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Vertical stratification of invertebrate assemblages in water-filled treeholes of a temperate deciduous forest

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Abstract

Water-filled treeholes provide temporal habitats and resources to detritus-based aquatic organisms in the above-ground forest strata. Treeholes are found at different vertical positions, and are often surrounded by dense understory vegetation, which may affect water volume and litter weight. Differences in water volume and litter weight are indicative of the habitat quantity and the quality of treehole communities. Therefore, in the present study, we used containers as artificial treeholes to examine the effects of these characteristics on treehole invertebrate assemblages in a broad-leaf deciduous forest in central-eastern Japan. We first generated two models: a direct-effect model that reflected the physical and chemical properties of treeholes (water volume, litter weight, and other measurable properties that might directly influence invertebrate survival and fitness); and an indirect-effect model that reflected the differences in vertical position and surrounding understory vegetation *per se*. We compared these models and found that species richness is better explained by the direct-effect model, whereas the indirect-effect model plausibly explains the differences in invertebrate abundances. Further analyses revealed that some species such as *Tripteroides bambusa* utilized lower treeholes, while higher treeholes had a greater abundance of Ceratopogonidae sp. A within dense understory vegetation. Our study demonstrates that treehole invertebrates are not only influenced by simple physicochemical properties, but also by ambient conditions. However, the response patterns were highly variable across species. Our approach provides insight for elucidating the key drivers of treehole detritivore diversity in vertically stratified environments.

Keywords: Mosquito; Phytotelmata; Treehole height; Understory vegetation

Introduction

The vertical positions of microhabitats determine the spatial distribution patterns of invertebrate assemblages (Basset, Hammond, Barrios, Holloway, & Miller 2003; Shaw 2004; Ulyshen 2011). In arboreal environments, habitat patches such as bryophytes, epiphytes, and treeholes (Shaw 2004; Sillett & Antoine 2004) are distributed across different vertical positions, and these patches provide important habitats for several vertebrate and invertebrate species (McCune 1993; Lindenmayer, Cunningham, Pope, Gibbons, & Donnelly

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2000; Whitford 2002; Krömer, Kessler, & Gradstein 2007; Fayle, Chung, Dumbrell, Eggleton, & Foster 2009). Biotic and abiotic factors vary along the vertical gradients of forests (Parker 1995; Ulyshen 2011), consequently influencing the distribution patterns of terrestrial organisms inhabiting arboreal habitat patches (Rodgers & Kitching 1998; Yoshida & Hijii 2005; Lindo & Winchester 2013). In the aboveground forest strata, water-filled treeholes provide habitats for detritus-based aquatic invertebrates by retaining rainwater and food resources (e.g., litter) (Kitching 1971). Treehole communities depend on the quality, quantity, and temporal fluctuations of allochthonous resources (i.e., food and water), which may be affected by forest structure characteristics (e.g., foliage availability) and the vertical position of the treeholes.

Although several studies have examined the vertical distribution of aquatic invertebrates (Scholl & DeFoliart 1977; Sinsko & Grimstad 1977; Lounibos 1981; Copeland & Craig 1990; Yanoviak 1999; Derraik, Snell, & Slaney 2005), little attention has been paid to the community structure in relation to environmental factors associated with vertical gradients (but see Blakely & Didham 2010). Species richness and the abundance of aquatic invertebrates are known to be influenced by abiotic factors such as drought susceptibility at higher strata (Yanoviak 1999; Blakely & Didham 2010) and the incursion of soil from rain splashes at or near the forest floor (Kitching 1971). Moreover, the understory vegetation may provide extra litter (Gilliam 2007; Welch, Belmont, & Randolph 2007) and intercept sunlight (Messier, Parent, & Bergeron 1998; Aubin, Beaudet, & Messier 2000), which could potentially affect treehole habitat conditions and the resulting structure of treehole faunal communities.

The effects of these abiotic factors associated with vertical gradients can be quantified using two models. A direct effect model reflects the physicochemical properties of treeholes (e.g., water volume, litter weight, and other measurable properties), which may directly influence the survival and fitness of individuals. In contrast, an indirect effect model reflects the differences in vertical position and surrounding understory vegetation *per se*, which encompasses variation in physicochemical (including variables in the direct-effect model) plus other unmeasured characteristics (e.g., habitat detectability and predation rate) that may influence the reproductive success, immigration, and extinction of treehole communities.

The direct effect model is related to the more individuals hypothesis (MIH) proposed by Srivastava and Lawton (1998), as treehole productivity is a parameter of the direct effect model. This hypothesis postulates that a habitat with higher productivity supports a large number of individuals, which reduces extinction risks of individual species, thereby resulting in higher species richness. The MIH was, however, rejected by the same authors (Srivastava & Lawton 1998), as their study found that treehole productivity was correlated with species richness, but not total abundance of aquatic insects. In contrast, another study by Yee and Juliano (2007) supported the MIH, as they found a significant indirect effect of treehole productivity through abundance on species richness of aquatic invertebrates.

In the present study, we used cylindrical containers as artificial treeholes to examine the effects of treehole height and understory vegetation on the aquatic assemblages. Our aim was to determine whether physicochemical properties, which have often been measured in previous studies, are sufficient to explain the variation in invertebrate community structures (direct effect model), or whether such community dynamics can be explained by unmeasured or unmeasurable properties related to habitat differences (indirect effect model). Artificial treeholes were used to standardize environmental factors such as habitat history, size, and initial resource quality and quantity, while attracting a similar set of species as natural systems (Yanoviak & Fincke 2005). We set these artificial treeholes at different vertical positions within habitats with dense or sparse understory vegetation to test the following hypotheses: (1) species richness and total abundance are explained by the different models; (2) habitat type (dense/sparse understory vegetation), height, and seasonality all, but differently, affect community composition and spatial distribution patterns of invertebrate species because of differences in habitat requirements and the life cycles of individual species.

Materials and methods

Site description

A field experiment was conducted in a broad-leaf deciduous forest in Karasawayama (36°21′N, 139°36′E), in the Kanto Plain of central Japan. This area is categorized as a monsoon Asian climatic zone with relatively high and low precipitation occurring June–September and December–January, respectively. Annual air temperature and precipitation in the study area averaged 13.9 °C and 1244.7 mm, respectively (1981–2010, Japan Meteorological Agency 2017). During the study period, the amount of precipitation was notably higher from July to September, but was very low in mid-October (see Supplementary Appendix A: Fig. 1). The forest is dominated by *Quercus serrata* Thunb., with a mean tree height of approximately 20 m. Dwarf bamboo was approximately 2 m high, and it was patchily distributed as understory vegetation. For comparison with the present study (in which we used artificial treeholes), we conducted preliminary surveys of natural treeholes in the Kanto Plain (see Supplementary Appendix B for more details).

Vertical stratification and presence of understory vegetation

On June 1, 2011, we selected 27 and 24 *Q. serrata* trees in dense and sparse understory vegetation habitats, respectively. Tree diameters ranged between 177 and 104 cm, and