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Linking species, traits and habitat characteristics of Collembola at European scale

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ABSTRACT

Although much work has been done on factors which influence the patterning of species and species trait assemblages in a variety of groups such as plants, vertebrates and invertebrates, few studies have been realized at a broad geographic scale. We analyzed patterns of relationships between species, species trait distribution/assembly, and environmental variables from the west of Europe to Slovakia, Poland and Sweden. We created a database by compiling traits and occurrence data of European collembolan species, using literature and personal field studies embracing a large range of environmental gradients (vertical stratification, habitat closure, humus form, soil acidity and moisture, temperature, rainfall, altitude) over which Collembola are supposed to be distributed. Occurrences of the 58 best-documented species, environmental variables and species traits allowed us to (i) show which environmental variables impact the distribution of the 58 species at broad scale and (ii) document to what extent environmental variables and species trait assemblages are related and which trends could be found in trait/environment relationships. The impact of vertical stratification, habitat closure, humus form, soil acidity, soil moisture, temperature, and to a lesser extent rainfall and altitude on species distribution, firstly revealed by indirect gradient analysis (correspondence analysis, CA), was further shown to be significant by direct gradient analysis (canonical correspondence analysis, CCA). RLQ analyses were performed to find linear combination of variables of table R (environmental variables) and linear combinations of the variables of table Q (species traits) of maximum covariance weighted by species occurrence data contained in table L. RLQ followed by permutation tests showed that all tested environmental variables apparently contributed significantly to the assemblages of the twelve species traits studied. A convergence was observed between traits related to vertical stratification and those related to habitat closure/aperture. Well-developed locomotory organs (furcula, legs), presence of sensorial organs sensitive to air movements and light (e.g. trichobothria and eye spots), spherical body, large body size, pigmentation (UV protection and signaling) and sexual reproduction largely occur in epigeic and open habitats, while most of woodland and edaphic habitats are characterized by short locomotory appendages, small body size, high number of defense organs (pseudocelli), presence of post-antennal organs and parthenogenesis. Climate and especially temperature exert an effect on the assemblage of traits that are mostly present aboveground and in open habitats. The contribution of combinations of some environmental variables to the occurrence of each species trait was tested by linear, logistic or multinomial regression (Generalized Linear Models). Vertical stratification, followed by temperature, played a dominant role in the variation of the twelve studied traits. Relationships between traits and environment tested here shows that it is possible to use some traits as proxies to identify potential ecological preferences or tolerances of invertebrate species. However, a significant part of species distribution remained unexplained, probably partly because some traits, like ecophysiological ones, or traits involved in biotic interactions (e.g. competition) were unavailable. The present work is thus a first step towards the creation of models predicting changes in collembolan communities. Further studies are required to inform ecophysiological traits, in order to complete such models. Moreover the niche width of species will have to be determined.

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1. Introduction

Identifying the main factors that drive the composition of communities and the distribution of species is a fundamental goal in community ecology and is of particular importance for predicting biodiversity responses to environmental changes (Belyea and Lancaster, 1999). Selection of species by habitat constraints (deterministic process) is one of the four classes of processes that influence patterns in the composition and diversity of species (Vellend, 2010). Functional traits, (named "traits" hereafter), are well-defined, measurable properties of organisms, used comparatively across species, and that strongly influence organismal performance (McGill et al., 2006). Focusing on the selection of species functional traits rather than only on species identity, allows to (1) identify mechanisms implied in the distribution of species and in the dynamics of biodiversity, (2) understand the mechanisms that shape communities comprised of many species (3) identify general patterns and hence, help to predict potential changes in the composition of communities, and consecutive ecosystem functioning, following disturbance (McGill et al., 2006; Vellend, 2010). The use of functional traits of species allowed to understand species responses to varied disturbances such as fragmentation, land use change or agricultural practices (Cole et al., 2002; Barbaro and van Halder, 2009; Ozinga et al., 2009; Vandewalle et al., 2010). For example, Ozinga et al. (2009) showed that differences between plant species in characteristics (traits) involved in dispersal processes contribute significantly to explaining losses in plant diversity in response to habitat degradation.

Species traits of diverse communities (plants, carabids, butterflies, birds, spiders) also have been shown to vary with environmental factors such as habitat fragmentation (Barbaro and van Halder, 2009), presence of planted hedgerows in highway verges (Le Viol et al., 2008), post-fire age (Langlands et al., 2011), salinity (Pavoine et al., 2011), agricultural land use and urbanization (Vandewalle et al., 2010). Nevertheless, the role of habitat constraints and dispersal abilities as filters, allowing only species with similar traits to assemble, has never been demonstrated at broad spatial scales, due to lack of suitable data, especially in soil invertebrates (Barbaro and van Halder, 2009; Decaëns et al., 2011; Makkonen et al., 2011; Pavoine et al., 2011). This may bias to a great extent the relationships between habitat preferences and species traits. Because the overall species response to habitat constraints involves trade-offs (Uriarte et al., 2012) between responses to different environmental factors (e.g. bedrock and climate, habitat openness and humidity, or temperature, or soil pH), it is easy to correlate erroneously a trait to an environmental factor. For example, the collembolan species *Heteromurus nitidus*, thought to strictly depend on soil pH since it was never found in soils at pH < 5 in North and West of France (Ponge, 1980, 1993), was later found in soils at pH < 4 in south-western mountains of France (Cassagne et al., 2003, 2004). One way of avoiding this error risk is to determine habitat preferences of species over a wide range of habitats, encompassing a variety of temperature and altitude levels, at a scale close to the geographic distribution range of the species.

Moreover, despite the abundance, high diversity and essential functional role of soil invertebrates (Hopkin, 1997; Coleman et al., 2004), trait-based approaches were not explicitly used to study species/environment patterns and processes in these animal groups (Vandewalle et al., 2010). Only studies focusing either on a restricted number of traits (especially dispersal), or of habitats have been made to assess the effects of land-use disturbance or climate change on soil communities (Ponge et al., 2006; Vandewalle et al., 2010; Decaëns et al., 2011; Makkonen et al., 2011; Bokhorst et al., 2012).

The taxonomic Class of Collembola is a good model to address such questions, because it comprises a high number of species, occupying highly diverse habitats over a broad biogeographic area (Hopkin, 1997). Moreover, some authors have hypothesized, from field observations, the existence of five or more "eco-morphological groups" based on conspicuous morphological differences among Collembola living in diverse habitats (Gisin, 1943; Delamare-Deboutteville, 1951; Rusek, 2007). They classified collembolan species according to the relationships between some morphological characteristics and different gradients of vertical stratification (edaphic, hemiedaphic, epigeic) and soil moisture (hydrophilic, xerophilic), but no attempt was made to rely statistically morphological characteristics (traits) to environmental variables. Europe, as a wide area including a high diversity of landscape and vegetation types, is a favorable terrain for exploring multivariate relationship between species trait values, assembly processes, and environmental factors.

In this study, we asked the following questions: (1) What is the pattern of relationships between species assemblages and environmental variables at broad geographic scale? (2) Which environmental variables are associated with trait variation in Europe and which environmental variables contribute to the assemblage of local communities?

To this end, we compiled a large volume of data about species traits and environmental characteristics of sites where species have been collected throughout Europe. To enable this, we created 'Coltrait', a database collating traits and occurrence data of European collembolan species across a wide range of habitats, mostly from Northwest Europe. Occurrence data and associated descriptions of samples and sampling sites were either provided by our own studies, or collected in the literature. For traits, we selected collembolan characteristics expected to explain the distribution of species and the subsequent composition of species communities through three processes that drive patterns of community composition, namely (1) Abiotic components of habitat, (i.e. environmental variables) adaptation/selection (e.g. sensorial organs, cuticle protection, reproduction type); (2) Dispersal ability (e.g. locomotory appendages); (3) Biotic components of habitat selection (predator defense, e.g. detection by sensory organs, excretion of repulsive substances).

We firstly analyzed the impact of environmental variables on the distribution of species in Europe, and then we analyzed patterns of trait/environment relationships.

2. Materials and methods

2.1. Data collection

2.1.1. Habitat characteristics and species occurrences

The Coltrait database comprises four tables that were used for the present study: a species traits table, a sample description table (environmental variables observed in samples or in sample sites to determine habitat characteristics), an occurrence/sample table and a bibliography table.

Habitat characteristics and occurrences of collembolan species in these habitats were provided either by our own studies (Ponge, 1980, 1993; Arpin et al., 1984, 1985, 1986; da Gama et al., 1994, 1997; Ponge, 2000; Loranger et al., 2001; Ponge et al., 2003; Gillet and Ponge, 2005) or were extracted from articles dealing with field studies on collembolan communities (e.g. Hågvar, 1982; Rusek, 1989, 1990; da Gama et al., 1994, 1997; Cassagne et al., 2003,