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Temporal abiotic variability structures invertebrate communities in agricultural drainage ditches

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A B S T R A C T

Abiotic variability is known to structure lotic invertebrate communities, yet its influence on lentic invertebrates is not clear. This study tests the hypothesis that variability of nutrients and macro-ions are structuring invertebrate communities in agricultural drainage ditches. This was determined by investigating invertebrate adaptations to disturbance using insect life-history strategies. Many low-lying agricultural areas contain drainage ditches which potentially provide suitable habitat for aquatic invertebrates. In the province of North Holland (The Netherlands) the extensive network of eutrophic ditches are hydrologically managed, creating seasonal variability of water quality arising from agricultural run-off and the inlet of mineral rich, river derived water. This temporal variability was analysed from monitoring data, collected over a 7 month period (February till August) and covering 84 ditches in three soil regions; sand, clay and peat. Invertebrate diversity was determined as local (α diversity), regional (γ diversity) and species-turnover (β diversity). We ran canonical correspondence analysis and linear mixed models to determine correlations between invertebrate diversity, functional community composition and specific abiotic parameters, including variability (expressed as the Median Absolute Deviation). Invertebrate α diversity was positively correlated to variability in water transparency and negatively correlated to average pH, with the two parameters reflecting a water quality gradient in the environment. Insect life-history strategies expressed adaptations to abiotic variability and harsh (eutrophic) conditions. These adaptations were mainly achieved through good dispersal abilities and developmental trade-offs. The results support measures to reduce influxes of excess nutrients to this network of ditches.

LRH: Whatley et al.
RRH: Abiotic variability structures invertebrate communities

Introduction

Agricultural landscapes cover approximately 38% of the Earth's total land area (Clay, 2004), thus it is important that we understand how management activities underpin biodiversity patterns in these landscapes. In The Netherlands the management intensity of agricultural landscapes has increased over recent decades (Kleijn et al., 2004). In the country's low-lying provinces the landscape is characterized by networks of drainage ditches, which potentially provide suitable habitat to a range of aquatic organisms including invertebrates (Beltman, 1983; Herzon and Helenius, 2008; Van der Hammen, 1992; Verdonschot, 2012). However, the diversity of invertebrates has declined dramatically over recent decades (Van Dam, 2009; Whatley et al., 2014).

Individual hydrological systems in North Holland, known as polders, include plots of land separated by ditches and surrounded by the larger arterial canal system. Polders are hydrologically managed to maintain artificially stable water tables suitable for agriculture. To this end, water is pumped out of polders during wet periods and mineral rich river water is let into polders during dry periods. This inlet of mineral rich water can have a strong effect on abiotic conditions by altering the pH and buffering capacity of waters and increasing sulphate concentrations, which then trigger the release of sediment bound phosphates leading to internal eutrophication (Lamers et al., 2002; Roelofs, 1991). Consequently, these agricultural ditches are eutrophic and exhibit a high degree of abiotic variability, related to the inlet of external waters as well as maintenance (i.e. vegetation removal and dredging) and nutrient rich run-off from surrounding agricultural land (Lamers et al., 2002; Twisk et al., 2000; Verberk et al., 2007; Verdonschot et al., 2012). Although abiotic variability is expected to influence biodiversity

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patterns in these areas, as has been demonstrated for invertebrates in lotic environments (McCabe and Gotelli, 2000), the importance of abiotic variability has not been investigated for lentic invertebrate communities in North Holland's heavily impacted environment.

Invertebrate community composition can be influenced by many factors, including patch size and habitat connectivity (i.e. the ability of individuals to colonize new habitats) as well as environmental filtering processes (Chase, 2003; Verdonschot et al., 2012). More specifically, the stability and predictability of an environment can influence the persistence of species based on their specific traits relating to dispersal, tolerances and reproductive behaviour. While an inherent degree of (temporal) variability exists in nature, unpredictable events like those described above in agricultural ditches can act as a disturbance for biological communities. Disturbance is defined here as an event which creates temporarily unsuitable abiotic conditions, such as anoxia, osmotic stress or decreased water transparency and which ultimately leads to the local reduction in invertebrate abundance or the complete removal of certain species. Disturbance events can cause a range of community responses and may promote diversity at intermediate levels by removing competitive and dominate species (i.e. the intermediate disturbance hypothesis, Connell, 1978). In general the greater the frequency and intensity of the disturbance the greater the chance it will lead to a decline in diversity.

Stable community equilibrium may not be reached in environments which experience regular disturbances and contain a range of species adapted to colonize newly available habitats (Connell, 1978; Huston, 1994, 1979). The rate at which a community can recover from a disturbance relates to habitat connectivity, the size of the available species pool (γ diversity) and species dispersal abilities. Therefore, it is important to consider multiple measures of diversity to understand how disturbance structures communities in any given environment (Chase, 2003; McCabe and Gotelli, 2000). Moreover, community dynamics are linked to the specific adaptations of individual species to cope with disturbances. Species life-history strategies reflect a species integrated response to their environment because temporal and spatial environmental factors can filter out species which do not have suitable life-history strategies (Poff, 1997; Southwood, 1977; Stearns, 1976; Verberk et al., 2013). The representation of specific life-history strategies may, therefore, reveal additional information about how environmental conditions are driving community composition (Verberk et al., 2013, 2010, 2008a).

Aside from environmental filtering, habitat size and geographical distance between suitable patches of habitat will also determine the ability of a population to recover from disturbance (MacArthur and Wilson, 1967). Indeed, invertebrate diversity in Dutch agricultural systems often varies between ditches and is likely to be associated with changeable environmental conditions (Verdonschot, 2012). Since the size and number of aquatic habitats are in decline as a result of increased agricultural intensity, it is important to understand the role of abiotic disturbance in structuring species diversity. A comprehensive study carried out over 20 years ago in the province of North Holland indicated that patterns in macroinvertebrate community composition were related to soil region, among other factors (Van der Hammen, 1992). These patterns were likely associated with differences in land use and hydrology in each soil region (Van der Hammen, 1992). However, land use has intensified over the past 20 years and it is not clear if these original patterns in diversity still hold true.

In this study we test the hypothesis that variability of nutrients and macro-ions are structuring invertebrate communities in an intensively managed low-lying agricultural landscape. We investigated this by analysing invertebrate adaptations to disturbance using insect life-history strategies. To this end we examined monitoring data collected in the province of North Holland from 84 drainage ditches situated in the three dominant soil regions (sand, clay and peat). We applied linear mixed models and canonical correspondence analyses (CCA) to investigate correlations between abiotic variability, average abiotic conditions and macroinvertebrate species-turnover and determine the importance of abiotic variability in driving invertebrate communities. In addition, the representation of specific insect life-history strategies (relating to dispersal, synchronized life-cycles, tolerance to abiotic extremes and reproductive strategies) were investigated to provide further insight into insect community structure. Relationships between the geographical distance between ditches and species-turnover were also assessed to determine if scale was an important factor structuring invertebrate communities within this landscape.

Materials and methods

Data collection and preparation

Abiotic parameters

Drainage ditches were sampled over a four year period (2008–2011) as part of the standard monitoring of waters in the province of North Holland, The Netherlands (Fig. 1). From the available data 84 drainage ditches (17 sand, 24 peat and 43 clay soil ditches) were selected. Selection was based on water type to include only secondary ditches (i.e. not part of the main transport system and thus not disturbed by large vessels) of small to medium size (width range 2–40 m, depth range 0.1–1.8 m), low salinity (average chloride concentrations <1000 mg/L) and sampled for invertebrates within the same season (i.e. between June and August). In the same ditches abiotic parameters were measured monthly, between February and August during the same year that invertebrates were sampled. Water transparency and pH were measured in the field (by Secchi disk and a WTW pH/Oxi 340i/set meter, respectively) and undisturbed, overlying water was collected for laboratory analyses of nitrogen (kjeldahl nitrogen

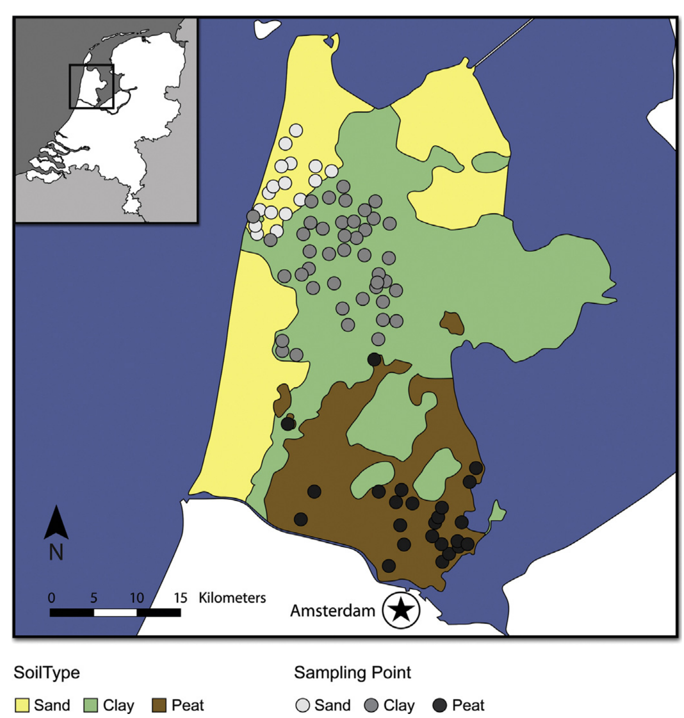

Fig. 1. Position of ditches sampled in the three soil regions. Invertebrates were collected once in the summer between June and August from each ditch in either 2008, 2010 or 2011. Abiotic variables were determined for all ditches at monthly intervals from February to August in the same year invertebrates were collected.