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Non-biting midges (Diptera: Chironomidae) from fountains of two European cities: micro-scale island biogeography

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We studied chironomid assemblages of 12 fountains located in Olomouc (Czech Republic) and in Copenhagen (Denmark). In total, 45 taxa of three subfamilies were recorded. The typical fountain assemblage was constituted of common species with very wide geographical distribution and ecological requirements as Cricotopus ornatus, C. sylvestris, Orthocladius fuscimanus, Psectrocladius limbatellus, Chironomus spp., along with tap-water species (Paratanytarsus grimmii), hygropetric and semi-terrestrial taxa (e.g. Orthocladius fuscimanus, Metriocnemus eurynotus). There was no linkage between taxa richness and fountain area or distance from the colonisation source. However, in Olomouc, with a single main colonisation source, a strong correlation between similarity of chironomid assemblage structures and distance to river was recognised. In Copenhagen, with a number of small water bodies, fountains were not correlated significantly with distance to sources. However, similarities of chironomid assemblage structures were negatively correlated with their geographical distances. Species temperature optima and preferences did not relate to distribution patterns. Generally, distance to natural aquatic sources, fountain proximity and regional factors determine the taxonomic composition of the nonbiting midges.

Keywords: Chironomidae; exuviae; fountains; artificial habitats; dispersal; colonisation

Introduction

Fountains in cities function as aquatic islands in a "terrestrial sea". They are artificial basins with sprinkling water and generally function as decoration of the cityscape. In fact, fountains can be considered as temporary pools existing from spring to late autumn. During this time they are colonised by aquatic insects from the surrounding water bodies. Although they represent very interesting habitat for aquatic organisms, little or almost no attention was paid to their biological inhabitants (Hamerlík 2006).

With this study we want to examine the following questions: (i) what chironomid species characterise the artificial fountain habitats, (ii) what are the differences in assemblage structures within and between the two regions/cities, (iii) what is the role

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of natural colonisation sources, and (iv) is there a small-scale biogeographical pattern among the fountains?

Study area

We studied 12 fountains of two cities: six in Olomouc (Central Europe), and six in Copenhagen (Scandinavia) (Figure 1). For coordinates and additional characteristics of the fountains, see Table 1.

Olomouc (OLO) ($49^{\circ}35'$ N and $17^{\circ}15'$ E, altitude ~220 m) is a Moravian town (Czech Republic) with an area of approx 103 km² and slightly more than 100,000 citizens. The fountains studied are of baroque origin, built in 1687–1735, and are situated in the frequently visited parts of Olomouc downtown. They consist of sandstone and vary slightly in size from ~20 to 45 m². They are supplied by tap water and they are functioning from spring (April) to autumn (October). During the winter period they are without water. There are no lakes or other considerable water bodies near to the fountains except on the right side arm of the Morava River (a lowland river) called Mlýnsky potok, flowing across the town near the city centre.

Copenhagen (CPH) (55°40′ N and 12°34′ E, altitude 0–15 m) is the capital and largest city of Denmark. It is situated on the islands of Zealand and Amager. The area of the city is approx 455 km²; the population is approx. 1.5 million in the city and urban areas. All fountains studied were made of sandstone, marble and andesite in the twentieth century, and similarly to OLO fountains, they are supplied by tap water and functioning from spring (April) to late autumn (end of October). They are scattered in different parts of the downtown. The city is surrounded by brackish water sea to the east, and there are plenty of natural and artificial freshwater lakes in it. There is no river or other running water sources of importance present.

Materials and methods

Sampling

Accumulated pupal exuviae were collected monthly from April to October from the water surface by drift net (300 μ m) in 2006 (Olomouc) and 2008 (Copenhagen). The



Figure 1. Location of the study fountains in Olomouc and Copenhagen. Black dots represent fountains, grey patches freshwater sources.

Site	N-coordinate	E-coordinate	Approx. area m ²	Min-max T °C	Mean T °C	Distance from source m
Olomouc	;					
OLO 1	49°35′46.18″	17°15′27.57″	27	14.5-18.4	16.1	196
OLO ²	49°35'30.51″	17°15′11.95″	42	14.8 - 18.8	16.3	218
OLO ₃	49°35′33.10″	17°15'08.57"	22	13.2-17.2	14.9	279
OLO 4	49°35′38.25″	17°15′07.92″	44	15.0-19.2	16.6	256
OLO ⁵	49°35′39.08″	17°15′03.69″	24	14.8 - 18.7	16.2	347
OLO ₆	49°35′43.10″	17°14′59.32″	25	14.3-18.7	15.9	445
Copenha	gen					
CPH 1	55°40′56.34″	12°33'29.61"	10	15.0-27.0	23.0	13
CPH ²	55°40′55.77″	12°33'31.14″	10	16.0-28.0	24.0	13
CPH ₃	55°40′54.94″	12°34'40.13"	28	11.5-21.0	17.5	360
CPH ⁴	55°40′54.19″	12°34'39.76"	28	11.5-22.0	18.5	360
CPH ⁵	55°40′33.98″	12°34'38.30"	214	10.5-22.5	17.6	480
CPH_6	55°42′11.95″	12°35′09.15″	16	10.5-22.0	17.6	780

Table 1. Basic parameters of the observed fountains.

material collected was placed into a plastic bottle, labelled and preserved with 75% ethanol. Pupal exuviae were mounted in Berlese fluid and identified under high magnification (400 x) to species level if possible. Identification keys by Langton (1991), Contreras-Lichtenberg (1986) and Vallenduuk and Morozova (2005) were used. The fountain water temperature was measured on every sampling date with a digital thermometer. Ecological requirements according to Moog (1995) and Bitušík and Hamerlík (2003) were used to divide chironomid taxa into feeding groups and flood preference groups. Temperature optima for the lotic chironomid taxa were estimated from the temperature vs. DCA-score relation presented in Lindegaard and Brodersen (1995, figures 5 and 6).

Data analysis

All analyses were performed based on binary data of chironomid assemblages. No down-weighting of rare species was made in the final analysis to give the maximum information from the study material. The pair-wise geographical distances among fountains were measured as the Euclidean geographical distance (EGD) from GPS coordinates (in decimal degrees). Distances from the water source were measured as the closest distance from the river (OLO), or from the nearest considerable freshwater source (CPH). Assemblage structure and beta diversity (species turnover) were measured using detrended correspondence analysis (DCA) with the gradient length expressed as standard deviations (SD) in the program CANOCO v. 4.5 (ter Braak and Smilauer 2002). Pair wise assemblage similarities based on binary species data were calculated using the Sørensen similarity coefficient, S (Magurran 1988). The ANOSIM permutation procedure was used to test for significant difference in assemblage structure between the two regions (Clarke and Green 1988). Small-scale biogeographical patterns among fountains were analysed by examining the correlation between pair wise assemblage similarities (S) and pair wise Euclidean geographical distances (EGD) (pair wise combinations = n(n-1)/2 = 15).

Results

Taxonomic composition

In total, nearly 10,000 chironomid pupal exuviae identified as 45 species/taxa were recorded in 12 fountains (Table 2). In both cities, species of subfamily Orthocladiinae dominated, followed by Chironominae and Tanypodinae (Figure 2). Taxa richness varied from 11 to 23 in OLO and 4 to 13 in CPH fountains. A single species, *Cricotopus (I.) sylvestris*, occurred in all 12 fountains; *Cricotopus (I.) ornatus*, *Orthocladius (Eud.) fuscimanus, Psectrocladius (P.) limbatellus, Chironomus* spp. and *Paratanytarsus grimmii* were the most frequent taxa recorded in ~70% and more of sites.

Five taxa occurred in all OLO fountains: *Procladius (H.) choreus, Cricotopus (I.) reversus, C. sylvestris, Psectrocladius limbatellus, Chironomus* spp.; two species, *Cricotopus ornatus* and *C. sylvestris*, were recorded in all CPH fountains.

Generally, almost half of the recorded taxa only occurred in a single fountain (21 out of 45). But while half of the OLO species occurred in a single fountain, this ratio was 32% in the case of CPH species/fountains. Furthermore, more than half of the CPH species colonised half and more of CPH fountains; in OLO it was only 35% of the species they were recorded in the half or more of the fountains.

The trophic structure in fountains of both regions was markedly similar (Figure 3a). Collectors made up approximately half of all the species, followed by scrapers and predators. Filter-feeders, represented by a single species, *Orthocladius fuscimanus*, presented the numerically marginal part of the assemblages.

In OLO fountains, a wide range of species from limnobionts to rheobionts occurred, however, rheophilic taxa along with rheobionts clearly dominated with 65% (Figure 3b). In CPH fountains, rheobionts were not present at all and limnophilic and limnobiontic species represented more than half of all taxa collected. Semi-terrestrial species were more represented than in OLO and made up 20% of the all taxa.

Beta diversity (species turnover) was high (2.4 SD, DCA) and there were significant differences in assemblage structures between OLO and CPH (p < 0.002, ANOSIM). From the 40 taxa recorded in OLO fountains, 26 did not occur in CPH; on the contrary, five taxa out of 19 collected in CPH fountains were not recorded in OLO. Fourteen taxa were common for both regions. From the most common taxa (present in both areas and in >58% of sites), only one was rheophilic (*O. fuscimanus*) and the rest were limno-rheophilic (*Cricotopus sylvestris*) and limnophilic (*Procladius choreus, Corynoneura scutellata* group, *Cricotopus ornatus, Psectrocladius limbatellus, Chironomus* spp., *Paratanytarsus grimmii*). Taxa only occurring in CPH fountains were species linked to standing waters and semiterrestric, while almost 60% of taxa only recorded in OLO were rheobionts and rheophilic (Figure 3c).

Chironomid assemblages/geographical pattern

In Copenhagen, the highest richness was recorded in the fountain with the biggest area (15, CPH_5), and in Olomouc the highest richness was found in the fountain most closely situated to the river (23, OLO_1). However, there was no correlation between fountain species richness nor fountain area, neither distance to sources, in the two cities (p > 0.05).

Table 2. List of chironomid taxa recorded in the studied fountains. Species and fountains are arranged according to axis 1 scores in DCA. CPH – Copenhagen, OLO – Olomouc.

	ZHJ	CPH_I	CPH_S	CPH_4	CPH_3	OTO_0	CPH_0	ULU_4				
Psectrocladius (P.) barbimanus (Edwards, 1929)	+	+	+	Ι	Ι	I	Ι	I	I	Ι	Ι	I
Psectrocladius (P.) sordidellus (Zetterstedt, 1838)/		+	+		I	Ι	Ι	I	I	I	Ι	I
ventricosus Kieffer, 1925												
Procladius (P.) flavifrons Edwards, 1929		Ι	+	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι
Micropsectra cf. lindrothi Goetghebuer, 1931	+	Ι	+	+	+	+	Ι	Ι	Ι	Ι	Ι	Ι
Metriocnemus (M.) eurynotus (Holmgren, 1883)		Ι	Ι	+	+	Ι	Ι	I	I		Ι	I
Pseudosmittia sp.	I	I	Ι	I	+	I	Ι	I	I	I	Ι	I
Nanocladius (N.) rectinervis (Kieffer, 1911)	I	I	Ι	I	I	+	Ι	I	I	I	Ι	I
Orthocladius (O.) rhyacobius Kieffer, 1911		I	I		I	+	Ι	I	I		Ι	I
Paratanytarsus bituberculatus (Edwards, 1929)	Ι	Ι	Ι	Ι	Ι	+	Ι	Ι	Ι	Ι	Ι	Ι
Acricotopus lucens (Zetterstedt, 1850)	+	+	Ι	Ι	Ι	+	Ι	+	Ι	Ι	+	Ι
Cricotopus (I.) sylvestris (Fabricius, 1794)	+	+	+	+	+	+	+	+	+	+	+	+
Cricotopus (I.) ornatus (Meigen, 1818)	+	+	+	+	+	I	+	I	+	+	+	+
Psectrocladius (P.) limbatellus (Holmgren, 1869)	+	+	+	+	+	+	Ι	+	+	+	+	+
Chironomus (C.) spp.	+	+	+	+	+	+	Ι	+	+	+	+	+
Corynoneura scutellata gr.	I	+	+	+	I	+	I	+	I	I	+	+
Limnophyes sp.	I	I	Ι	+	+	+	+	+	+	I	Ι	+
Orthocladius (O.) cf. oblidens (Walker, 1856)	Ι	Ι	Ι	Ι	Ι	Ι	Ι	+	Ι	Ι	Ι	Ι
Dicrotendipes nervosus (Staeger, 1839)	I	Ι	Ι	Ι	Ι	Ι	Ι	+	Ι	Ι	Ι	Ι
Polypedilum (U.) cultellatum (Goetghebuer, 1931)	I	Ι	Ι	Ι	Ι	Ι	Ι	+	Ι	Ι	Ι	Ι
Macropelopia nebulosa (Meigen, 1804)	Ι	Ι	Ι	Ι	+	+	Ι	Ι	Ι	Ι	+	Ι
Thienemannimyia pseudocarnea Murray, 1976	I	I	Ι	I	I	I	I	I	+	I	I	I
Paratanytarsus grimmii (Schneider, 1885)	I	Ι	+	+	+	+	Ι	+	Ι	+	+	+
Orthocladius (Eud.) fuscimanus (Kieffer, 1908)	I	I	+	+	+	Ι	+	+	+	+	+	+
Zavrelimyia nubila (Meigen, 1830)	I	I	Ι	I	I	I	I	+	+	+	I	I
Bryophaenocladius subvernalis (Edwards, 1929)		I	+		I	I	Ι	+	I	I	Ι	+
Procladius (H.) choreus (Meigen, 1804)	I	I	Ι	I	+	+	Ι	+	+	+	+	+
Tanytarsus mendax Kieffer, 1925	I	I	+	I	I	I	I	I	I	I	Ι	+
Paratrichocladius ruftwentris (Meigen, 1830)	Ι	Ι	I	I	Ι	+	Ι	+	+	I	+	+
											(co	ntinued)

Table 2. (Continued).												
	CPH_2	CPH_1	CPH_5	CPH_4	CPH_3	0L0_6	CPH_6	OLO_4	0L0_3	OLO_2	0L0_5	OL0_1
Cricotopus (I.) reversus Hirvenoja, 1973	I	Ι	I	Ι	Ι	+	I	+	+	+	+	+
Parachironomus arcuatus gr.	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	+	Ι	Ι
Orthocladius (O.) rubicundus (Meigen, 1818)	I	I	I	I	I	I	I	I	I	I	+	I
Synorthocladius semivirens (Kieffer, 1909)	Ι	I	I	I	Ι	I		I	I	I	+	Ι
Cryptochironomus obreptans (Walker, 1856)	I	I	I	I	I	I	I	I		I	+	I
Microtendipes rydalensis (Edwards, 1929)	I	I	I	I	Ι	I	I	I	Ι	I	+	Ι
Polypedilum (P.) sp.	I	I	I	I	I	I	I	I	I	I	+	Ι
Cricotopus (C.) bicinctus (Meigen, 1818)	Ι	I	I	I	Ι	I	I	I	I	+	+	+
Ablabesmyia monilis (Linnaeus, 1758)	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	+	Ι	+
Dicrotendipes notatus (Meigen, 1818)	Ι	Ι	Ι	Ι	Ι	Ι	I	Ι	Ι	Ι	+	+
Glyptotendipes (G.) barbipes (Staeger, 1839)	Ι	Ι	I	Ι	Ι	Ι	Ι	Ι	Ι	Ι	+	+
Procladius (H.) sp. A	Ι	Ι	I	Ι	Ι	Ι	I	Ι	Ι	Ι	Ι	+
Zavrelimyia melanura (Meigen, 1804)	Ι	Ι	I	Ι	Ι	Ι	I	Ι	Ι	Ι	Ι	+
Eukiefferiella claripennis (Lundbeck, 1898)	Ι	I	I	I	Ι	I		I	I	I	I	+
Orthocladius (Euo.) thienemanni Kieffer, 1906	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	+
Thienemanniella cf. vittata (Edwards, 1924)	I	Ι	Ι	I	Ι	Ι	Ι	I	I	I	I	+
Kiefferulus tendipediformis (Goetghebuer, 1921)	Ι	I	I	I	I	I	I	I	I	I	I	+
Number of taxa	7	8	13	10	12	15	4	16	11	12	20	23



Figure 2. Subfamily structure of chironomid assemblages of Olomouc (OLO) and Copenhagen (CPH) fountains.

The assemblage structure in the OLO fountains (DCA axis 1) was strongly correlated with longitude and thus also with distance to river source (r = -0.88 and 0.86; p < 0.05), respectively. Minimum temperature was correlated with DCA axis 2 due to one cold fountain (OLO_3). The assemblage structures in CPH fountains were not significantly correlated with distance to sources (r = 0.63; p > 0.05), but the secondary gradient (DCA axis 2) was strongly correlated with minimum temperature (r = -0.94; p < 0.01).

The pair wise similarities in chironomid assemblage structures from CPH fountains were negatively correlated with the geographical distance between fountains (r = -0.87; p < 0.01) (Figure 4). For OLO fountains, also a negative relationship was found, although not significant (r = -0.49; p > 0.05).

Discussion

Up to 23 species of one insect family in the temporary and artificial fountain habitats is fascinating. Dealing with life in temporary and unstable habitats may require adaptations such as high potential for rapid colonisation, omnivorous diets, and specialised survival strategies. The studies of the fountains as aquatic biotopes revealed 12 species recorded for the first time in the Czech Republic and two species recorded for the first time in Denmark (Hamerlík 2007; Hamerlík et al. in press). An untraditional ecological approach such as this thus has high value for diversity and faunistic studies.

The occurrence of the most common taxa, such as *Cricotopus ornatus*, *C. sylvestris*, *Procladius choreus*, *Corynoneura scutellata* group, *Psectrocladius limbatellus* and *Chironomus* spp., in the majority of fountains of both regions is not surprising. They are widespread in the Palaearctic and Holarctic or have even almost worldwide distribution patterns (*C. sylvestris*) (Sæther and Spies 2004). Moreover, they are common in a wide variety of habitats from the littoral zone of lakes and ponds to lowland rivers (Moog 1995). The fact that except the *C. scutellata* group, all the taxa mentioned were able to colonise waters in the Azores islands



Figure 3. Structure of chironomid assemblages of Olomouc and Copenhagen fountains. (a) Feeding groups, (b) preference of flood, (c) preference of flood of taxa occurring only in one region. Abbreviations: Fil – filter-feeders, Col – collector-gatherer, Pre – predator, Scr – scraper; LB – limnobionts, LP – limnophils, L-R – limno-rheophils, RP – rheophils, RB – rheobionts, ST – semi-terrestrial.



Figure 4. Correlations between the pair wise similarities in chironomid assemblage structures and pair wise distances between fountains. Copenhagen, r = -0.87, p < 0.01; Olomouc, r = -0.49, p > 0.05.

located ~ 1500 km from the European coast, also underlines their good colonisation potential (Murray, Hughes, Furse and Murray 2004).

A few taxa, however, may be characteristic of fountain habitats without respect of surrounding water bodies. They are species typical of artificial worldwide distribution (Langton, Cranston and Armitage 1988). It has achieved notoriety as a pest in tap-water habitats as *Paratanytarsus grimmii*, dwelling hygropetric biotopes as *Metriocnemus eurynotus*, *Orthocladius fuscimanus* and *Limnophyes* sp., or semiterrestrial as *Bryophaenocladius subvernalis* and *Pseudosmittia* sp. (Armitage, Cranston and Pinder 1995).

Paratanytarsus grimmii is a parthenogenetic species with almost worldwide distribution (Langton et al. 1988). It has achieved notoriety as a pest through its capacity to breed in water distribution system. Preimaginal stages of *P. grimmii* were recently found in a filter-bed of a waterworks (Hamerlík et al. in press). It is possible that in nature the species lives in hyporheic habitats (Armitage et al. 1995). The most likely source of *P. grimmii* in fountains may be refugia in the tap water networks.

Orthocladius fuscimanus is one of the few chironomid species restricted to hygropetric biotopes (Oliver and Sinclair 1989). Cranston (1984) noted the occurrence of O. fuscimanus in sewage lagoons and in percolating filter beds of sewage works. This can be regarded as the ecological equivalent of natural organic rich hygropetric biotopes. A number of other typical madicolous species, such as Metriocnemus eurynotus and Limnophyes minimus (Meigen 1818) have also been found in sewage filters (Cranston 1984).

The restricted occurrence of *Procladius (P.) flavifrons* to the CPH fountains as opposed to *Thienemannimyia pseudocarnea, Cricotopus (I.) reversus, Polypedilum cultellatum, Cryptochironomus obreptans* and *Kiefferulus tendipediformis* only in OLO fountains may be explained by regional scale distribution of chironomid species. The first species has not been registered in the Czech Republic (Bitušík and Brabec 2006) while the following five species have not yet been recorded in Denmark (Lindegaard 1997).

Despite the high morphological similarity within the family Chironomidae there is a huge variability in mechanisms of feeding. The most common factors influencing the feeding behaviour of larval midges are larval size, food quality and sediment composition (Armitage et al. 1995). Consequently, trophic structure of chironomid assemblages reflects quality and quantity of food resources in their habitat. Considering the fact that fountain substrate resembles a uniform and compact face of a large rock, without an obvious layer of accumulated organic matter, we expected a predominance of scrapers in the fountains. In both regions, however, species primarily feeding as collectors, also called deposit feeders, dominated (Moog 1995). This feeding group predominates when fine particulate organic matter (FPOM) accumulates, such as in lakes and in places of reduced current velocities in rivers. It can reflect the original source of fountain species (slow flowing lowland rivers in OLO, lakes in CPH). This result supported the well known flexibility in the feeding mode of chironomids when they can shift from one mode to another. Furthermore, Zah, Burgherr, Bernasconi and Uehlinger (2001) documented that aquatic invertebrates are more plastic in utilising food resources on extreme environmental conditions as has been expected. However, it can also suggest that even small patches and a thin layer of FPOM are adequate to allow collectors to dwell on such a uniform habitat. Moreover, according to our knowledge, the study fountains are not cleaned during the season, what allows adequate accumulation of detritus to support the high proportion of collectors.

Variables closely linked with periphyton growth such as light conditions and growth season were not estimated in this study. These factors, however, could help to explain the trophic structure of particular fountains and should be included in future studies.

There were considerable differences in water temperature (both ranges and means) between the two sets of fountains. These differences were most likely caused by the combination of volume of fountain water and arrangement of flow. The smallest fountains with low volume reached the highest temperatures. At the same time, it was a lower temperature range in OLO fountains with lower variability in size than in CPH fountains with higher size diversity. However, the temperature optima for 26 taxa (57% of total) showed that cold as well as warm water species were present in both regions (Figure 5). The estimated optima ranged from 9 to 23°C, indicating that temperature was not an important factor determining the species distributions in fountains.

The difference in running water sources in OLO (Mlýnsky potok) versus standing water sources in CPH was clearly reflected in the assemblage structures. The contribution of rheophilic taxa was markedly higher in OLO, whereas limnophilic species dominated in CPH. Moreover, while in OLO rheobionts represented a significant part of the assemblage, in CPH they were not recorded at all. The fountain habitat itself may usually be considered as well mixed and turbulent waters offering conditions for both rheo- and limnophilic species. This study demonstrates that both types coexist and that colonisation source type and source distance have an effect on the chironomid assemblages. However, the proportion of taxa with different flood preferences in particular fountains could also be influenced by different water exchange and arrangement of water flow of the fountains. Even though we have not focused on water exchange/chironomid assemblage structure interactions in this study, it should be, together with light condition/trophic structure interactions, the objective of future surveys.

The surprisingly high taxa richness could be due to lack of inter-specific competition. All the fountains studied function from the spring to late autumn,



Figure 5. Temperature optima for 26 lotic taxa estimated according to Lindegaard and Brodersen (1995).

when they are emptied. Consequently, they are re-colonised by insects from the surrounding water sources every year. This can represent a disturbance which avoids the fountain assemblage to develop a stable community with competition and allows high species richness.

The midge assemblages from this study demonstrate some basic aspects of island biogeography. According to the equilibrium model suggested by Preston (1962) and MacArthur and Wilson (1967), there might be a balance of immigration and extinction of the island biota. An increase in distance from the source of colonisation lowers the immigration rate, while an increase in island area lowers the extinction rate. Area, however, seldom exerts a direct effect on species presence. The most obvious reason why larger areas contain more species is that larger areas typically encompass more different habitat types. In case of fountains, however, area was not correlated wit taxa richness. The likely reason is that fountains represent extremely uniform biotope with homogenous substrate and base rock, so increased area does not necessarily give rise to higher heterogeneity. Besides, the fountain areas varied only slightly in this study.

The pair wise similarities in chironomid assemblage structures in CPH fountains were negatively correlated (Figure 4) with the geographical distance between fountains. Thus, fountains that were far apart had low similarity in species composition, whereas fountains with high proximity also had similar species compositions. The correlation was clear in CPH where the average inter-distance among fountains was 1.5 km (maximum 3.0 km), indicating that species interchanges between

fountains may be important but also that the neighbouring fountains are also nearer to the water body they both are colonised from. In OLO, the average inter-distance among fountains was almost five times less (0.33 km, maximum 0.57 km), and the correlation was not significant. The distance to the source, however, had significant influence on the chironomid species assemblages. Consequently, even though there was no relationship between taxa number and distance from the source in OLO, distance from the source apparently influences the structure of chironomid assemblage. With increasing distance from the river, other water bodies such as colonisation sources can take over.

With this study we have shown that the temporary and artificial fountain habitats have an interesting diversity of aquatic and semi-terrestrial midge species. Some species are characteristic of the "tap-water environment", but the overall diversity is highly dependent on colonisation, dispersion and interchanges of species among the fountain islands in the cityscape. Distance to natural aquatic sources, fountain proximity and regional factors determine the species composition of the non-biting midges.

Summary

(1) The typical fountain assemblage is constituted of species linked with tap-water, hygropetric and semi-terrestrial habitats as well as more common species with very wide geographical distribution and ecological requirements. These taxa will probably occur in most of the temperate fountains independently of the main source. (2) There was no linkage between taxa richness and fountain area or distance from the colonisation source. (3) In OLO, where a single strong lotic colonisation source was present, there was a strong correlation between the similarity of chironomid assemblage structure and distance to river source. (4) In CPH, there was a number of small water bodies scattered all over the city, and fountains were not significantly correlated with distance to sources. However, pair wise similarities in chironomid assemblage structures from CPH fountains were negatively correlated with the geographical distances among fountains. (5) With this study we have shown the great potential of the fountain habitats for studying dispersal and colonisation of aquatic insects. For general patterns of interactions between fountains are needed.

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