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How do patch quality and spatial context affect invertebrate communities in a natural moss microlandscape?

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ABSTRACT

Globally, moss associated invertebrates remain poorly studied and it is largely unknown to what extent their diversity is driven by local environmental conditions or the landscape context. Here, we investigated small scale drivers of invertebrate communities in a moss landscape in a temperate forest in Western Europe. By comparing replicate quadrats of 5 different moss species in a continuous moss landscape, we found that mosses differed in invertebrate density and community composition. Although, in general, richness was similar among moss species, some invertebrate taxa were significantly linked to certain moss species. Only moss biomass and not relative moisture content could explain differences in invertebrate densities among moss species. Second, we focused on invertebrate communities associated with the locally common moss species *Kindbergia praelonga* in isolated moss patches on dead tree trunks to look at effects of patch size, quality, heterogeneity and connectivity on invertebrate communities. Invertebrate richness was higher in patches under closed canopies than under more open canopies, presumably due to the higher input of leaf litter and/or lower evaporation. In addition, increased numbers of other moss species in the same patch seemed to promote invertebrate richness in *K. praelonga*, possibly due to mass effects. Since invertebrate richness was unaffected by patch size and isolation, dispersal was probably not limiting in this system with patches separated by tens of meters, or stochastic extinctions may be uncommon. Overall, we conclude that invertebrate composition in moss patches may not only depend on local patch conditions, in a particular moss species, but also on the presence of other moss species in the direct vicinity.

1. Introduction

With over 12,000 moss species described (Goffinet and Buck, 2004), bryophytes are a diverse group of plants that cover over 250 million hectares of our planet's surface (Bond-Lamberty and Gower, 2007). By housing nitrogen fixing cyanobacteria (DeLuca et al., 2002; Lagerström et al., 2007) and capturing organic debris, mosses play an important role in the carbon and nitrogen cycle (Lindo and Gonzalez, 2010; Turetsky, 2003). Furthermore, mosses also form microhabitats for a diverse set of other organisms that remain poorly studied. Besides associated fungi and micro-organisms, the invertebrate bryofauna forms the dominant component of a complex detrital food web (Hunt et al., 1987). Oribatid and prostigmatid mites and springtails are the most abundant decomposers of organic material in moss ecosystems (Block, 1982). These, in turn, are the main food source for mesostigmatid mites (Crotty et al., 2014) and many larger arthropods including centipedes (Chilopoda), spiders (Arachnida) and rover beetles (Staphylinidae). The combination of above and belowground tissues of mosses, their associated organisms and processes has been defined as the bryosphere (Lindo and Gonzalez, 2010). Recent surveys continue to expand the list of species representing the global bryofauna (Anderson, 2006; Boeckner et al., 2006; Lindo, 2009). However, worldwide relatively few areas have been surveyed and reported diversities are underestimations due to the paucity of taxonomical literature and difficulties with species delineation in speciose groups such as oribatid mites (Borcard et al., 1992).

Although moss fauna surveys are relatively scarce, mosses are regularly used in ecological experiments. The typical patchy nature of the habitat, in combination with the ease of manipulation, has stimulated their use as natural model systems for studying spatial and temporal community dynamics (Srivastava et al., 2004; Turetsky, 2003). Mosses grow on different substrates including soil and live or dead wood. From an ecological perspective, moss patches on dead tree trunks are interesting habitats because they can be quite isolated from other patches in the surrounding landscape matrix. Currently, research on bryofauna is mainly confined to northern regions including tundra areas and conifer

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forests (Chapin et al., 1987; Jonsson et al., 2015; Schwarz et al., 1993; Skubaa and Gulvik, 2005; Usher and Booth, 1986). Yet, little is known about invertebrates associated with moss in temperate and (sub)tropical forests. In addition, most current research has focused on experiments in semi-natural conditions, while datasets that can associate species distribution patterns to environmental conditions, spatial location and the landscape context are still scarce (Caruso et al., 2013; Gerson, 1982; Jonsson et al., 2015).

Mosses commonly occur in patches as a mixture of species. This could potentially promote animal biodiversity, either by increasing habitat heterogeneity, as shown by Heikkinen et al. (2004) or when moss species with typical infauna boost the diversity in neighboring moss vegetation due to a flux of dispersing invertebrates that would otherwise not be able to persist there. Indications for such so called mass effects, however, have only been found in experimental semi-natural moss patch systems (Chisholm et al., 2011). Finally, moss species richness may also promote invertebrate biomass and diversity via increased water retention capacity of a moss patch if the complementarity of competing moss species results in denser growth and improved capillarity of the rhizoids (Michel et al., 2012).

Although mosses and several of the organisms that inhabit them, can survive desiccation (Carleton and Dunham, 2003), most of the invertebrates strongly depends on moisture for growth and reproduction. Therefore, the ability of different moss species to retain water might be an important variable explaining the community composition of moss inhabiting invertebrates. In addition, the mainly detritivorous invertebrates also predominantly depends on leaf litter input as the primary food source. As such, canopy cover which modulates both leaf litter input and evaporation is likely to be linked to the abundance and richness of moss invertebrate communities on the forest floor. However, this has been poorly investigated (but see Suominen et al., 1999; Eissfeller et al., 2013; Leonard et al., 2017). Whether certain moss species are more likely to house specific invertebrate taxa also remains largely obscure (Jonsson et al., 2015).

In this study, we aimed to assess the importance of several rivalling drivers of moss invertebrate composition in a Western European deciduous forest habitat. Using both a continuous mat landscape of moss and a more isolated set of moss patches on dead tree trunks, we tested whether invertebrate diversity and community composition are dominantly driven by habitat characteristics provided by different moss species or by the landscape context including patch isolation and the presence of multiple co-occurring moss species. To this end, we combined survey data with experimental measurements of water retention in different moss species.

Our first objective was to determine whether invertebrate communities inhabiting several common moss species differ in richness, abundance or species composition. Second, we verified whether potential differences in invertebrate composition among moss species are linked to their species-specific water content. Third, we wanted to determine whether small scale spatial community patterns of invertebrate in isolated moss patches support predictions of classical island biogeography theory (IBT) and metacommunity ecology. If so, variables such as patch size and connectivity should be important predictors of the invertebrate community composition (Holyoak et al., 2005; Leibold et al., 2004; Logue et al., 2011; MacArthur and Wilson, 1967). Alternatively, invertebrate diversity and abundance might depend more on environmental conditions such as canopy cover and habitat heterogeneity.

2. Methods

In the first field survey of the study, we contrasted abundance, diversity and composition of the invertebrate fauna associated with five different moss species that co-occur in mats on the forest floor. We hypothesized that some mosses would house more individuals and more or different invertebrate taxa than others and that differences in water retention ability might be an important underlying explanation. For this, we collected a total of 40 moss samples belonging to five different species (8 replicates per species) in the Sonian forest (Zoniënwoud; 50.798N 4.486E) in Jezus-Eik (Belgium) on March 22nd, 2016. As samples, we collected 10 cm × 10 cm quadrats of five moss species by cutting them out of larger moss cushions. Most of the collected species formed a layer above the litter and were easy to extract: *Kindbergia praelonga* (Hedw.) Ochyra (1982), *Rhytidiadelphus squarrosus* (Hedw.) Warnstorf (1906), *Brachythecium rutabulum* (Hedw.) Bruch, Schimper & Gümbel (1853), *Pseudoscleropodium purum* (Hedw.) Fleischer ex Brotherus (1925). Only *Polytrichum formosum* Hedwig (1801) rooted itself into the soil with extended rhizoids. Samples were transported to the lab in individually sealed, plastic bags.

In the lab, the invertebrate communities of 20 samples (5 moss species × 4 replicates) were extracted using individual Berlese-Tullgren funnels (Caruso et al., 2013; Edwards, 1991). Moss patches were put on a 1 cm × 1 cm metal grid in a funnel which was put on top of a 300 mL glass jar with 50 mL of 70% ethanol. Then, the funnel was placed under a 60Watt lamp for 12 h. The heat of the lamp forced the invertebrates to move in the opposite direction and, intoxicated by the alcohol fumes, they then fell in the jar filled with ethanol solution which preserved them. All invertebrates were counted and identified using a 40× magnification stereomicroscope (MOTIC SMZ-171) and a 100× magnification microscope (Leica DMIC).

The other set of twenty samples (5 moss species × 4 replicates) was used to quantify the actual and relative water content and the initial weight of the moss samples. Also dry weight and the maximum water content were measured for each sample, yet these variables were strongly correlated to the actual water content (all correlation coefficients $r \geq 0.93$). Therefore, we just used actual and relative water content as measures for the water content of the mosses in all analyses. After being transported in sealed bags to maintain their humidity, the samples' initial weight was measured in the lab. Next, we sprayed the moss patches extensively with water and put them for 24 h in a humid, warm room, in a closed box with a layer of water at the bottom. Then, samples were weighted again after maximum saturation. Afterwards, they were placed at room temperature with moderate humidity for drying until they reached their equilibrium dry weight. Actual and maximum water content were calculated by subtracting dry weight from initial and saturated weight respectively. Relative water content was calculated as the actual water content divided by the initial weight.

In the second field survey of this study, we explicitly considered the landscape context. For this, we focused on one focal moss species (*Kindbergia praelonga*) that occurs in isolated patches on dead beech trunks in another section of the same forest. The trunks are remnants of a forest stand that was cut approximately 25 years ago and moss patches on top of these trunks are therefore relatively young, compared to moss patches on the floor of the forest. In this part of the forest, moss patches are quite isolated because they can only grow on trunks as the soil is covered by a dense layer of dead beech (*Fagus sylvatica*, Linnaeus 1753) leaves (Appendix A). We assessed the relative importance of patch size (surface area of the moss patch), - heterogeneity (richness of moss species in the patch), trunk height (elevation of moss patch above forest floor), canopy cover (completely covered or half open) and connectivity (Probability of Connectivity Indices, explained below) on patterns of invertebrate abundance and diversity. Often, other moss species than the focal species co-occurred on these tree trunks and we aimed to test whether moss diversity in the patch potentially promoted invertebrate diversity in the sampled *K. praelonga* quadrats. To test these questions, additional samples were taken in a different location in the Sonian forest (Zoniënwoud; 50.799N 4.486E) on April 13th, 2016. We collected 32 moss samples (10 cm × 10 cm) on trunks of different patch size, trunk height, canopy cover and moss diversity. All trunks contained *K. praelonga* which was the focal species of this survey and therefore the only species that was sampled. The second most common species on the trunks was *B. rutabulum*. Less encountered species were