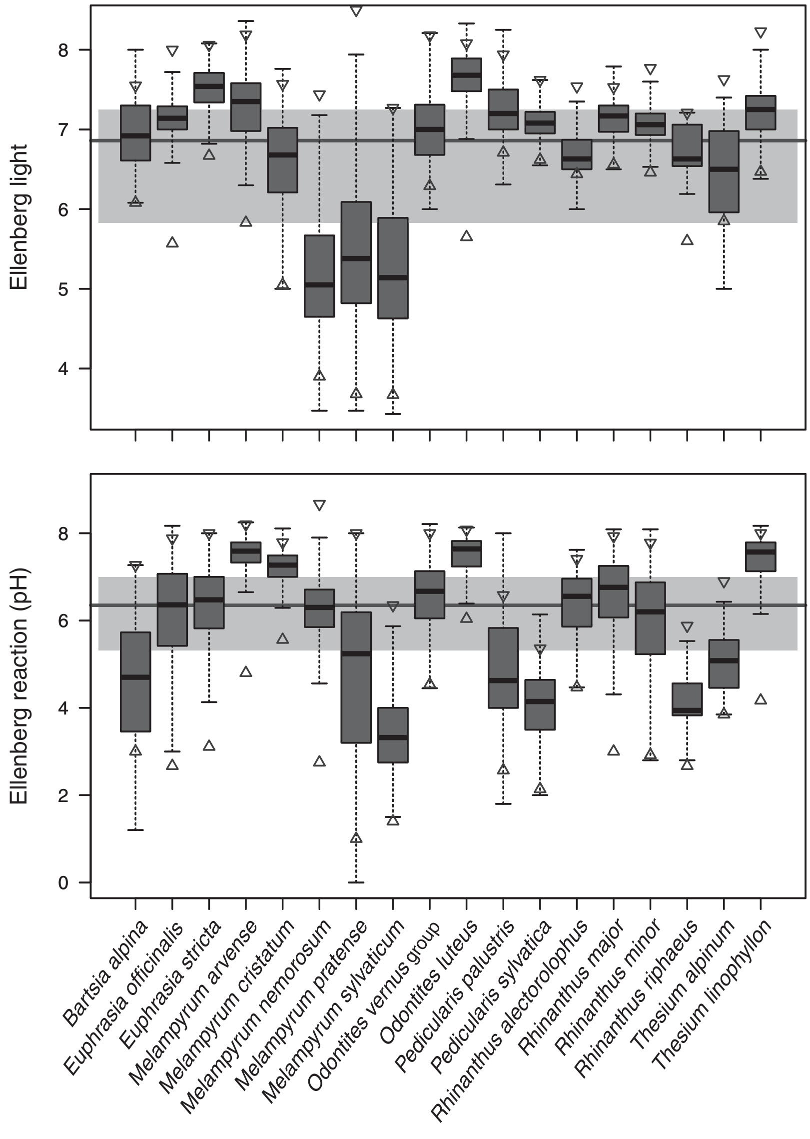

Fig. 5. – Positions of occupied and suitable sites for the root hemiparasites along gradients of Ellenberg indicator values for light and soil reaction. Median, quartiles and non-outlier ranges are displayed. Dark-grey line and grey belt display the median and inter-quartile range of the whole database. Up- and down-pointing triangles display the range of values at occupied sites.

series of hemiparasites with some species being associated with a high and others with a low value. All species of root hemiparasites grow in vegetation largely dominated by perennials (Fig. 7), except *Melampyrum arvense*, *Odontites vernus* group and *Rhinanthus alectorolophus*, which also occur in agroecosystems with numerous annual species.

The analysis of variation in the predicted habitats using sets of descriptors identified EIVs as the most correlated variables followed by climatic variables and LHS traits

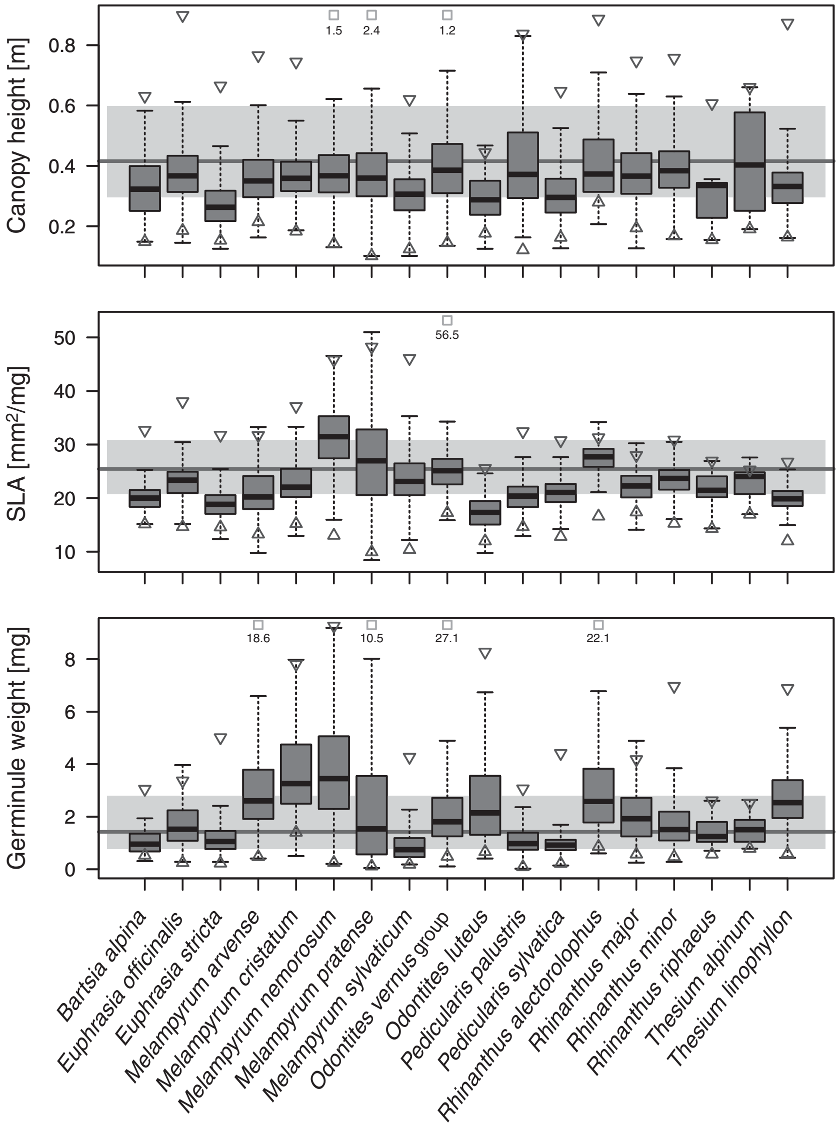

Fig. 6. – Positions of occupied and suitable sites for the root hemiparasites along gradients of CWMs of functional traits canopy height, SLA and seed weight. Median, quartiles and non-outlier ranges are displayed. Dark-grey line and grey belt display the median and inter-quartile range of the whole database. Up- and down-pointing triangles display the range of values of occupied sites. Boxes display extremes that are outside of the axis ranges and their values are indicated by numbers.

(Table 1) for most species. Large proportions of the variation in the predicted habitat were also accounted for by the shared effects of EIVs and LHS traits, and EIVs and climate. Climate alone or in combination with EIVs was, however, the best descriptor for some of the species, namely *Bartsia alpina*, *Rhinanthus riphaeus*, *Thesium alpinum* and *Melampyrum sylvaticum.*

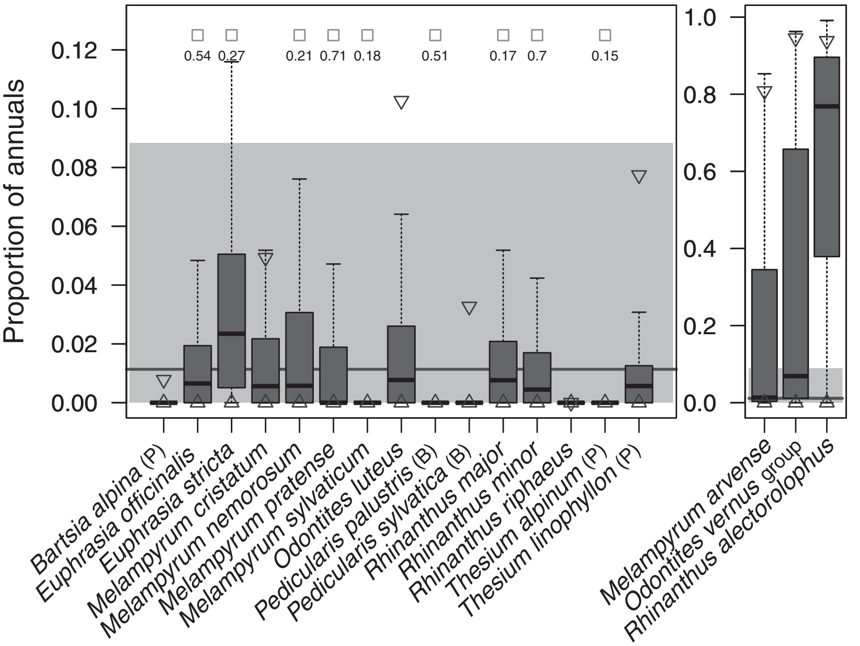

Fig. 7. – Proportion of annual species in communities at occupied and suitable sites for the root hemiparasites. Life span of perennial (P) and biennial/monocarpic perennial (B) hemiparasitic species is indicated. The other species are annuals. Median, quartiles and non-outlier ranges are displayed. Dark-grey line and grey belt display the median and inter-quartile range of the whole database. Up and down triangles display the range of values at occupied sites. Boxes display extremes that are outside of the axis ranges and their values are indicated by numbers.

Table 1. – Percentages of variation in habitat suitability explained by individual habitat descriptor groups and their shared effects (overlap; e.g. climate+EIVs corresponds to overlap of effects of climate and EIVs, not to their interactions).

Species	Climate	EIVs	LHS traits	Climate +EIVs	EIVs +traits	climate +traits	climate +EIVs +traits
Bartsia alpina	36.0	21.4	1.9	0.6	4.7	0.0	8.3
Euphrasia officinalis	2.0	30.0	1.7	1.1	24.4	0.1	0.0
Euphrasia stricta	0.2	20.0	2.9	5.3	24.0	0.1	1.7
Melampyrum arvense	0.8	17.0	3.4	6.9	21.4	0.1	5.4
Melampyrum cristatum	1.5	30.2	3.1	1.2	19.1	0.5	2.5
Melampyrum nemorosum	1.6	33.6	1.5	3.7	17.6	0.3	0.8
Melampyrum pratense	2.5	43.5	1.7	0.0	2.9	0.5	0.0
Melampyrum sylvaticum	7.4	14.7	1.5	18.4	5.5	0.3	7.7
Odontites vernus group	0.8	15.5	6.6	1.9	5.0	0.0	0.0
Odontites luteus	1.8	9.4	2.3	6.3	34.8	0.3	11.9
Pedicularis palustris	1.1	26.9	4.2	3.4	15.4	0.1	0.0
Pedicularis sylvatica	0.9	30.8	0.9	7.3	20.1	0.1	3.2
Rhinanthus alectorolophus	2.7	19.4	5.5	0.0	8.7	0.3	0.9
Rhinanthus major	1.6	16.3	1.5	1.3	23.0	0.0	0.0
Rhinanthus minor	0.7	30.4	2.4	2.4	26.5	0.0	0.0
Rhinanthus riphaeus	17.7	15.6	5.3	19.8	6.9	1.0	0.4
Thesium alpinum	30.1	20.6	4.5	12.5	9.8	0.0	0.0

Discussion

Characteristics of habitats favourable for hemiparasitic plants

Several trends shaping the niches of root-hemiparasitic species are apparent from their occurrence in different types of vegetation and the descriptions of their habitats in terms of EIVs and functional traits. The types of vegetation favourable for most species of root hemiparasites are open ones in which there is a high availability of light in the herb layer, which is dominated by low (low canopy height) and slow-growing species (low SLA). Favourable sites are subject to moderate levels of disturbance (e.g. mowing and grazing) and in which there are moderate levels of water and macronutrients. Suitability of the habitats of the three most frequent species of root hemiparasites, *Melampyrum pratense*, *Rhinanthus minor* and *Euphrasia officinalis*, is clearly co-limited by abundance of water and mineral macronutrients (Fig. 4). Most hemiparasitic species, however, are not recorded at heavily disturbed places and sites severely limited by both a scarcity of water and mineral macronutrients. Exceptions are *Odontites vernus* and *Pedicularis palustris* with ecological niches that include macronutrient-rich and wet sites, and *Odontites luteus* and *Thesium linophyllon* that grow at dry oligotrophic sites.

Interpretation of habitats in terms of niches

The favourable habitats for most of the species of hemiparasites studied provide strong support for the hypothesis that there is a strong and interactive effect of water and mineral macronutrient availability on the performance of root hemiparasites (Těšitel et al. 2015). This hypothesis, based on the results of manipulative experiments, suggests that the performance of root hemiparasites should be best at sites where water and mineral macronutrients are available in moderate amounts, or if one of these is abundant, the other is scarce. Simultaneous abundance of both diminishes the hemiparasite's benefit based on efficient, yet low-cost access to these resources (Irving & Cameron 2009) and results in their competitive exclusion from the community (Van Hulst et al. 1987, Matthies 1995, Hellström et al. 2004, Mudrák & Lepš 2010, Hejcman 2011, Těšitel et al. 2013). In contrast, simultaneous scarcity of these resources may reduce hemiparasites' shoot growth to such extent that it reduces their ability to derive resources from host root xylem (Těšitel et al. 2015) as also suggested by a mathematical model (Fibich et al. 2010). This substantial update of the resource-limitation hypothesis that states that hemiparasitism is most beneficial in low-productive habitats where these resources are scarce (Matthies 1995, Borowicz & Armstrong 2012).

The abundance of the below-ground resources has other effects on hemiparasites beside the increase in competitive pressure. Hemiparasites can benefit from abundant mineral macronutrients to a similar extent as non-parasitic plants by improving the efficiency of physiological processes, especially photosynthesis (Phoenix & Press 2004, Těšitel et al. 2015). This results in a more vigorous growth and greater fecundity of established individuals (Van Hulst et al. 1987, Mudrák & Lepš 2010, Těšitel et al. 2013). Some of the hemiparasitic species are able to inflict extensive damage on their hosts by inducing strong water stress at dry macronutrient-rich sites, which possibly reduces competitive pressure from the host community (Těšitel et al. 2015). Moreover, Demey et al. (2015) have demonstrated that root hemiparasites may prefer to parasitize clonal plants, which may be higher quality hosts due to resource withdrawal from the whole clonal network. In addition, damage inflicted on the clonal hosts might decrease competitive pressure of these frequently dominant competitors, thereby improving establishment success of hemiparasite seedlings (Lepš & Těšitel 2015). In general, hemiparasites are able to suppress their hosts to a variable extent (Těšitel et al. 2015) and reduce total community productivity (Ameloot et al. 2005) and thus the intensity of above-ground competition. This is one of the principal factors underlying persistence of competitively inferior, mostly annual or short-lived monocarpic perennial hemiparasites (Electronic Appendix 2) in perennial-dominated grassland communities (Strykstra et al. 2002; Fig. 7). Moderate disturbance such as grazing and mowing of meadows is another key factor reducing competition and litter production, which strongly facilitates survival of hemiparasite seedlings (Mudrák et al. 2014). In contrast, strong disturbance occurring during a hemiparasite's growth period may have fatal consequences for a population (Mudrák et al. 2014) since the regenerative ability of most species of hemiparasites is very limited (Klimešová & de Bello 2009).

Odontites luteus and *Thesium linophyllon* are the only hemiparasites of all the species studied that conform to the resource limitation hypothesis and occur in low-productive habitats stressed by macronutrient and water deficiency. In contrast to the other species studied, they are, however, unable to colonize less extreme habitats. This may be due to a trade-off between host resource conservation in extreme habitats and host suppression in more productive habitats. Although there are no ecophysiological data for either of these species, *Santalum acuminatum*, which is distantly related to *T. linophyllon* and grows in macronutrient-poor semi-desert habitats, is known to display such a hemiparasitic resource conservation strategy (Tennakoon et al. 1997).

The *Odontites vernus* group and *Pedicularis palustris* present exceptions to the resource-competition niche hypothesis that suggests sites with simultaneous high macronutrient and water availability are unsuitable. The high proportion of annuals and moderate canopy height and SLA values of habitats favourable for the *O. vernus* group indicate they are subject to high levels of disturbance, which decreases the competitive pressure (Grime et al. 1997) and allows establishment of this small-seeded (Těšitel et al. 2010b) annual hemiparasite. This was also demonstrated by Gilhaus et al. (2013) who revealed a strongly positive association between grazing and *O. vernus* dominance in floodplain meadows. In contrast, *P. palustris* grows at wet and frequently waterlogged sites where productivity might be limited by oxygen stress (Schulze et al. 2002). In addition, *P. palustris* is able to suppress tall sedges (e.g. *Carex acuta*), its principal hosts but also strongest competitors in its habitat (Decleer et al. 2013). *Melampyrum sylvaticum*, *M. pratense* and *M. nemorosum* are exceptional in their ability to grow in shaded habitats in forest understory (Fig. 5, Electronic Appendix 2). This is probably because they germinate in autumn and hibernate in epicotyl dormancy, which enables them develop quickly in spring, and have a long lifespan (for an annual), which enables them to exploit resources throughout the whole growing season (Průšová et al. 2013). Ecophysiology of forest-understory hemiparasites, in particular their energy budget, however, remains a challenging question for further research.

The mechanistic interpretation of other distinct patterns in habitat suitability is less straightforward than those dependent on below-ground resources and light availability. The suitability of sites with a cold climate for *Bartsia alpina*, *Rhinanthus riphaeus* and

Thesium alpinum might fit within the competition framework as a short growing season imposes stress on communities, which reduces competitive pressure. However, all of these species are rare and their habitat models are not robust enough to present a solid basis for mechanistic interpretations. Apparent suitability of sites with high soil pH for *Melampyrum arvense*, *M. cristatum*, *Odontites luteus* and *Thesium linophyllon* (Fig. 5) is another distinct pattern. While soil pH is one of the strongest factors affecting species richness and composition of plant communities in central Europe (Ewald 2003), its ecophysiological effect on hemiparasites remains unclear. Therefore, the association with high soil pH in these species might in fact reflect the habitat suitability of communities occurring at calcareous sites in the Czech Republic underpinned by factors (low competition, low primary macronutrient availability, low water availability) other than soil pH.

Implications for ecological restoration and conservation

The identification and description of properties of favourable habitats is crucial for restoration projects that use hemiparasites as ecosystem engineers (Pywell et al. 2004, Westbury et al. 2006, Westbury & Dunnett 2007, Hellström et al. 2011). It can facilitate decisions such as when to use hemiparasites as ecosystem engineers, which species to choose and which additional measures to apply to ensure their establishment. For instance, more intense mowing (twice per season) is likely to be necessary for establishing *Rhinanthus* species and reducing the negative effect of litter at productive restored sites close to the suitability limit (Fig. 4). However, in such cases, the first mowing should always be scheduled for after the seeds of *Rhinanthus* ripen (Blažek & Lepš 2015). In addition, our results suggest possible use of *Pedicularis palustris* and *Odontites vernus* as ecosystem engineers at wet sites with high macronutrient availability where *Rhinanthus* species cannot establish due to competition. While an ecosystem engineering role is established for *P. palustris* (Decleer et al. 2013), it has never been considered in the case of *Odontites*.

Another important message comes from the ratio between numbers of occupied and suitable sites (Electronic Appendix 2). The low values ranging between 0.05 and 0.3 recorded for many species suggest that species of root hemiparasites do not occupy most of the suitable sites. This can be ascribed to limitations on dispersal as many of the species have large seeds and have no efficient means of seed dispersal (Těšitel et al. 2010b), demographic effects limiting fitness in small populations (Schmalholz & Kiviniemi 2007, Kiviniemi 2008) and the high demographic stochasticity of hemiparasite populations (Ameloot et al. 2006). The implication for restoration projects is that an introduction of hemiparasites by sowing can be successful even at sites not occupied by any hemiparasitic species (Mudrák et al. 2014), whereas spontaneous colonization is unlikely.

The majority of the root-hemiparasitic taxa that are reported to occur or have occurred in the Czech Republic are listed in the national Red List (Grulich 2012). Some of these threatened species are listed due to their general rarity caused by the rarity of their habitats (*Bartsia alpina*, rare subalpine species of *Euphrasia*, *Pedicularis sudetica*). Most hemiparasites are Red-Listed due to a recent decline, which is probably connected with landscape-level eutrophication, intense large-scale disturbances and intensification of agriculture during recent decades. This is the case for the meadow species *Euphrasia*, *Melampyrum arvense*, *M. cristatum*, *M. nemorosum* var. *praecox*, *Odontites luteus*, *O. vernus* subsp. *vernus*, *Pedicularis palustris*, *P. sylvatica*, *Rhinanthus alectorolophus*, *Rhinanthus riphaeus* and most *Thesium* species. Both causes underlying their threatened status (rarity and decline) may be valid for some species (*Odontites luteus*, some *Thesium* species). Conservation of the former group of endangered hemiparasites requires only protection of the habitat from destruction and usually no specific management measures are needed. In contrast, the second group is dependent on the existence of sites with limited below-ground resource availability and a moderate disturbance regime, which decreases competition and promotes seedling establishment. Such sites may be fairly variable, ranging from mesic and dry grasslands (favourable for most *Orobanchaceae*) to more disturbed habitats (e.g. several *Thesium* species).

Assessment of the habitat suitability modeling approach

Our study is not the first attempt to explore plant species habitats and ecological niches using vegetation databases, functional traits and EIVs. For example, Hölzel (2003) studied the ecological niches of floodplain-meadow violets. In our study, we further developed this approach by incorporating a distinction between habitat models and ecological niches (Kearney 2006) and the species-pool concept (Eriksson 1993, Zobel et al. 1998, Münzbergová & Herben 2004). This resulted in a three-step approach consisting of building the habitat models, their description and mechanistic interpretation (Fig. 2). The distinction between these steps is crucial. The habitat models are based on an analysis of 'hard' data on species co-occurrence available in a vegetation-plot database using appropriate statistical techniques. Few compromises in the requirements of these techniques need to be made when using a stratified set of vegetation plots (Roleček et al. 2007). In the second step, the nature of the descriptions of the habitat models does not allow the use of formal statistical testing due to non-independence of the data (Zelený & Schaffers 2012). Therefore, only a graphical representation of the patterns is reported here. From this perspective, the partitioning of variation in the habitat models explained by descriptor groups might appear in conflict with the recommendation of Zelený & Schaffers (2012) not to combine individual EIVs (or functional traits) as predictors in a single analysis. However, this is not a classical statistical analysis in which predictors compete to be included in (or omitted from) the model during the model-building procedure. The final step of our approach, mechanistic interpretation of the described models aims to identify niches of species by incorporating knowledge of the ecological interactions of these species with the environment and co-occurring vegetation. Such information cannot be derived from the data in the database. Therefore, results of other experimental studies (such as those of Mudrák & Lepš 2010, Těšitel et al. 2011, 2013, Demey et al. 2015 in case of the current study) are needed to provide this essential information required for identifying their ecological niches.

See www.preslia.cz for Electronic Appendices 1–3

Acknowledgements

We are grateful to Jiří Sádlo, Andreas Demey and an anonymous reviewer for their exceptionally insightful comments on a previous version of this manuscript. We would like to thank Petr Blažek for his help with data processing and Tony Dixon for improving our English. The study was supported by the Czech Science Foundation. J. T., P. F., F. B. and J. L. were supported by project no. P505/12/1390 and M. C. by project no. 14-36079G.

Souhrn

Kořenoví poloparaziti představují specializovanou funkční skupinu rostlin. Jsou to zelené fotosyntetizující rostliny, které ale paraziticky získávají živiny z kořenů ostatních rostlin. Někteří kořenoví poloparaziti výrazně ovlivňují biotické vztahy v temperátních travinných společenstvech, zatímco jiní patří mezi druhy ohrožené vyhynutím. V naší studii jsme na základě dat z České národní fytocenologické databáze vytvořili modely vhodnosti biotopů pro kořenové poloparazity vyskytující se v České republice. Tyto modely, založené na formalizované klasifikaci vegetace, vzájemné závislosti výskytu druhů ve vegetačních třídách a aktuálním výskytu poloparazitů ve snímcích v databázi určily pro každý poloparazitický druh soubor snímků, v nichž by se tento druh mohl vyskytovat. Tento soubor snímků byl následně popsán pomocí klimatického modelu, Ellenbergových indikačních hodnot a funkčních vlastností zastoupených druhů, což umožnilo charakterizovat vlastnosti vegetace příhodné pro jednotlivé poloparazitické druhy. Díky znalostem ekofyziologických principů poloparazitismu z experimentálních studií bylo možné interpretovat vlastnosti vhodné vegetace jako faktory určující ekologickou niku zkoumaných druhů. Jednotlivé typy vegetace se svou vhodností pro různé druhy kořenových poloparazitů značně liší. Zároveň je ale téměř každý široce vymezený typ vegetace České republiky (s výjimkou vodní vegetace) ekologicky příhodný pro alespoň některý z poloparazitických druhů. Pro poloparazity je vhodná zejména vegetace přirozených nebo polopřirozených trávníků, kde se vyskytuje i největší počet poloparazitických druhů. Podobně hojní jsou poloparaziti i v lesích, ale počet druhů je zde podstatně menší a prakticky omezený pouze na druhy rodu *Melampyrum*. Většina poloparazitických druhů není schopna růst v extrémních biotopech s intenzivním stresem nebo disturbancemi. Stejně tak živinami bohatá a dostatečně vlhká místa, kde dominují rychle rostoucí, konkurenčně silné druhy, nejsou vhodná pro výskyt poloparazitů. Tato omezení vyplývají z podstaty poloparazitizmu, jehož hlavní výhodou je parazitický zisk podzemních zdrojů. Aby bylo možné tuto výhodu využít, je třeba dostatek světla a alespoň relativně příznivé podmínky pro růst. To platí zejména pro jednoleté poloparazitické druhy, které převažují v květeně ČR. Tyto ekologické nároky poloparazitů byly dříve předpovězeny matematickými modely a prokázány ve skleníkových ekofyziologických pokusech, ale naše studie ukazuje jejich platnost v krajinném měřítku. Kromě nich ale mohou jednotlivé poloparazitické druhy vykazovat různé další nároky na podmínky prostředí a růst v různých typech vegetace.

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Received 21 November 2014
Revision received 12 March 2015
Accepted 2 April 2015