Diving Beetle (Coleoptera: Dytiscidae) Community Dissimilarity Reveals How Low Landscape Connectivity Restricts the Ecological Value of Urban Ponds

Wenfei Liao (wenfei.liao@helsinki.fi)
University of Helsinki: Helsingin Yliopisto https://orcid.org/0000-0002-1583-0408

Stephen Venn
University of Helsinki: Helsingin Yliopisto

Jari Niemelä
University of Helsinki: Helsingin Yliopisto

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Abstract

Context: Structural and functional connectivity, as subconcepts of landscape connectivity, are key factors in biodiversity conservation and management. Previous studies have focused on the consequences of connectivity for populations of terrestrial organisms, which may not be appropriate for aquatic organisms.

Objectives: As landscape connectivity critically affects the potential value of ponds for biodiversity, here we used diving beetles (Dytiscidae), an indicator taxon of wetland biodiversity, to investigate how structural connectivity affects functional connectivity to aquatic invertebrates in an urban landscape.

Methods: We assessed pairwise similarities of dytiscid community, i.e. the variation of species composition between clustered and isolated ponds in the Helsinki Metropolitan Area, Finland. We investigated how dytiscid community similarity is affected by Euclidean distances between ponds, as an indicator of structural connectivity.

Results: We found that clustered ponds shared more species than isolated ponds. Dytiscid species community similarity responded negatively to increasing Euclidean distance between ponds. Effectively dispersing species were widely distributed across the landscape, while poor dispersers were scarcely distributed in the same landscape.

Conclusions: Structural connectivity determines which species are able to disperse successfully, with poor dispersers restricted to well-connected ponds. The different responses of effective dispersers and poor dispersers to the same structural connectivity indicates that functional connectivity determines species composition. We recommend providing well-connected aquatic habitats in urban landscapes and the implementation of measures to reduce isolation of wetland assemblages. Even clustered ponds need dispersal from other habitats to ensure their contribution to urban biodiversity.

Introduction

Landscape connectivity refers to “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993). Structural connectivity and functional connectivity are subconcepts within the topic of landscape connectivity. Structural connectivity determines the spatial relationship between habitat patches in a landscape, while functional connectivity accounts for behavioural responses of organisms to the landscape structure (Taylor et al. 2006). In urban contexts, landscapes are highly fragmented and vulnerable to habitat loss, consequently resulting in decreasing structural connectivity and increasing isolation of habitats (Concepción et al. 2015). Impermeable surfaces and structures, such as buildings and roads, constitute ecological traps and movement barriers, obstructing the dispersal of organisms and thereby decreasing functional connectivity of habitats (Horváth et al. 2009; Muñoz et al. 2015). Most research about structural and functional connectivity has focused on organisms in terrestrial ecosystems, which can differ considerably from the needs of aquatic organisms (Pringle 2006; Villalobos-Jimenez et al. 2016).

Urban ponds are crucial components of urban green-blue infrastructure, providing essential habitats to support biodiversity (Hill et al., 2017). They harbour a wide range of organisms, including macrophytes (e.g. Gledhill et al. 2008), invertebrates (e.g. Liao et al. 2020), amphibians (e.g. Mazgajska 1996), and waterbirds (e.g. Murray et al. 2013). Although urban ponds are discrete and often surrounded by inhospitable terrestrial landscapes, they can be functionally connected if species can cross the intervening habitat matrices and disperse between ponds (Tischendor & Fahrig 2000). Previous research has shown that structural connectivity can increase functional connectivity for aquatic taxa that disperse via terrestrial routes, such as amphibians (e.g. Ribeiro et al. 2011) and aquatic reptiles (e.g. Pereira et al. 2011). Structural connectivity, however, is not the only factor determining functional connectivity (Taylor et al., 2006) and affecting species distributions.

As functional connectivity accounts for behavioural responses of organisms to environmental changes in landscapes, changes in habitat-specific environmental factors can affect the dispersal of organisms and species distribution. Matrix habitat quality affects the dispersal of organisms (Clobert et al. 2009) and their potential to colonize new habitats (Moilanen & Hanski 1998). In aquatic ecosystems, predator-prey dynamics affect species survival (e.g. Goertzen & Suhling 2013; Liao et al. 2020), which also affects the potential of dispersing individuals to establish a new population. As habitats are not uniform in quality (Moilanen & Hanski 1998), it is necessary to consider habitat-specific environmental factors when we investigate functional connectivity.

Previous research on the effects of landscape connectivity on the movement of aquatic taxa between habitats has mainly focused on organisms dispersing via terrestrial routes (e.g. Ribeiro et al. 2011; Pereira et al. 2011). Little knowledge is available on the effects of landscape connectivity on aquatic organisms that use aerial dispersal. To enhance the capacity of urban blue infrastructure to support biodiversity, it is crucial to understand how landscape connectivity affects taxa with different dispersal capacity, so that we can generate reliable recommendations for conservation planning and the design of urban blue infrastructure.

In this study, we use diving beetles (Dytiscidae) as a study taxon. Dytiscids are a family of aquatic insects, in which most species disperse primarily using aerial flight (Nilsson & Holmen 1995). Dytiscids have been recommended as an indicator taxon for rapid assessment of pond biodiversity (Bilton et al. 2006; Becerra-Jurado et al. 2014), but their diversity depends on both pond quality and landscape connectivity (Iversen et al. 2013, 2017). Here, we use community similarity/dissimilarity, i.e. the variation in species composition, to investigate the responses of dytiscids to habitat isolation. Specifically, we aim to answer the following questions: 1) How does structural connectivity affect dytiscid community dissimilarity between urban wetlands? 2) Do clustered ponds have better functional connectivity for dytiscids than isolated ponds? Finally, we consider the presence or absence of predatory fish as a habitat-specific factor for dytiscid population persistence (Goertzen & Suhling 2013; Liao et al. 2020) to address 3) How does the presence/absence of fish affect dytiscid community dissimilarity?

Methods

Study Site and Data collecting

We surveyed 26 urban ponds at 11 sites in the Helsinki Metropolitan Area, Finland (60.1699º N, 24.9384º E; Fig. 1). Six ponds (I1 – I6) were isolated, with at least 1 km distance to other ponds, while the other 20 ponds comprise five groups (2–8 ponds per site). Fifteen ponds were fishless, and eleven ponds had fish (Fig. 1). Some ponds, such as the ponds at site G4, were formed due to sand extraction in areas with abundant groundwater. The fish in some of the ponds were introduced by local residents for recreational purposes (Liao, 2017). The pond sizes varied from 0.013 to 1.18 hectare (mean = 0.27 ± 0.32 hectare), with shoreline perimeter of 59–559 m (mean = 210 ± 132 m).

We operated 1-L activity traps horizontally in the water for 48 hours (Elmberg et al. 1992) in May and July 2017 – 2019. We did not use bait in activity traps, in order to avoid sample bias caused by bait effects. The number of traps set in each pond was determined according to the available shoreline length during the trapping period (see Liao et al. 2020). We use activity traps to sample dytiscids instead of handnet sweeping in our urban ponds to avoid destruction in vegetation caused by handnetting and reduction in the aesthetic appearance of urban ponds. The dytiscid specimens were preserved in 70% ethanol until identification. We identified the specimens to the species level according to Nilsson and Holmen (1995) and followed the nomenclature of Nilsson and Hájek (2021). We also operated a fish trap for 24 hours in each permanent pond, to determine the presence or absence of fish. We estimated the Euclidean distance between ponds using the City of Helsinki Map Service (2019), as an indicator of structural connectivity between ponds (Kindlmann & Burel 2008).

Statistical Analysis

We applied the function “hclust” in the “vegan” package (Oksanen et al., 2019) to perform hierarchical clustering with average linkage in R software (version 3.6.3, R Core Team 2020). We conducted hierarchical clustering with the presence or absence of all recorded species during the three years (Appendix 2 & 3), to investigate the similarities between isolated ponds and clustered ponds. Twenty-four ponds at the 11 sites were included in the analysis; two ponds were excluded from the analysis because no beetle was caught during the three sampling years. Furthermore, we applied the hierarchical clustering with the species that occurred in at least two out of the three sampling years in a pond (Appendix 2), to investigate how differently isolated ponds and ponds in groups support dytiscids. A total of nineteen ponds at eight sites were included in this analysis.

To compare dytiscid assemblages between ponds with different Euclidean distance, we first applied the function “vegdist”, in the “vegan” package, to obtain Jaccard pairwise dissimilarity index values between ponds from the dytiscid presence/absence data. The Jaccard index values varied between 0 and 1, with 0 meaning the species compositions are the same, and 1 meaning the species compositions are totally different. Next, we used the “glmmTMB” package (Brooks et al. 2017) to fit generalised linear models (GLM) with a beta distribution (Smithson & Verkuilen 2006). To avoid zeros and ones in the response variable, we rescaled the dissimilarity values to lie within the interval (0, 1). As the presence of predatory fish affects dytiscid species composition (Liao et al. 2020), we considered the presence or absence of

fish in our data analyses. In the GLMs, covariates included the Euclidean distances between ponds, the presence/absence of predatory fish in each pair of ponds in the semi-matrix, i.e. “fish in neither”, “fish in one but not the other”, and “fish in both”, and these variables in interaction. The full model is described in Appendix 1 and we used the function “drop1” to select the optimal model, based on the lowest Akaike information criterion (AIC) values (Zuur & Ieno 2016).

Results

In total, we recorded 60 dytiscid species in the 26 study ponds. Thirty species occurred in at least one of the ponds during two out of the three sampling years (Appendix 2), while the other 30 species were recorded in only one of the sampling years (Appendix 3).

Our hierarchical clusters showed that ponds within a site share more dytiscid species than ponds at different sites, but the presence of predatory fish can lead to high dissimilarities between ponds within the same site (Fig. 2a). Ponds with fish were less likely to have dytiscids than ponds without fish. Only 6 out of 11 ponds with fish supported at least one dytiscid species, and these species include *Cybister lateralimarginalis* and *Dytiscus marginalis* (Fig. 2b & Appendix 2). By contrast, 13 out of 15 ponds without fish supported dytiscids (Fig. 2b). Clustered ponds supported certain numbers of dytiscid species, while isolated ponds without fish shared similar species composition with ponds at other sites (Fig. 2b; Appendix 2). Poor disperser species, such as *Hyphydrus ovatus* and *Graphoderus* spp., had a greater probability of occurrence in clustered ponds (Appendix 2).

The GLM result shows that the community dissimilarity index increased with increasing Euclidean distance between two ponds (p-value < 0.001, Fig. 3a – c; Appendix 1). However, there is also considerable variation between the assemblages of adjacent ponds (community dissimilarity index 0.2–1.0). With the pond combination “both fishless” as reference, the other two pond combinations had larger positive effects on the community dissimilarity indices than the Euclidean distances between ponds (Appendix 1). Community dissimilarity index was significantly lower between the combination of two fishless ponds (0.69 ± 0.19) than between a fishless pond and a pond with fish (0.79 ± 0.19, p-value < 0.001), and between two ponds with fish (0.77 ± 0.24, p-value < 0.001). The combination of a fishless pond and a pond with fish had no significant difference in community dissimilarity indices with the combination of two ponds with fish (p-value = 0.553, Fig. 3d).

Discussion

In this study, we investigated how structural connectivity between urban ponds affects the community dissimilarity of dytiscids, and how the presence/absence of predatory fish affects dytiscid species similarity between ponds in the landscape. We found that dytiscid community dissimilarity increases with decreasing structural connectivity between urban ponds. Ponds close to other ponds generally share more species and thus have higher functional connectivity than isolated ponds. The presence of

predatory fish, however, can make ponds functionally disconnected to most dytiscid species, even though they are located close to other ponds.

High pond density increases structural connectivity

Dispersal is crucial for maintaining populations of aquatic invertebrates occupying relatively isolated habitats, because it facilitates the colonisation of new habitats and increases gene flows (Bilton et al. 2001). Our results show that although community similarities have large variances, adjacent ponds have higher dytiscid community similarities than distant ponds (Figs. 2 & 3). This implies that increasing structural connectivity can facilitate dispersal and reduce the isolation of potentially suitable habitats for dytiscids. However, the extent to which dytiscids can benefit from high structural connectivity varies between species (Appendix 2). Higher structural connectivity may reduce the search time for new habitats, thus enhancing the potential of species to disperse successfully (Tischendorf & Fahrig 2000). In particular, high structural connectivity will benefit those species with weaker dispersal capacity, which rarely disperse successfully in landscapes with low structural connectivity. Also, clustered ponds may have more similar environmental conditions than isolated ponds, which may help species with limited flight capacity to find suitable new habitats nearby and establish a new population within a cluster of ponds, and subsequently to other ponds in different directions from the cluster.

Through its impact on dispersal, structural connectivity can affect the diversity of many aquatic taxa both at the local level and at the landscape level. These taxa include aquatic amphibians (e.g. Semlitsch 2000; Ribeiro et al. 2011), reptiles (Pereira et al. 2011), invertebrates (e.g. Gledhill et al. 2008), and macrophytes (e.g. Linton & Goulder 2003). Our finding that more dytiscid species are shared between clustered ponds than between isolated ponds (Figs. 2 & 3) indicates that structural connectivity is beneficial in facilitating successful dispersal and improving the functioning of ponds with regard to dispersal. Structural connectivity can be enhanced by increasing the provision of ponds, creating a ‘pondscape’ of suitable habitats (Gledhill et al. 2008; Hill et al. 2017).

In a given landscape, however, the same level of structural connectivity may constitute different levels of functional connectivity to different taxa or species. We found that species that are poor fliers, such as *Graphoderus* spp., are scarcely distributed in the landscape with co-occurrence only between ponds less than 1 km apart, while strong-flying species, such as *Hydaticus seminiger*, are more widely distributed across the same landscape (Appendix 1). In the conservation literature, structural connectivity is often misinterpreted as an equivalent of functional connectivity (Taylor et al. 2006; Ribeiro et al. 2011). Our study demonstrates that functional connectivity is species specific. Similarly, Gledhill et al. (2008) found that pond density has the largest effect on the species richness of aquatic invertebrates at the radius of 1000m, while it has significant effects on aquatic plants already at a radius of 250m radius.

Species traits determine functional connectivity of urban ponds for dytiscids

Functional connectivity depends on behavioural responses of organisms to changes in the landscape structure (Taylor et al. 2006), which are affected by a mixture of biotic and abiotic factors that determine “gap-crossing ability” of organisms (Tischendorf & Fahrig 2000). In our study, strong dispersers, such as *Acilius canaliculatus*, occur in ponds across the whole landscape, while poor-flying species, such as *Hyphydrus ovatus* (Jackson 1972) and *Graphoderus* spp. (Lundkvist et al. 2002), appeared mostly in multiple ponds within the same sites (Appendix 1). Thus, ponds that are clustered have higher functional connectivity than isolated ponds for species with limited dispersal capacity.

Although many dytiscid species are capable of dispersing several kilometres (Lundkvist et al. 2002; Matsushima & Yokoi 2020), urban landscapes contain dispersal barriers (Johnson & Munshi-South 2017). According to our results, ponds that are distant from each other share few dytiscid species and strong dispersers are more likely to occur in isolated ponds than poor dispersers (Fig. 3 & Appendix 2). We have previously demonstrated a negative response of species richness to the increasing cover of impermeable surfaces in pond surroundings (Liao et al. 2020), which suggests a negative response to decreasing structural connectivity. It is also highly likely that aquatic insects such as dytiscids encounter more ecological traps in more urbanized landscapes than in forested or agricultural landscapes. These ecological traps include artificial surfaces, such as vehicle windows and roofs (Nilsson 1997; Horváth et al. 2009), which can polarize 95–100 % reflected light. By contrast, natural water bodies polarize only 30–80 % reflected light (Robertson et al. 2017). Thus, inhospitable non-habitat matrices of urbanized landscapes can reduce functional connectivity for aquatic insects by increasing search time and mortality during dispersal. Therefore, when managing habitat for the diversity of aquatic organisms such as dytiscids, in addition to habitat quality in focal habitats, it is also essential to consider the role of secondary habitats, such as matrix habitats used for dispersal, and their level of permeability.

Predators may decrease pond functioning for biodiversity

Predation is the primary regulator of a prey population (Schowalter 2016). Predatory fish are known to modify community composition of aquatic invertebrates (Wittwer et al. 2010; Liao et al. 2020). In ponds with predatory fish, the decreasing abundance in most taxa, including dytiscids, is mainly due to direct effects of predation rather than predation-induced dispersal (Dahl & Greenberg 1999). In this study, we found that predation by fish can lead to high community dissimilarities between ponds (Fig. 3d & Appendix 2), even within the same site (Fig. 2). We consider that the high community dissimilarity between a pond with fish and a pond without is due to the vulnerability of some dytiscid species to fish predation, especially small-sized species, such as *Hydrophorus* spp. (Liao et al. 2020), even though the dispersal capacity of such species enables them to access these ponds. The high community dissimilarities between ponds with fish may have resulted from the quality and quantity of spatial prey refuges available in different ponds (Donelan et al. 2017; Liao et al., unpublished data). Predatory fish, thus, may decrease ponds’ capacity to support species.

As many species of dytiscid have poor capacity of co-exisiting with predatory fish (Liao et al. 2020), ponds with fish may become sink-habitats, especially when a pond lacks habitat heterogeneity. The availability of prey refuges, however, can ease predation pressure and increase the survival of vulnerable

species (Ghosh et al. 2017). Our previous study shows that emergent plants as spatial prey refuges can enhance dytiscid species richness and abundance, and also facilitate the co-existence of predator and prey species (Liao et al. unpublished data). Adequate provision of ponds with prey refuges and clusters of ponds, can therefore enhance the diversity of the urban fauna.

Conclusion: Supporting Urban Aquatic Biodiversity

Species are more likely to disperse and colonise successfully within a short distance than a long distance in urban landscapes. Changes in both abiotic (e.g. habitat isolation) and biotic (e.g. introducing fish for recreational purposes) environmental factors can affect behavioural responses of organisms. To support aquatic invertebrate diversity in urban landscapes, we recommend:

1. supplementing pond networks by increasing pond density in urban landscapes to reduce isolation of wetland habitats;
2. maintaining or creating multiple ponds at the same sites to facilitate dispersal between ponds serving as stepping ponds or extra habitats, especially for species with limited dispersal capacity;
3. retaining fishless ponds to conserve predator-intolerant invertebrates and maintain structural connectivity of ponds and functional connectivity to species;
4. providing aquatic vegetation as prey refuges to enhance the survival of aquatic invertebrates, especially in ponds with predatory fish.

Declarations

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Data Availability

We will make the data available on fairdata.fi when the manuscript is accepted.

Ethical Statement

The authors declare no conflict of interests.

Authorship

Wenfei Liao designed the study, collected and analysed the data, and led the writing. Stephen Venn and Jari Niemelä revised the manuscript critically for important intellectual contents and structure. All authors gave final approval for publication.

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Figures

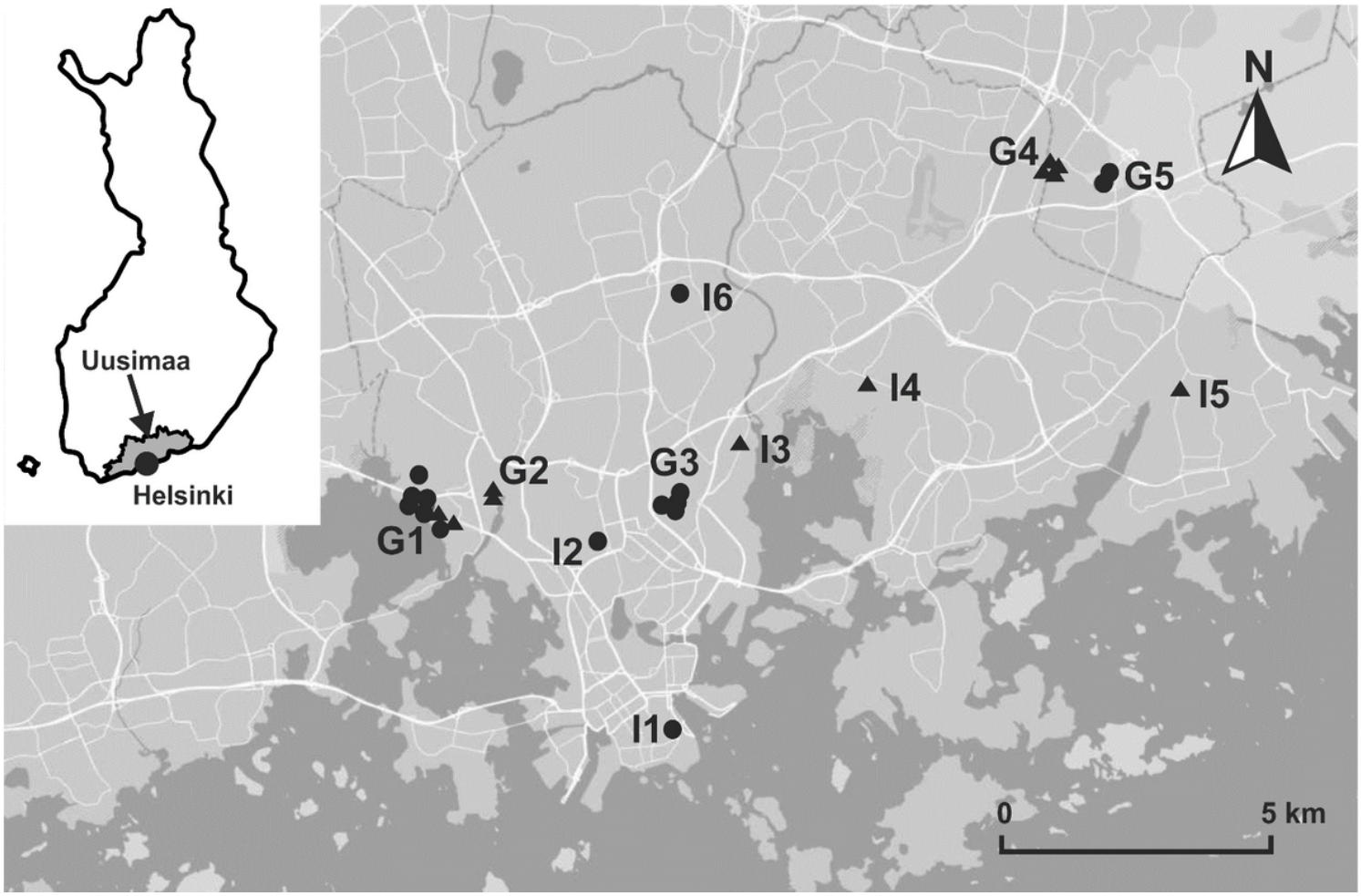

Figure 1

Map of study ponds in the Helsinki Metropolitan Area, Finland. Triangles represent ponds with fish, while filled dots represent fishless ponds. The ponds are located at 11 sites. Sites labelled with ‘I’ are isolated ponds, and sites labelled with ‘G’ are ponds in groups. Note: The designations employed and the

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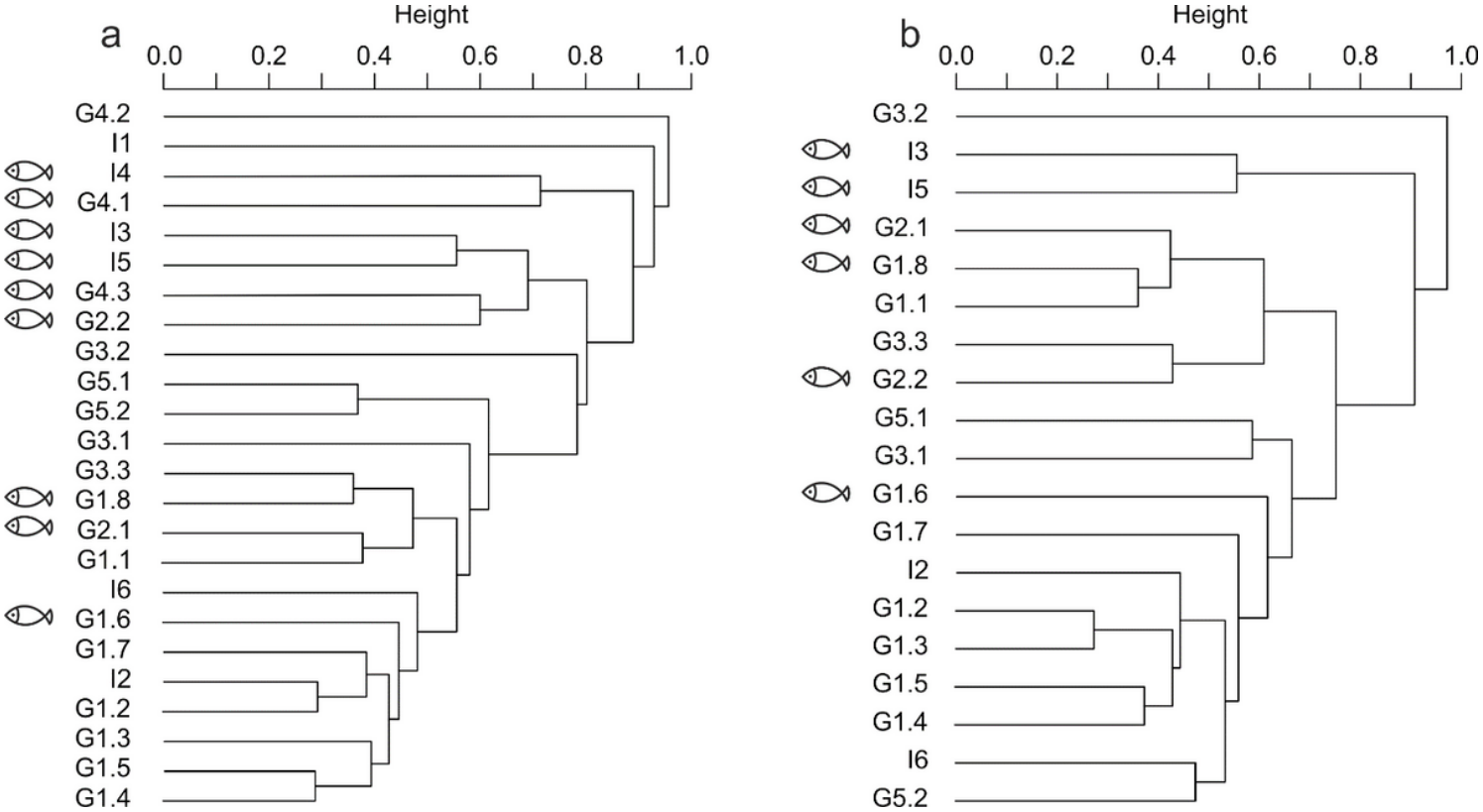

Figure 2

Cluster analysis of pond dytiscid species similarities: (a) all dytiscid species occurred during the sampling years are included in the analysis; (b) species that occurred during at least two out of the three sampling years, were included in the analysis. The clusters show ponds and sites that fit the analysis requirements. The fish symbols represent ponds with fish. Ponds labelled with ‘I’ are isolated ponds, and ponds labelled with ‘G’ are ponds in groups.

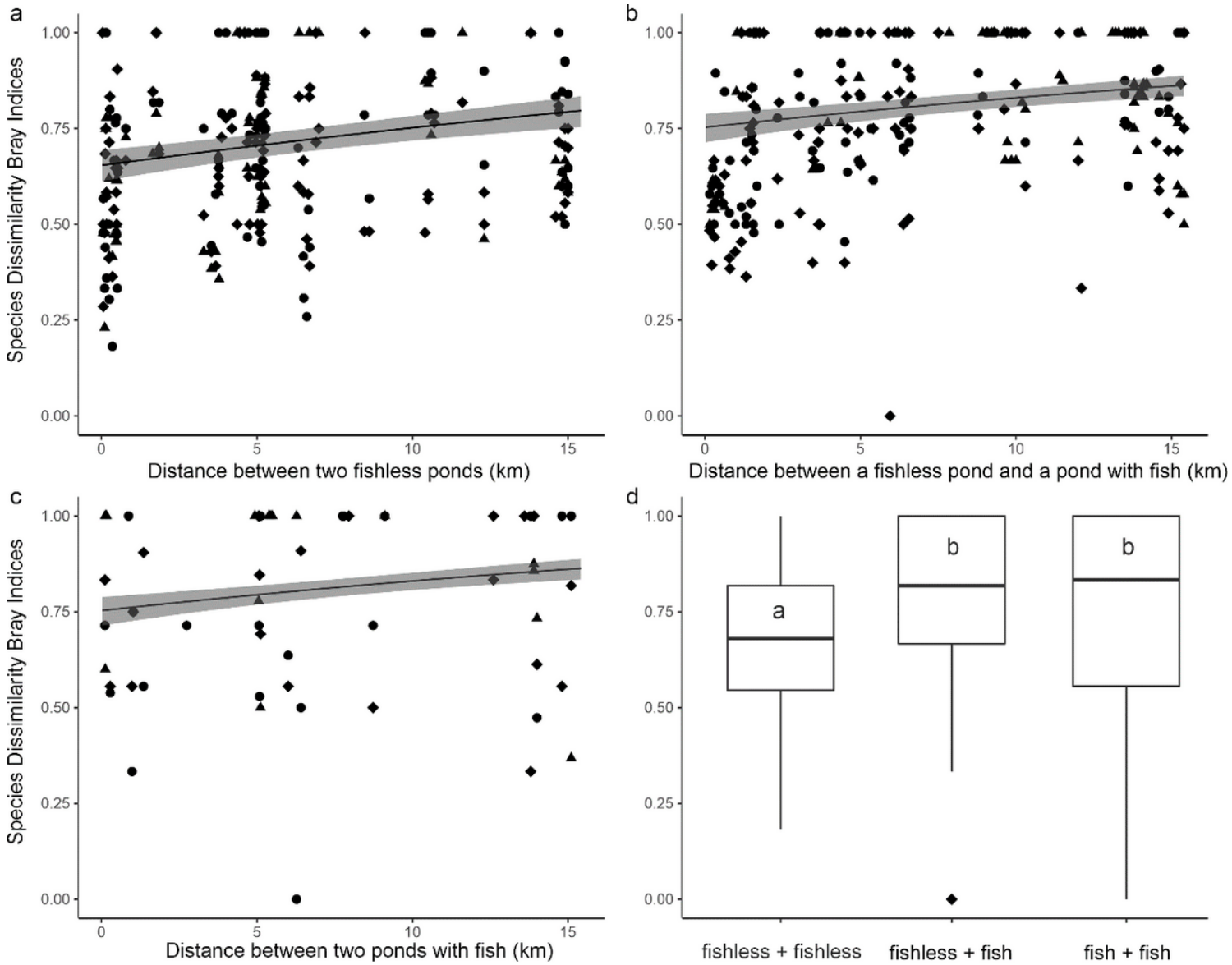

Figure 3

Dytiscid community dissimilarity index increases with distance (a) between two fishless ponds, (b) between a fishless pond and a pond with fish, (c) between two ponds with fish. (d) Dytiscid community dissimilarity index is lower between fishless ponds than between the other two pond combinations. The triangles represent community dissimilarities between ponds in 2017, the diamonds 2018, and the solid circles 2019. The letters in (d) represent significant differences between pond combinations, while the same letter indicates no significance between the scenarios.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Appendix.docx
- Supportmaterials.docx