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Long-term monitoring reveals decreasing water beetle diversity, loss of specialists and community shifts over the past 28 years

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Abstract. 1. Lentic freshwater organisms are influenced by a multitude of factors, including geomorphology, hydrology, anthropogenic impacts and climate change. Organisms that depend on patchy resources such as water beetles may also be sensitive to anthropogenic habitat degradation, like pollution, eutrophication, water level or management alteration.

2. To assess composition and ecological trends in the water beetle communities of Central Europe, we sampled water beetles (Dytiscidae, Haliplidae, Noteridae) in 33 water bodies in Southern Germany from 1991 to 2018. We used manual, time-standardised capture during three periods: between 1991 and 1995, 2007 and 2008, and 2017 and 2018.

3. During the 28-year survey period, we captured a total of 81 species. We found annual declines in both species number (ca -1%) and abundance (ca -2%). Also, community composition showed significant changes over time. The significant impact of pH on the community composition suggests that the recorded changes through time partly reflect natural succession processes. However, a pronounced decline of beetle species belonging to the moor-related beetle associations indicated that Central European water beetles are also threatened by non-successional factors, including desiccation, increased nitrogen input and/or mineralisation, and the loss of specific habitats. This trend to physiological homogenisation resulted in corresponding community composition shifts.

4. To effectively protect endangered species, conservation strategies need to be aimed at regularly creating new water bodies with mineralic bottom substratum, and maintenance of moor water bodies that represent late successional stages.

Key words. Biodiversity, lentic inland water bodies, long-term monitoring, time series, water beetles.

Introduction

Species declines accompanying climate change have been recorded for many taxa including insects, and in many regions and their respective habitat types (Thomas *et al.*, 2004; Barnosky *et al.*, 2011; Sánchez-Bayo & Wyckhuys, 2019). A recent study

in Central Europe reported large declines in terrestrial insect biomass in protected areas embedded in agricultural landscapes, presumably due to increasing land-use intensification (Hallmann *et al.*, 2017). This biomass-related study highlights the overall trend, but the interpretation (politically and practically) is controversial in terms of the mechanistic causes of decline, as the specific biology and population trend of most of the affected species is not taken into account in such large-scale studies. Also specific species declines in insects have been shown for different target taxa and habitats (e.g. Seibold *et al.*,

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2019), and species extinctions are often reported to be non-random, reflecting trait-mediated selective processes (Cardillo *et al.*, 2005; Seibold *et al.*, 2015; Habel *et al.*, 2016). However, major freshwater groups like water beetles received little attention and analyses so far.

Lentic inland water bodies form discrete habitat patches in landscapes (Pope *et al.*, 2000; Hof *et al.*, 2008) and are influenced by factors that include geomorphology (e.g. sinks, pondages, barriers), hydrology (e.g. water inflow and runoff, drainage, inundation, precipitation, evaporation), succession, sedimentation, and anthropogenic impacts (e.g. utilisation, pollution, water management, fishery, recreation). The main drivers of their physicochemical features are the chemistry of the subsoil (Molinari *et al.*, 2012), evaporation (Townsend, 2002) and the collective nature of a water body resulting from the surface flume of its catchment area (Sioli, 1975). Organisms dwelling and breeding in lentic inland water bodies are inescapably subject to their physicochemical and structural characteristics (Hansch & Fujita, 1963; Rohr & Crumrine, 2005). Consequently, anthropogenic influences (Fairchild & Eidt, 1993; Dudgeon *et al.*, 2006; Perrett *et al.*, 2006; McMahon *et al.*, 2012) and/or climate change (Stocker *et al.*, 2013; Richman *et al.*, 2015), threatening these lentic water bodies, can lead to species losses at rates comparable to those in tropical forests (Ricciardi & Rasmussen, 1999). Moreover, different species may differ in their response to habitat change. For example, moor specialists may be negatively affected by high nitrogen levels (Smith *et al.*, 1999; Galloway *et al.*, 2004; Holden *et al.*, 2007), while, in general, species dwelling in small water bodies are relatively insensitive to compounds that contribute to eutrophication (Rosset *et al.*, 2014).

The identification of true declines in arthropods requires standardised long-term data (Jeffries, 2011; Ewald *et al.*, 2015; Habel *et al.*, 2016). Yet, in most studies on lentic water bodies either the survey was conducted for only a few years (Jeffries, 1994; Chase, 2007; Florencio *et al.*, 2009; Ripley & Simovich, 2009 but see, e.g., Ovaskainen, 2019), or a space-for-time substitution approach was used across chronosequences of successional stages (Palik *et al.*, 2001; Marchetti *et al.*, 2010; Sferra *et al.*, 2017). Accurate estimates of the biodiversity in various water bodies must take into account not only temporal but also spatial scales (Cayrou & Céréghino, 2005). Small lentic water bodies constitute a mosaic of different conditions at a regional scale (Rosset *et al.*, 2014). In these pond-scapes, a high gamma diversity is achieved as a result of a high beta diversity among ponds (Davies *et al.*, 2008). Accordingly, by obtaining samples from different types of small lentic water bodies at a regional scale, both the diversity and the trends of their water-dwelling organisms can be assessed.

Water beetles form a diverse invertebrate group (Jäch & Balke, 2008) and their ecology, especially that of the family Dytiscidae, has been well-studied (Wesenberg-Lund, 1943; Galewski, 1971; Yee, 2014; Miller & Bergsten, 2016). In freshwater ecosystems, water beetles have been used as indicators of biodiversity and ecosystem health (Bilton *et al.*, 2006; but see Rosset *et al.*, 2014). Among the factors that influence water beetle diversity are latitude, elevation, subsoil, and beetle life history (Flechtner, 1983; Vamosi *et al.*, 2007; Abellán *et al.*, 2012),

temperature, pH, and conductivity (Heino, 2000; Schmidl, 2003; Gutiérrez-Estrada & Bilton, 2010) as well as fish density and the species composition of water plants (Fairchild *et al.*, 2000; Gioria *et al.*, 2010).

To determine whether there was a change in diversity and change of composition of water beetle communities, we used the water beetle association concept of Schmidl (2003), which relates species assemblages to successional stages of vegetational and physiographical development of water bodies. We carried out time-standardised, repeated surveys of water beetle communities (Dytiscidae, Haliplidae and Noteridae) in water bodies of different habitat types and successional status, within one region and over 28 years (1991–2018). These surveys covered the whole range of available natural or near-to-nature water bodies in the study area, comprising early successional water bodies with no or little vegetation and mineralic substratum (the corresponding term for the typical water beetle association in these water bodies is mineralic substratum association), pools and ponds in open landscape rich in vegetation and with a substratum made of sludge and coarse detritus (detritus association), and mature old fen and moor water bodies (moor association) with a soil substratum made of dense and thick layers of vegetation and detritus, which chemically separates the water body from the subsoil. To disentangle the effects of this natural succession pathway, climate change and land-use intensification, we analysed physical and chemical parameters in parallel with our water beetle monitoring.

We predicted that (i) water beetles species of the mineralic substratum association would disappear nearly completely from the sampled water bodies because of the natural succession of vegetation and accumulation of detritus over the 28 years of the study; (ii) moor dwelling species (moor association) would also be negatively affected, due to increased eutrophication which shifts community composition towards detritus related species associations (detritus association); and thus (iii), these species associations typical for detritus-rich waterbodies would be the least affected.

Material and methods

Study sites

From 1991 to 2018, 33 lentic water bodies were monitored over a spatial extent of ~120 km² in southern Germany (Supporting Information Fig. S1). The mean annual temperature in the study region is 11–13 °C, with an annual rainfall of 600–960 mm (Dietmar *et al.*, 2007) (See Supporting Information Fig. S2 for annual mean temperatures and rainfall in the study area from 1991 to 2018). The investigated water bodies ranged from very small and partially ephemeral pools (6 m²) to mid-size ponds (1 ha). Fifteen water bodies were in open land, 15 in forests, and three were old sand pit water bodies. Eight of the 33 water bodies were extensively managed carp ponds.

Initially, in 1991, the 33 water bodies could be assigned to the following different successional stages and categories of habitat types (see above): four mineralic substratum water bodies, 14 moor and fen water bodies in forests, and 11 ponds in open

landscape (eight carp ponds and three unmanaged ponds), with four water bodies being in a transitional stage between mineralic and detritus-accumulated substratum. The sites were sampled in 1991, 1993 and 1995, in 2007 and 2008, and in 2017 and 2018. In the 1990s, 12 of the 33 water bodies were resampled between one and five times, yielding 75 survey events. In the 2000s, 16 of the 33 sites were resampled once each, for a total of 49 data sets. During the last survey decade, seven of the 33 water bodies were either desiccated or no longer existed (four moor and fen water bodies, two ponds, and one mineralic substratum pool). Thus, only 26 sites could be resampled in 2017 and 2018. In this decade, three ponds were resampled once each, resulting in 29 additional data sets. In total, 153 surveys were conducted from 1991 to 2018 (see Table 1).

Beetle sampling and classification

Water beetles were collected using a time-standardised direct search and always either collected or supervised by J.S. Each water

Table 1. Number of surveys per water body and year.

Water body/ Year	1991	1993	1995	2007	2008	2017	2018
1	1	0	0	2	0	1	1
2	3	0	0	2	0	1	0
3	0	0	1	2	0	1	0
4	0	0	1	2	0	1	0
5	3	3	0	1	0	1	1
6	3	2	0	1	0	1	1
7	1	0	0	1	0	1	0
8	1	0	0	2	0	1	0
9	1	0	0	1	0	1	0
10	0	3	0	2	0	1	0
11	3	3	0	1	0	0	0
12	1	3	0	2	0	0	1
13	3	3	0	2	0	0	0
14	1	3	0	2	0	0	0
15	1	0	0	2	0	1	0
16	3	3	0	2	0	0	0
17	1	0	0	2	0	1	0
18	0	1	0	2	0	0	1
19	1	0	0	1	0	1	0
20	0	1	0	2	0	1	0
21	2	0	0	1	0	1	0
22	0	1	0	1	1	1	0
23	1	0	0	1	0	0	0
24	0	3	0	1	0	1	0
25	0	1	0	1	1	0	0
26	1	0	0	1	0	1	0
27	1	0	0	0	1	0	0
28	3	3	0	0	1	1	0
29	0	1	0	0	1	1	0
30	0	1	0	0	1	1	0
31	1	0	0	0	1	1	0
32	0	1	0	0	1	1	0
33	0	1	0	0	1	1	0

body was sampled by hand for 90 min, using a colander (25 cm diameter and 0.7 mm mesh size) in water containing dense vegetation, and a net (20 cm diameter, 1.0 mm mesh size) in open water bodies. All captured beetle specimens were collected. Collecting was done during the day, between 12:00 and 18:00, but not on rainy days. This ensured comparable data, with respect to the water parameters (see below). Only water beetles belonging to the Hydradephaga were considered, but Gyrinidae (whirligig beetles) were excluded as these require different collecting methods. Specimens from the hydradephagan families Dyticidae (excluding the genera *Dytiscus* and *Cybister*), Halipilidae, and Noteridae were determined to species level by J.S. Nomenclature follows the catalogue of Nilsson & Hájek (2019). The water beetle association concept of Schmidl (2003) was used to classify species and associations ecologically, with respect to the physiographical status and successional gradient of water body and vegetation development, respectively.

This concept recognises three main associations and eight sub-associations along the successional and pH-related gradient: Species of the mineralic substratum association (A-category) are found in new or disturbed water bodies devoid of detritus and vascular plants on the mineralic ground; therein, species within the mineralophilous sub-association (A1) require water bodies with an argillaceous, hardness-component-rich substrate, and those within the psammophilous sub-association (A2) water bodies with a sandy, hardness-component-poor substrate. With further succession of the vegetation, water beetle communities develop towards detritus associations (B-category), which occur in higher-successional-level water bodies in open landscape that are characterised by sludge and/or coarse detritus accumulation and decreasing pH values. The accrual of species of the argillophilous sub-association (B1) results in a transitional species community that is followed by a community of species of the limnophilous sub-association (B2). The latter species are typically found in mature meso- and eutrophic ponds and pools containing extensive vascular plant vegetation and organic detritus, thus shielding the water body from the mineralic subsoil. Species of the acidophilic sub-association (B3) are found in water bodies affected by siltation, fens and low moors with strong accumulations of detritus, and sub-dystrophic water caused by dissolved humus. The marshland forest association (B2/C1) is a transition between limnophilous detritus association B2 and acidic, oligo- to mesotrophic, shady forest water bodies of umbrophilic moor associations C1. Moor associations (C-category) may either be umbrophilic (umbrophilic sub-association C1), with species occurring mostly in small shady forest pools with a litter layer and a few algae, or sphagnophilic (sphagnophilic sub-association C2), comprising tyrphophilic or tyrphobiontic species that colonise peat bogs with significant *Sphagnum spp.* cover (over raised bog formations) and a low pH (see Supporting Information Table S1 for species list).

Water bodies and water parameters

The physical and chemical parameters of the water bodies were determined at each survey date. The maximum depth at 1 m from the edge and the elevation of the water body was

recorded, and pH and temperature ($^{\circ}\text{C}$) were measured using the pH 320 pH-metre fitted with a SenTix 41 pH-sensor (both from WTW, Weilheim). A WTW Oxi-Meter Oxi 320 and CelloX 325 electrode (both from WTW, Weilheim) were used to measure oxygen saturation (%). Furthermore, nitrite (mg l^{-1}) and chloride (mg l^{-1}) were determined using a PF 10 filter-photometer (Macherey-Nagel, Düren), and the conductivity (μS) using a LF91 conductivity metre with a KLE1/T conductivity sensor (both from Macherey-Nagel, Düren). Total hardness (dH°) and carbonate hardness (dH°) were determined by titration. The water used in the chemical analyses was taken 1 m from the water's edge at a depth of 10–50 cm depending on the total depth of the water. Spearman correlation between the measured parameters were calculated using the *cor* function within the stats package in R (R Core Team, 2018).

Statistical methods

Changes in water beetle communities through time were quantified using four measures: species richness, abundance, relative richness and community composition. Species richness and abundance of each association was calculated per survey in order to include association as an explanatory variable in the models.

Hierarchical generalised additive models (HGAM) sensu Pedersen *et al.* (2019) were used to model species richness and abundance. Relative richness was also modelled with species richness as dependent variable, while abundance was included as explanatory variable. These models are extensions of the standard generalised additive model (GAM) framework (Hastie & Tibshirani, 1990) and allow smooth functional relationships between predictor and response to vary between groups (Pedersen *et al.*, 2019). These are implemented in the *mgcv* package (Wood, 2017) in R (version 3.5.2) (R Core Team, 2018), which was used for all statistical analyses. The year was modelled in an overall smoother and in an additional smooth term, which specified the group-level smooth terms in a factor-smooth interaction, in order to show group-specific deviations from the global function (see Supporting Information S3 for model formula). Elevation of the water bodies, water temperature, oxygen saturation, total hardness, carbonate hardness, nitrite concentration, chloride concentration, pH and conductivity as well as water depth and the day of the year (1–365 further referred to as season) were included in the model as global smooth terms. Latitude and longitude were wrapped in the same smooth term (see Supporting Information S3). All the continuous variables used thin plate splines as basis function within the smoothers except for the season where cubic cycle splines were used as basis function. The initial waterbody type and the survey ID were wrapped in smoothers as discrete random effects. The survey-level random effect accounts for frequently observed overdispersion in models of count data (Harrison, 2014). Furthermore, it accounted for the fact that sampling intensity differed between the decades. A Tweedie error distribution with a log-link function was used, which is appropriate for data with a non-zero probability of zero observations (Gilchrist & Drinkwater, 2000). Restricted maximum likelihood (REML) was

used as the smoothing parameter estimation method. Finally, variable selection was performed with the *gam* internal argument 'select = T'.

Canonical correspondence analysis (CCA) was used in order to analyse whether the patterns found via the HGAMs translate into community composition shifts, while also controlling for explanatory variables using the *cca* function within the *vegan* package (Oksanen *et al.*, 2018). Communities were computed at the survey level, temperature, oxygen saturation, conductivity, total and carbonate hardness, chloride and nitrite concentration, pH and temperature as well as the year were used as environmental variables. Variable selection was performed with a stepwise model selection using the *ordistep* function.

Results

In total, 19 232 specimens (average 126 per sample, range 4–487) were recorded, belonging to 81 different water beetle species (average 11 per sample, range 2–25) in all water bodies sampled since 1991 (see Supporting Information Table S2 for species list and abundance per survey year). Surveyed water bodies ranged from a minimum pH of 3.9, which is near the lower end of the pH range of natural water bodies (e.g. in raised bogs), and a maximum pH of 10.1, which is close to the upper end of the pH gradient of natural water bodies. pH and conductivity were positively correlated (Spearman $\rho = 0.56$) in real-time comparison (Supporting Information Table S3).

Abundance and richness

The total abundance and the species richness of the water beetles per survey decreased by approximately 2% and ca 1%, respectively (Figs. 1 and 2a–c). Thus, mean abundance and species richness per survey decreased from 151 to 74 individuals (Fig. 1a), and from 13 to 7 species (Fig. 1b), respectively. Furthermore, abundance increased with increasing nitrite and total hardness and decreased with increasing temperature, pH, conductivity and depth (Table 2; Supporting Information Fig. S3). Species richness decreased with increasing elevation and conductivity (Table 2; Supporting Information Fig. S4). Relative richness decreased yearly and increased slightly with increasing depth of the waterbodies. It was also significantly influenced by the elevation (Table 2; Supporting Information Fig. S5). Survey ID had a significant effect on abundance, species richness and relative richness. The initial water body type had a significant effect on abundance and species richness.

Associations

Overall, we recorded five species belonging to mineralic substratum associations (A1/A2), 47 species belonging to detritus association (B1, B2, B3) and the transitional marshland forest association (B2/C1), and 16 species belonging to the moor association (C1/C2). The association–year interaction was significant

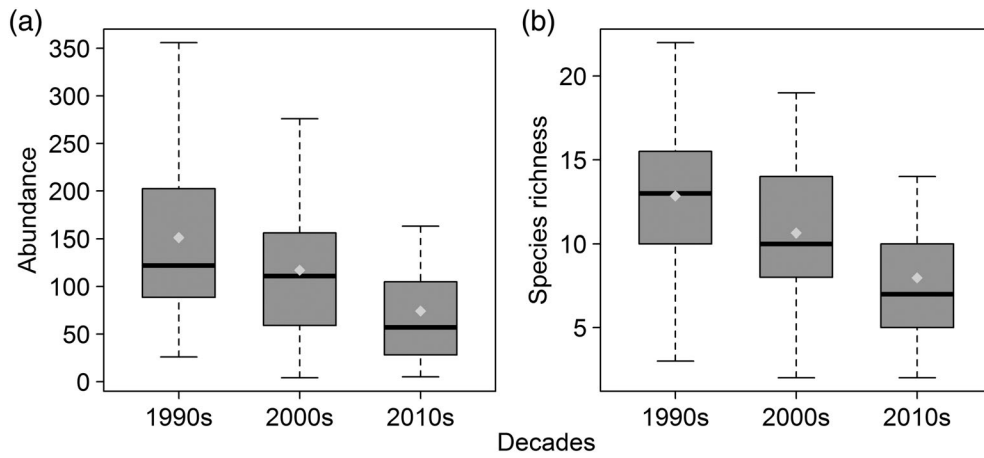


Fig. 1. Boxplots of water beetle abundance (a) and species richness (b) per survey and decade. Light grey rhombs indicate means.

for all three dependent variables and showed high effect sizes (Table 2). The group specific deviation from the overall temporal trend was most pronounced in mineralophilous and psammophilous water beetle associations (mineralic substratum sub-

associations A1/A2), which indicates that the species belonging to these associations showed the greatest declines over time (Fig. 2d–d). The species belonging to the umbrophilous and sphagnophilous species (moor sub-associations C1/C2) also

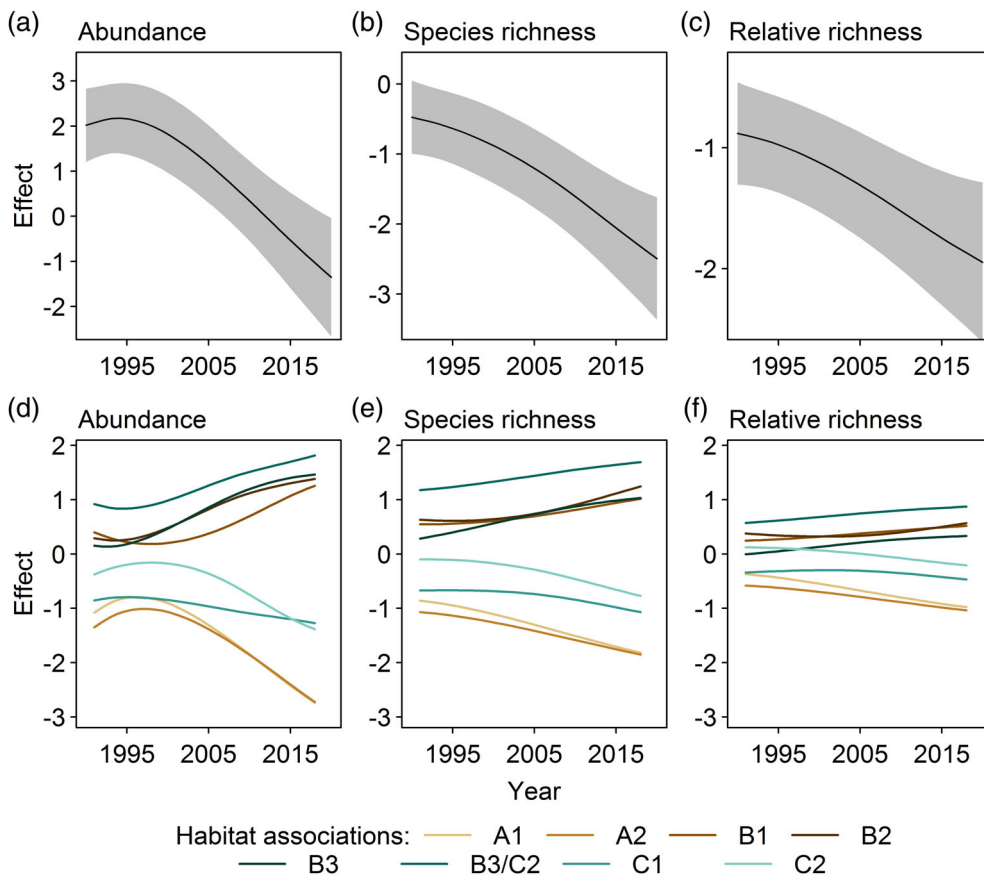


Fig. 2. Effect sizes of the year as global function and association specific deviations from the main trend for abundance (a,d), species richness (b,e) and relative richness (c,f). The A-categories are mineralic substratum associations, the B-categories detritus associations and the C-categories moor associations. [Color figure can be viewed at wileyonlinelibrary.com]

Table 2. Summaries of hierarchical generalised additive models for the dependent variables abundance, species richness and species richness corrected for abundance (relative richness).

Term	Abundance		Species richness		Relative richness	
	<i>F</i>	Significance	<i>F</i>	Significance	<i>F</i>	Significance
Year	1.921	***	2.413	***	1.030	**
Year:association	8.640	***	21.788	***	4.966	***
Season	–		–		–	
Survey ID	0.509	***	0.989	***	0.471	***
Initial type	7.809	***	1.914	*	1.011	
Lon/Lat	0.431		1.337	*	–	
Elevation	–		3.373	**	4.513	*
Temperature	0.451		0.513		0.239	
Oxygen saturation	–		–		–	
Total hardness	2.579	**	–		–	
Carbonate hardness	–		–		–	
Nitrite	5.833	***	–		–	
Chloride	–		–		–	
pH	1.971	**	0.688		–	
Conductivity	2.608	***	0.837		–	
Depth	1.842	**	0.001		0.807	
Abundance	NA	NA	NA	NA	102.705	***

Dashes indicate variables, which did not contribute to the according models and were thus excluded. NAs indicate variables, which were not included in the according model from the start.

deviated negatively from the overall trend, although the deviation was less pronounced than for the mineralic substratum associations (Fig. 2c–f). The trend for the species belonging to the ecological mid-position associations (detritus associations B1, B2, B3 and marshland forest association B2/C1) deviated positively from the overall temporal trend (Fig. 2c–f). This means that species belonging to detritus sub-associations did not decrease but show rather stable trends, in contrast to mineralic substratum and moor association related species. The deviation patterns from the overall trend were similar for abundance, species richness and relative richness.

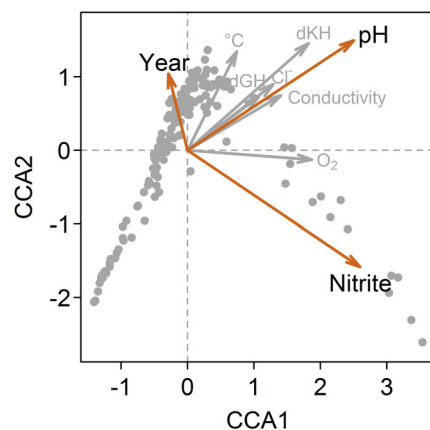


Fig. 3. CCA ordination with main gradients highlighted in orange. [Color figure can be viewed at wileyonlinelibrary.com]

Community composition

The stepwise model selection for the CCA showed that all included parameters had a significant influence (Supporting Information Table S6). Thus, all of them were kept in the CCA. CA inertia was 11.55, CCA constrained 2.18 (19%). CCA axes 1–4 cumulatively explained 73% (30.3, 50.5, 62.6, and 73.0) of the total constrained variation (Supporting Information Tables S4 and S5 for further details). The main gradient was defined by nitrite, pH and carbonate hardness (Fig. 3). Conductivity, chloride and total hardness gradients values are rising co-linear with pH and carbonate hardness. High values of nitrite are found mainly in young water bodies with mineralic substratum. Year (time) is another quite independent gradient in the community composition, with rising temperature being the most closely correlated parameter.

Discussion

Within the total temporal range of our observation of 28 years, nearly 50% of all species belonging to the three water beetle families Dytiscidae, Haliplidae, and Noteridae recorded in Germany (Spitzenberg *et al.*, 2016) were sampled. As the temperature had no significant effect on abundance and richness in our calculations, effects attributable to climate change may have been mediated by the observed decrease in water depth and by resulting increases in conductivity and total water hardness by concentration effects. Note that especially abundance was significantly influenced by these parameters. The negative effect of rising maximum depth (measured 1 m from the water's edge) on abundance can also be explained by the steep slopes at the banks of

the surveyed water bodies (esp. ponds) with larger depths, resulting in fewer habitat structures and water plants, both of which provide breeding sites for water beetles (Nilsson *et al.*, 1994; Fairchild *et al.*, 2003). The decrease in richness with increasing elevation is in line with previous findings (Vamosi *et al.*, 2007), although the maximal elevation difference in our study area was only ~100 m a.s.l.

Effects of pH and conductivity on water beetle abundance and richness

We found more specimens in water bodies with lower pH, which is in line with previous studies (Nilsson & Soderberg, 1996; Batzer *et al.*, 2004 but see Arnott *et al.*, 2006). However, although our samples covered nearly the entire gradient of the naturally occurring pH range, we could not detect a clear threshold at which this trend decreased or changed (Supporting Information Fig. S3). In near-to-nature lentic water bodies, pH is mainly influenced by the geological substratum and the amount of plants and detritus (succession). Under natural conditions, a lower pH correlates with increases in the amounts of plant matter and humus (Vuorenmaa *et al.*, 2006) and increasing isolation of the water body from geological underground (Schmidl, 2003, but see Carvalho *et al.*, 2005 for laboratory conditions and Yee & Juliano, 2007 for rotholes). Detritus accumulation in turn enlarges the structural diversity of a habitat and therefore water beetle abundance (Schmidl, 2003).

We found a positive correlation of pH and conductivity (Supporting Information Table S3), and at the same time decreasing abundances and species richness with increasing conductivity (Supporting Information S3). This is in line with the above outlined, corresponding effects of detritus on pH, but is in contrast to the observations of some studies in which rising conductivity was shown to have a positive effect on species richness (Eyre *et al.*, 1990; Heino, 2000; Bilton *et al.*, 2006), at least up to a threshold of around 600 μS (Gutiérrez-Estrada & Bilton, 2010). Our results suggest that water bodies with lower abundances of water beetles and fewer species had conductivity levels exceeding this 600 μS threshold; however, there was no such clear threshold in our data set. Increasing levels of conductivity are often a result of a concentration effect (Townsend, 2002) arising from increased evaporation or a deficient water supply. Our finding of decreasing water levels comply with this and may have led to water bodies that negatively influenced abundances and species numbers (Blasius & Merritt, 2002).

Effects of time on water beetle abundance and richness

For all of the surveyed water types, time (year) had a significant negative effect on abundance, species richness, and relative richness. A negative effect over time has been previously reported but variably interpreted. According to Nilsson (1984), succession in lentic water bodies is accompanied by a decline in species numbers, whereas Fairchild (2000) demonstrated higher diversities in older water bodies and other studies reported no change in species richness or abundance during

succession (Spieles *et al.*, 2006; Miguel-Chinchilla *et al.*, 2014). Thus, while the reductions in abundance and diversity can in part be attributed to natural succession (see below), they cannot be clearly separated from time-related effects, such as trophic or structural disturbances or chemical disturbances such as insecticides (Fairchild & Eidt, 1993; Fairchild *et al.*, 2000; Wood *et al.*, 2003; Death & Zimmermann, 2005; Rohr & Crumrine, 2005). As habitat availability in lentic water bodies tends to influence beetle species richness positively (Dehling *et al.*, 2010), the observed losses might also have resulted from habitat loss at the landscape level or by *in situ* losses of structural and vegetational diversity. Alternatively, the frequency of drought events may have increased as a consequence of climate change, as noted previously. Drought has been shown to affect water beetles negatively by reducing the number and type of their habitats (Kholin & Nilsson, 1998). In fact, an attempt to start a similar monitoring programme in moor water bodies in 2015 and subsequent years in the same study area failed, because nearly all water bodies were dried up in summer.

Association specific deviations from overall temporal trend

Over the 28 years of this study, the observed association range narrowed, with the opposing changes at both ends of the successional gradient shown in the year–association interaction (Fig. 2). Species belonging to the mineralic substratum associations (A1, A2) vanished naturally during progressive succession (Schmidl, 2003). At the other end of the successional gradient instead, species losses and decreases in total abundances occurred that could not be attributed to natural succession. Water bodies initially suitable for moor association species (C1, C2) gradually lost their specific habitat quality for the respective species sets. This might have been due to increases in air-borne nitrogen inputs (De Schrijver *et al.*, 2011) or to the transient complete desiccation of these water bodies, accompanied by remineralisation effects and reverse vegetational alterations (Limpens *et al.*, 2011). Although eutrophication may not necessarily pose a major threat to water beetle diversity in small water bodies (Rosset *et al.*, 2014), special habitats such as nutrient-poor moors and fens and their faunas suffer generally from eutrophication (Holden *et al.*, 2007).

Declines both in mineralic substrate and moor associations led to a *bidirectional* homogenisation (Figs. 2 and 3) of communities towards *detritus* associations. This is in line with the general findings in insects of a loss of habitat specialists and the homogenisation of insect communities in land habitats (Augenstein *et al.*, 2012; Gossner *et al.*, 2016). Both should be carefully considered in conservation strategies in which the creation and maintenance of water habitats are important issues and a practical tool for nature conservation (Davies *et al.*, 2008; Brainwood & Burgin, 2009; Thiere *et al.*, 2009; Gioria *et al.*, 2010). Based on our results, conservation efforts should routinely include the creation of new water bodies with mineralic bottom substratum. In addition, moor water bodies should be actively promoted in suitable areas and soils and existing moor water bodies maintained. Restoration of moor and fen water bodies requires a long period of development until they become suitable

for the typical species sets (Więcek *et al.*, 2013). Also, the presence of an appropriate source habitat is crucial for successful recolonisation (Van Duinen *et al.*, 2003). Accordingly, the conservation of water bodies and their fauna should be organised at a landscape scale to take also organisms into account, which are poor dispersers (Kehl & Dettner, 2007; Lønsmann Iversen *et al.*, 2013).

Our findings showed that detritus associations were not negatively affected over time. Ponds in open landscape are still used and maintained by humans for fishery but also for nature conservation issues. Mature ponds with a high structural diversity (different reed and water plant formations, shallow water body sides, coarse detritus, etc.) and higher nutrition levels are still present in the study area, thus supporting higher species richness and abundances (Fairchild *et al.*, 2000; Palik *et al.*, 2001; Schmidl, 2003). While early successional pools with no or little vegetation and mineralic substratum are transitional by nature, the ecological nodus (*sensu* Ellenberg, 1988, see also Austin *et al.*, 1989) of pond associations currently is enlarged in the successional continuum by the discussed nutrient input, which suppresses or retards the development towards dystrophic moor associations, or even reverses the latter back into the nutrient richer detritus habitat type.

Shifts in community composition

Community composition was strongly driven by pH (Fig. 3), which is a good proxy for succession (Schmidl, 2003). This finding was in line with the results of earlier studies showing that pH is one of the most important chemical factors correlating with the species composition of small lentic water bodies (Larson, 1985; Eyre *et al.*, 1990; Zikeli *et al.*, 2002; Fritz *et al.*, 2004). Nitrite was another key determinant of community composition in our study and its concentration decreased over time (Fig. 3). Nitrite accumulation is a prominent feature of fresh, mineralic substrate water bodies and it occurs before the bacterial flora has become established (Smith *et al.*, 1997), i.e. the denitrification cascade is not well developed yet. Thus, as the sampled water bodies underwent succession, their nitrite levels naturally dropped, because of the decreasing pH, the development of the denitrifying bacterial flora and the pH-related transition of nitrite to ammonium (Suzuki *et al.*, 1974; Grunditz & Dalhammar, 2001; Strauss *et al.*, 2002; Jiménez *et al.*, 2011).

Prospects

This study shows that especially mineralic substratum and moor water-beetle associations are facing threats and declines in diversity and abundance, correlating with changes in the physicochemical setting especially of these water types. Despite the fact that the time range of 28 years is a long survey period, some of the evaluated factors could be counterchecked by comparable surveys in forest areas, where changes on landscape (alteration of water catchment, agricultural nutrient input) or climate level are more moderate, compared to open landscapes. Methodologically, a more continuous survey would allow greater power to

evaluate variation through time, and the regular inclusion of newly created water bodies with mineralic substratum to the surveying scheme would allow assessment of the status of the corresponding beetle associations at the landscape scale correctly. Furthermore, though time standardised collecting is a reliable tool for assessing water beetle fauna of small to mid-sized water bodies, a sampling with standardised traps would be a way of excluding sampler biases, which is especially important when considering long time spans and essential for establishing a general tool for bioindication.

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Conflict of Interest

The authors declare that there is no conflict of interest.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Study area in southern Germany. Scale bar indicates kilometres. The reference system is WGS84. Inset: location in Central Europe.

Figure S2. Mean temperature [$^{\circ}\text{C}$] (A) and mean precipitation [l/m^2] the study area between 1991 and 2018. Dotted lines represent overall means. Data was recorded by the German Meteorological Service (DWD) and provided by <http://skilma.de>.

Table S1. Species per associations and sub-associations, with additional character species for each association (if applicable)

Figure S3. Partial effect plots of significant explanatory variables for abundance.

Figure S4. Partial effect plots of significant explanatory variables for species.

Figure S5. Partial effect plots of significant explanatory variables for relative richness.

Table S2. List of captured and analysed beetle species per year. n water bodies specifies in how many waters it was found in the corresponding year. Individuals is the sum of total catches per year.

Table S3. Spearman correlation matrix of measured water parameters

Table S4. CCA eigenvalues and their contribution to the scaled Chi-square

Table S5. Partitioning of scaled Chi-square

Table S6. Variable selection results table

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