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Unravelling the correlates of species richness and ecological uniqueness in a metacommunity of urban pond insects

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ABSTRACT

City ponds have the potential to harbour a rich biodiversity of aquatic insects despite being located in an urban landscape. However, our current knowledge on the correlates of pond biodiversity is limited and even less is known about the factors that influence the ecological uniqueness of urban ponds. The multiple environmental gradients, at different spatial scales, that may affect biodiversity and ecological uniqueness of urban ponds can thus be seen both as an opportunity and as a challenge for a study. In this study, we aimed to fill this gap by focusing on aquatic insect assemblages in 51 ponds in the Swedish city of Stockholm, using a metacommunity perspective. We found that species richness was primarily determined by the density of aquatic insects, water depth and proportion of buildings around the pond. The uniqueness of ponds was estimated as local contributions to beta diversity (LCBD), and it was primarily related to the proportion of arable land and industry around the ponds. With regard to the metacommunity we found two interesting patterns. First, there was a negative relationship between richness and LCBD. Second, biodiversity was spatially independent, suggesting that spatially-patterned dispersal did not structure species richness or LCBD. These last two patterns are important when considering conservation efforts of biodiversity in city ponds. We hence suggest that the conservation of insect biodiversity in urban pond should consider the surroundings of the ponds, and that high-richness ponds are not necessarily those that require most attention because they are not ecologically the most unique.

1. Introduction

Metacommunity ecology, a recently-emerged branch of ecology, aims to find underlying causes for variation in biodiversity across a landscape. Current ideas in metacommunity ecology emphasize that not only local environmental conditions (e.g. productivity, ecosystem size and predation pressure) but also dispersal between localities affect biodiversity (Leibold et al., 2004). Disentangling the roles of environmental conditions and dispersal for biodiversity may be difficult (Cottenie, 2005), since it requires dispersal proxies (Jacobson and Peres-Neto, 2010) and because there might be spatial autocorrelation in local environmental conditions and biological data (Pinel-Alloul et al., 1995). However, provided that there is low spatial autocorrelation in environmental conditions, two scenarios can be expected with regard to the roles of local environmental conditions and dispersal in affecting biodiversity. First, if species are able to track environmental heterogeneity, then we should see hot-spots and cold-spots in biodiversity scattered across the landscape. Second, if dispersal limitation is important, then we should see spatial structure in biodiversity, such that localities situated far from each other harbour different levels of biodiversity partly irrespective of local environmental conditions (Heino et al., 2015). Here, we focus on two aspects of biodiversity (i.e. species richness and ecological uniqueness of a biological community) and examine spatial patterns in an insect metacommunity of urban ponds.

Freshwaters harbour very high levels of biodiversity in relation to the areal extent they cover (Dudgeon et al., 2006). Biodiversity in freshwater ecosystems is affected by factors operating at both local and landscape scales (Allan, 2004). Natural local factors

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of importance to biodiversity include the classical effects of area (i.e. increasing species richness with increasing ecosystem size; MacArthur and Wilson, 1967; Sepkoski and Rex, 1979), habitat heterogeneity (i.e. higher species richness with increasing habitat heterogeneity; e.g. Stein et al., 2014) and passive sampling (i.e. a higher number of individuals sampled results in higher species richness; e.g. Kuusela (1979). A positive relationship between species richness and number of individuals may also arise due to relevant ecological processes because high population sizes are associated, for instance, with high resource availability and low rates of local extinction (Gotelli and Colwell, 2001).

Other typical factors affecting biodiversity in freshwater ecosystems include nutrients (i.e. species richness either increasing or decreasing with nutrients levels; e.g. Heino, 2009) and acidity (i.e. species richness is typically lower in acidic freshwater ecosystems; e.g. Brönmark and Hansson, 2005). Also, landscape degradation, including conversion of riparian forest to agricultural and urban land-uses, may affect biodiversity in freshwater systems (Allan, 2004; Smith et al., 2009). While such effects of local and land-use factors have been extensively studied in stream systems (Sandin and Johnson, 2004; Heino et al., 2007), few studies have focused on their relative roles in urban freshwater systems (Goertzen and Suhling, 2013; Teittinen et al., 2015).

Urban landscapes are typically complex mixtures of built-up areas, roads, parks and green corridors (Goertzen and Suhling, 2013), contributing to environmental heterogeneity and dispersal routes for species (Smith et al., 2009). Urbanization may either decrease or increase environmental heterogeneity of urban ecosystems, such as freshwaters, which may have important consequences for biodiversity (McKinney, 2006; Hassall, 2014). Freshwater ecosystems in urban landscapes are also to some degree isolated from each other by not only spatial distances but also by degraded riparian zones, roads and built-up areas unsuitable for dispersal between localities. However, these issues have been little studied so far (Smith et al., 2009). Taken together, it is still premature to suggest generalities as to the roles of environmental conditions and dispersal for freshwater biodiversity in urban landscapes.

Urban ponds are a special type of freshwater ecosystems (Chester and Robson, 2013). Biodiversity of urban ponds varies much but is often surprisingly high (Hassall, 2014), and it may sometimes be comparable to that found in natural freshwater ecosystems (Hassall and Anderson, 2015). For example, studying stormwater management ponds in the Canadian city of Ottawa, Hassall and Anderson (2015) found that macroinvertebrate diversity was roughly similar to that in more natural ponds. Goertzen and Suhling (2013) found that dragonfly species richness varied from zero to 17 in urban ponds in the German city of Dortmund, and that species richness was mainly related to aquatic vegetation in and terrestrial vegetation surrounding a pond. These studies also underscore the importance of urban ponds in maintaining biodiversity (Goertzen and Suhling, 2013) and providing ecosystem services, as well as aesthetic and educational value (Hassall, 2014).

Biodiversity in urban ponds has rarely been studied from a metacommunity perspective. We aimed to fill this gap by focusing on aquatic insect assemblages of ponds in an area of the Swedish city of Stockholm. Stockholm harbours ca. 100 ponds, which are typically located in parks or less populated areas of the city. Specifically, we focused on the spatial patterning and determinants of species richness (i.e. number of insect species in a pond) and ecological uniqueness (i.e. the contribution of a locality to total beta diversity; see Legendre and De Cáceres, 2013). Our aim was to disentangle the roles of environmental conditions measured at different scales (in-pond and land use variables) underlying biodiversity variation in an urban landscape. We hypothesised that insect biodiversity would be primarily determined by local environmental variables, as has been found in more natural lentic (e.g. Heino, 2013) and lotic freshwaters (e.g. Landeiro et al., 2012), and suggested by findings from urban ponds (e.g. Goertzen and Suhling, 2013). However, we also expected that land use and geographic position affect biodiversity.

2. Methods

2.1. Study area

Our study was conducted in the core area of the city of Stockholm, capital of Sweden, and includes 51 ponds (i.e. covering all ponds) in the northern half of the city (Fig. 1). The sampled area covers 50% of the city area and should thus be representative for the whole city. The city has ca. 900 000 residents, but the metropolitan area is home to approximately 1.5 million inhabitants. We defined city ponds as natural or man-made water bodies with an area between 2 m^2 and 2 ha and holding water for at least 4 months of the year (Biggs et al., 2005). Ponds were selected from maps and by using information from municipalities' officials. Since our focus was on the densely-populated areas in the city, we divided Stockholm into 1×1 km squares and only considered squares where > 75% of the area is covered by developed area as defined in a terrain map (Terrängkartan^{TM}) of the Swedish mapping, cadastral and land registration authority (Lantmäteriet). Hence, ponds located in golf courses or large forested areas, most often situated outside the populated areas, were not included, even though these golf courses have shown a great potential for fostering biodiversity in urban areas (Colding et al., 2009). All ponds were sampled in May or June 2013 and 2014, and the resulting database was originally used to study the effects of socio-economic factors and management on biodiversity (Malgorzata et al., 2016a, 2016b). However, those two studies did not study metacommunity aspects and beta-diversity patterns as we do here.

2.2. Local variables

The following local environmental variables were measured for each pond: area, maximum depth, pH, total phosphorus (total P), total nitrogen (total N), total organic carbon (TOC), and macrophyte cover, and presence/absence of fish and newts. These variables have been shown to affect biodiversity in many rural ponds and were therefore selected in this study on urban ponds (e.g. Hassall et al., 2011). Pond area was estimated from the Terrängkartan^{TM} map from Lantmäteriet (The Swedish mapping, cadastral and land registration authority) using the software ArcGIS 9 (Environmental Systems Research Institute, 2009), and water depth with a ruler in the deepest part of the pond. Water chemistry variables were sampled in May-June 2013/2014 and analysed at the Limnology laboratory at Uppsala University. Macrophyte cover was estimated visually in August in units of 10, ranging from 0 to 100% of cover and included submerged, floating and emergent vegetation. Initially the presence/absence of fish and newts were also included, but they were removed from the dataset since they did not affect species richness or LCBD.

2.3. Land use variables

The following land use or landscape variables were estimated: distance to the nearest pond, and the land cover variables percentage of water, forest (deciduous + coniferous), area with buildings (low rise + high rise buildings), area with industry and arable land. Past studies have shown that many of these variables affect terrestrial biodiversity (e.g. McKinney, 2008), but few studies have used them for urban pond biodiversity. They were retrieved from the