



Collembolan preferences for soil and microclimate in forest and pasture communities



Charlène Heiniger^a, Sébastien Barot^b, Jean-François Ponge^{c,*}, Sandrine Salmon^c, Jacques Meriguet^d, David Carmignac^d, Margot Suillerot^a, Florence Dubs^a

^a IRD, UMR BIOEMCO, Centre France Nord, 93143 Bondy, France

^b IRD, UMR BIOEMCO, ENS, 75006 Paris, France

^c MNHN-CNRS, UMR 7179, 91800 Brunoy, France

^d ENS, UMR BIOEMCO, ENS, 75006 Paris, France

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ABSTRACT

The goal of the present study was to determine whether the habitat preference of collembolan species is more influenced by soil properties or by microclimate and whether the preference for a given soil matches the preference for the corresponding microclimate. To answer these questions, we set up a soil core transfer experiment between a forest and an adjacent pasture. We first eliminated the entire soil fauna from forest and pasture soil cores and inoculated them with a new community originated from forest or pasture. After enclosing them, in order to prevent exchanges of soil animals between treated soil and surrounding environment, soil cores were transplanted back to the field for four months and a half. The experimental design comprises every combination of three factors (community origin, soil nature and microclimate) for a total of 8 treatments. Twenty-two species were present in the experiment, 16 of which were present in more than 10% of the experimental soil cores. We determined habitat preference for these 16 species using a large dataset comprised of field observations in the same region. Results showed that most forest species did not withstand pasture microclimate, although some of them preferred pasture soil. Likewise several pasture species were favoured by the forest microclimate, some of them also preferring forest soil. We concluded that forest species were absent (or less abundant) in pastures because they are not resistant enough to drought, while pasture species were absent (or less abundant) in forests because of food requirements, and/or soil physicochemical properties such as soil pH and organic carbon content, and/or were less competitive. Moreover, when selecting their habitat, some species are submitted to a trade-off between preferences for different habitat features.

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1. Introduction

The search for unifying principles in community ecology led to the identification of three processes that interact to shape species assemblages: 1) habitat selection, 2) dispersal and 3) biotic interactions (Weiher and Keddy, 2001; Wardle, 2006; Mayfield et al., 2009). Understanding the factors that determine the preference of a species for a given habitat is thus essential to predict species distribution and local community composition. In most habitats, many different factors (biotic and abiotic) interact, creating environmental conditions that allow or impede species persistence and

reproduction (Bull et al., 2007). Furthermore, different species show different levels of specialization for a given habitat, from specialists which are only found in a restricted array of environmental conditions to generalists which are found in a wide array of environmental conditions (Egas et al., 2004; Julliard et al., 2006). The extent to which a species is specialist of a given habitat probably depends on how much it is adapted to the different habitat features and the level of specialization is likely to differ between habitat features.

For invertebrate species inhabiting soil and litter layers, habitat is at least twofold. First, the nature of the soil and the humus form are very influential: (1) they determine the availability and quality of resources such as organic matter, which in turn determines the composition and activity of microbial communities, one of the main food sources of soil invertebrates (Ponge, 1991; Murray et al., 2009;

* Corresponding author. Tel.: +33 6 78930133.

E-mail address: ponge@mnhn.fr (J.-F. Ponge).

Sabais et al., 2011); (2) soil and humus through several physico-chemical properties, such as pH, moisture, structure, carbon content, etc., are critical parameters for collembolan survival (Ponge, 1993; Berg et al., 1998; Loranger et al., 2001). Second, the type of vegetation is also influential: (1) it influences the quality and quantity of organic matter inputs; (2) it influences the local microclimate and interacts with soil and humus to determine temperature and moisture levels which prevail within the soil (Chen et al., 2008; Ponge, 2013). For example tree canopy cover in forests prevents most UV radiation from reaching the ground surface and creates lower soil temperatures in forests compared to pastures (Scott et al., 2006).

Collembolan communities have been shown to vary according to vegetation types, e.g. open vs closed vegetation (Ponge et al., 2003; Vanbergen et al., 2007). Forests (closed vegetation) benefit from high inputs of litter which create thick organic (and organic-mineral) layers. High soil carbon content induces both low pH and high soil moisture and creates conditions favouring overall collembolan abundance and diversity (Hopkin, 1997). In addition, high organic inputs in forests provide abundant trophic resources. In contrast, open vegetation (e.g. any habitat without trees such as pastures or meadows) is characterized by intense export through mowing, grazing, or harvesting, and more active decomposition, which induces lower organic contents and reduced or absent organic layers (Compton and Boone, 2000). Additionally, the absence of tree cover induces higher temperatures in summer and lower soil moisture than in forests (Batlle-Aguilar et al., 2011). Thus, in collembolan communities, specialists of a given habitat should be intolerant to at least one feature of non-preferred habitats (microclimate, resource quality and/or availability, physicochemical factors): for example, forest specialists should be intolerant either to soil properties or microclimate of open habitats. In contrast, generalist species should be generalist for both soil and microclimate.

In their experiment, Auclerc et al. (2009) determined habitat preference and dispersal ability of a large set of collembolan species. Using a soil transplant experiment between a forest and a meadow, they showed that several forest-preferring and forest-strict species actually colonized more efficiently meadow soil transferred to forest than non-transferred forest soil. They suggested that certain forest species, more abundant in the transplanted meadow soil, could not survive in the meadow because of its microclimate. However, in their study the effect of species ability to colonize both soil types through dispersal was difficult to distinguish from the effects of actual preferences for a given habitat. Moreover, Auclerc et al. (2009) only transplanted soil cores from one type of habitat to another but did not submit collembolan communities to a different microclimate. This did not allow a full disentanglement of the effects of soil and humus nature from the effects of microclimate determined by plant cover.

The present experiment thus aimed at addressing the two following questions. Are forest or pasture species excluded from (or less abundant in) pastures and forests, respectively, because they do not withstand differences in temperature and related soil moisture (microclimate) in these habitats, or because they do not find appropriate trophic resources and suitable physicochemical conditions (soil nature)? Are generalist species tolerant to both soil and microclimate? We hypothesize that forest and pasture species are not primarily influenced by the same habitat features. Forest species would be absent (or less abundant) in pastures because of physiological requirements for forest microclimate (i.e. higher humidity and lower temperature) whereas pasture species would be absent (or less abundant) in forests because they do not find appropriate trophic resources in them.

Given our choice of a transfer experiment in which animals cannot freely move to find suitable conditions for their growth and

reproduction, preferences will be only inferred from their ability to survive and multiply better under certain conditions than others. This is also the sense given to the word “affinity” in similar experiments (Huhta, 1996) but we here refer to the definition given by Pey et al. (2014) of “ecological preference” as “the optimum and/or the breadth of distribution of a trait on an environmental gradient”, considering “ecological preference” as the result of multiple interacting ecophysiological traits each species display and “habitat preference” as a subset of “ecological preference”.

2. Material and methods

2.1. Study site

The study was set up in a forest and an adjacent pasture in the Morvan Regional Natural Park at the same location as the experiment reported in Auclerc et al. (2009). The Morvan Natural Park is located in the centre of France (Burgundy) and has a submontane-atlantic climate with continental influence (mean annual rainfall 1000 mm and mean temperature 9 °C). The bedrock is granite and soils are moderately to strongly acidic (pH < 5). The forest canopy is comprised of deciduous trees (*Fagus sylvatica* and *Quercus petraea*) and has been in place over at least a century, according to stand structure. The forest soil is an Acrisol and the humus form is a dysmoder sensu Brêthes et al. (1995). The nearby pasture used to be mowed every year in spring and then grazed by cattle in summer and autumn, but mowing had been abandoned for several years because of poor forage production due to several consecutive drought years. The pasture soil is a Cambisol and the humus form is an eumull. The transition between forest and pasture is sharp.

2.2. Experimental design and soil core manipulation

We designed a soil core transplantation experiment between forest and pasture (closed vs. open vegetation, respectively) coupled with a manipulation of invertebrate communities. Eight treatments (five replicates each) corresponded to all possible combinations of three factors: community origin, COM (forest vs. pasture), soil origin, S (forest vs. pasture) and microclimate, CLIM (forest vs. pasture) (Fig. 1, see also Fig. 2 for a global view of manipulation steps). The setup took place between March and June 2011 (fauna removal, inoculation and transplantation) and the experiment ended in the beginning of November 2011.

2.2.1. Fauna removal and re-inoculation

In order to control the communities present in both soils (forest and pasture), we first removed the fauna and re-inoculated it with a new community extracted from a fresh soil core. This allowed us to have a forest community in the pasture soil and conversely a pasture community in the forest soil. Thirty soil cores (20 cm diameter × 10 cm depth) were taken in both forest and pasture (60 soil cores in total, i. e. the soil, including the soil biota, was sampled by taking of soil samples) and brought back to the laboratory. Soil fauna was then eliminated by repeatedly freezing soil cores. Each soil core was dipped in liquid nitrogen for 45 min. This was repeated after a week interval, in order to eliminate possible resistant eggs that could have been stimulated to hatch by the first freezing. In between, soil cores were stored in a cold chamber at 15 °C.

We then inoculated each soil core with a new community. To do so, 48 soil cores (24 for each soil) of the same volume (20 cm diameter × 10 cm depth) were taken at the same site. These cores were split into four equal parts in the field, packed into semi waterproof bags (plastic bags with holes allowing gas exchanges) and brought back to the lab within two days. They were

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