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Restoration of raised bogs–Land-use history determines the composition of dragonfly assemblages

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ABSTRACT

Even though bogs function as the most important terrestrial carbon store on Earth and play a crucial role in the conservation of highly endangered species, the area covered by peatlands is declining globally. Consequently, numerous restoration efforts within degraded bogs have been realized. In many cases, however, it is unknown whether the conservation measures have been successful.

We used Odonata (hereafter referred to as dragonflies) as ecological indicators to evaluate the restoration success of rewetting measures in central European degraded raised bogs. Depending on their land-use history (rewetted industrial peat cuts with and without former agricultural use), two types of bog restoration were compared with rural peat cuts (control).

Our study demonstrated that restored bogs are important habitats for dragonfly conservation. Both types of restored bogs were as diverse in overall species richness as the control plots. However, land-use history had a strong effect on restoration success. All raised-bog species of the study area were able to recolonize at least some of the nutrient-poor restored bogs. The situation was different for the nutrient-rich restored bogs. Due to the high nutrient content – caused by the former agricultural use – the characteristic dragonfly fauna of raised bogs will be unlikely to be able to recolonize in these locations in the long term. Nevertheless, the nutrient-rich restored bogs represent an important secondary habitat, especially for transition-bog species. In conclusion, the conducted restoration measures created a network of small oligo- to mesotrophic water bodies, which fosters aquatic macroinvertebrate diversity in bogs.

1. Introduction

Natural bogs are highly complex ecosystems that are formed by slowly accumulating plant material (mainly peat mosses, *Sphagnum* spp.) (Joosten and Clarke, 2002). They function as the most important terrestrial carbon store on Earth and supply multiple other ecosystem services, such as climate regulation, water purification and storage (Parish et al., 2008; Rydin and Jeglum, 2013; Andersen et al., 2017). In addition, they are characterized by a highly specific flora and fauna, resulting in a high nature conservation value (Spitzer and Danks, 2006; van Kleef et al., 2012; Beadle et al., 2015).

Peatlands are mainly distributed in the northern hemisphere, where cool climates and relatively high precipitation lead to a waterlogged environment (Joosten and Clarke, 2002; Bragg and Lindsay, 2003; Spitzer and Danks, 2006). Under these conditions, peat bogs developed over millennia in large areas of the temperate and boreal zone. At least 80% of the global share of peat bogs can be found in this part of the world (Rydin and Jeglum, 2013). However, most bogs have been modified by human activities. In Europe, their drainage for peat cutting, agriculture and forestry began already in medieval times (van Dam, 2001). However, the most severe changes took place after 1950 (EC, 2007). Systematic cultivation of formerly intact peatlands – including the application of mineral fertilizer to improve the agricultural productivity of the naturally nutrient-poor ecosystems – resulted in severe area loss (Joosten and Clarke, 2002; Bragg and Lindsay, 2003; Rydin and Jeglum, 2013). Particularly in central Europe, the decrease was dramatic, with only 1% of the original bog area remaining (Joosten and Couwenberg, 2001). As a result, today, numerous characteristic bog species are endangered or already extinct (e.g., Topic and Stancic, 2006; Hughes et al., 2008). Consequently, most European bog types are protected under the EU Habitats Directive, including raised and transition bogs (Annex I habitats 7110, 7120 and 7140, respectively; EC,

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2007).

As an important refuge for rare and endangered bog specialists, but also as a carbon store, numerous restoration efforts within degraded bogs have been realized, especially in Europe with the beginning of the EU Life Program in the early 1990s (EC, 2007; Andersen et al., 2017). Conservation managers commonly used drainage blocking (rewetting) to improve the hydrological function of peatlands (e.g., Armstrong et al., 2009; Wilson et al., 2011; Holden et al., 2017). Nevertheless, most restoration studies have been carried out on single bogs (e.g., Howie et al., 2009; Ketcheson and Price, 2011) or focused on plants, in particular peat-building *Sphagnum* mosses (e.g., Pellerin and Lavoie, 1999; Farrell and Doyle, 2003; Campeau et al., 2004). Studies evaluating the fauna of restored bogs are comparatively rare, although some groups of species have already been tested as ecological indicators for the success of habitat restoration (e.g., van Duinen et al., 2003; Mazerolle et al., 2006; Taillefer and Wheeler, 2012).

In aquatic habitats, Odonata (hereafter referred to as dragonflies) are particularly suitable as bioindicators for assessing the success of restoration measures as they reflect the response of other taxonomic groups to environmental change most consistently (e.g., Briers and Biggs, 2003; Simaika and Samways, 2011; Hassall, 2015). Consequently, this group of insects may function as a cross-taxon surrogate to represent broader freshwater diversity patterns (Bried and Samways, 2015).

We therefore used dragonflies as ecological indicators to evaluate the restoration success of rewetting measures in central European degraded raised bogs. Depending on their land-use history (rewetted industrial peat cuts with and without former agricultural use), two types of bog restorations were compared with rural peat cuts. The latter function as a control as they represent the most natural bog pools present in the degraded raised bogs of the study area. Particularly, this study aimed to answer the following questions:

(i) To what extent were target (raised-bog and transition-bog) species able to establish within the restored bogs?
(ii) Do the dragonfly assemblages differ between the three bog types?
(iii) Which environmental parameters explain the observed diversity patterns?

2. Materials and methods

2.1. Study area

The study area ('Diepholzer Moorniederung') covers an area of about 1180 km^2 (Belting and Obracay, 2016) and is located in north-western Germany, in the southern part of the federal state of Lower Saxony (52°36′ N, 8°22′ E). The climate is subatlantic with mean monthly temperatures of 1.1 °C in January and 16.9 °C in August. Annual precipitation amounts to 710 mm. After the last ice age, Lower Saxony developed – due to its humid climate – into being the bog-richest federal state in Germany (Grosse-Brauckmann, 1997). However, bog cultivation and peat harvesting within the last 100 years have led to a severe decline of the peatland area. Today, only 3% of the remaining peatlands in Lower Saxony are characterized by semi-natural conditions (NLWKN, 2006) and intact bogs have been completely destroyed (Grosse-Brauckmann, 1997). Among the remaining peatlands, the study area represents one of the largest raised-bog areas in Lower Saxony and is therefore of trans-regional importance for the conservation of typical bog species in central Europe (NLWKN, 2006).

2.2. Subareas and plots

Within the study area, we investigated nine raised bogs (subareas) (Table A1), where restoration measures have taken place during the last 30 years (Belting and Obracay, 2016). The size of these bogs varied between 376 ha and 16,098 ha (mean: 3476 ha ± 1623 SE). To avoid problems with potential spatial autocorrelation, we used the variable subarea as a random effect (see also Section 2.5). Within the nine subareas, dragonfly species richness and abundance were studied in 33 plots. The number of plots per subarea depended on their availability and varied between two and eight per subarea (mean: 3.7 ± 0.9 SE). In order to evaluate the effects of bog restoration, we compared the dragonfly assemblages of restored bogs with two different land-use histories (cf. Rosinski, 2012):

(i) Nutrient-rich restored bogs (n plots = 9): raised bogs, which were largely drained and then used as grassland. Since the 1980s agricultural use was replaced by industrial peat cutting. Restoration of these sites has taken place 8 to 31 years ago by rewetting of the industrial peat cuts. However, there is still evidence of nutrient enrichment from the past agricultural use, as indicated by a high cover of *Juncus effusus*.
(ii) Nutrient-poor restored bogs (n plots = 12): raised bogs, which were largely drained and subsequently used for industrial peat extraction. These bogs were restored using the same methods and within the same time period as the nutrient-rich restored bogs (see above). The nutrient supply was low as indicated by a high cover of the oligotrophic species *Eriophorum angustifolium* and/or *Eriophorum vaginatum*.

As a control, rural peat cuts (n plots = 12) were used, since they are considered the most natural bog pools that are still being present in the degraded raised bogs of north-western Germany. The exact age of the rural peat cuts was unknown, but all were created before 1980.

2.3. Habitat characteristics

Several biotic habitat quality parameters were recorded per plot (Table A2): the cover of *Sphagnum* mosses (submerged or floating), as well as the cover of the vascular plants *E. angustifolium*, *E. vaginatum* and *J. effusus*, were estimated as indicators of habitat productivity. Both *Eriophorum* species prefer oligotrophic conditions (Ellenberg nutrient indicator value [ENIV]: 2 and 1, respectively); in contrast, *J. effusus* is typical of more mesotrophic habitats (ENIV: 4) (Ellenberg et al., 2001; Grime et al., 2007). Additionally, the cover of all other vascular plants (usually *Molinia caerulea*) was estimated. All 33 plots were free of shrubs and trees (cover < 10%). During the field survey, no evidence of fish occurrence was found at any of the plots.

As abiotic habitat characteristics, pH, the water surface extent (ha), the water level (cm) and the electrolytic conductivity (µS/cm) were measured five times over the course of the summer. For further analysis of pH and conductivity, we pooled the data by using the mean values of each variable. The water level values were used to determine the loss of water surface extent (%) and as a substitute for the plot size served the maximum water surface extent (ha) (Table A2).

2.4. Dragonfly sampling

The survey was carried out from the beginning of May to the end of August 2011. We sampled dragonfly exuviae because they indicate successful reproduction and are, thus, much more suited for ecological studies than the highly mobile adults (Raebel et al., 2010). This is especially true for temperate zones like central Europe, where the exuviae are well known and moderate rainfalls usually did not cause substantial exuviae loss (cf. Bried et al., 2012). Exuviae data sets were collected six times in three week intervals. At each plot, exuviae were sampled within a ring of 0.5 m^2 size, which was randomly placed ten times around the shoreline of the water body (total area: 5 m^2) (cf. Holtmann et al., 2018, 2019). Exuviae were determined in the laboratory using the identification key of Heidemann and Seidenbusch (1993).

Based on their ecological requirements, we defined the target species of (semi-)natural bogs. According to Sternberg and Buchwald (1999, 2000), two groups can be differentiated (Table A3):

(i) Raised-bog species: These species are characteristic of the oligotrophic pools in the degraded raised bogs of the study area and have the highest (regional) habitat specificity.
(ii) Transition-bog species: This group of species has a broader spectrum of colonized habitats and can be found in more mesotrophic pools of peat- and/or heathlands.

2.5. Statistical analysis

Intercorrelations of predictor variables were examined prior to multiple regression analysis (see below) by applying a Spearman's correlation matrix that included all metric predictor variables. Strongly intercorrelated variables (Spearman's rank correlation, $|r_s| > 0.6$) were excluded from the models (Table A2; cf. Dormann et al., 2013).

In order to analyze the environmental parameters (Table A2) that explained the species richness and abundance of the target dragonfly species, we conducted generalized linear mixed-effects models (GLMM: glmer, Bates et al., 2015) with a Poisson error structure. If overdispersion was detected, standard errors were corrected using negative binomial GLMM (Crawley, 2007). For all GLMM, the variable *subarea* (Section 2.2) was setup as a random factor. In order to increase model robustness and to identify the most important environmental parameters, we applied model averaging based on an information-theoretic approach (Grueber et al., 2011). Model averaging was conducted using the ‘dredge’ function (R package MuMIn; Bartón, 2017), and only included top-ranked models within ΔAICc < 3 (cf. Grueber et al., 2011). To avoid overfitting the model, the analysis was performed in three steps: (i) The first model was exclusively fitted with the abiotic variables (Table A2); (ii) we calculated a GLMM with all biotic variables (Table A2); and (iii) finally, a synthesis model was conducted, which included the significant predictor variables from steps i and ii.

Plot age, the time since the creation of the water body, could not be used for the analysis, because it was unknown for the control plots (Section 2.2, cf. van Duinen et al., 2003). However, we tested whether there was a relationship between plot age and the species richness of raised-bog and transition-bog species. Therefore, we conducted two univariate generalized linear models (GLM) with a Gaussian or Poisson error structure, respectively.

We also analyzed whether species data (species richness and abundance of all, raised-bog and transition-bog species) and the environmental variables (Table A2) differed between the three bog types. Accordingly, GLMM with a Poisson or negative binomial error structure and *subarea* as a random factor were performed. All correlations, GLM and GLMM were done with R 3.3.2 (R Development Core Team, 2018).

In order to identify indicator species for each bog type, an indicator species analysis (ISA) was carried out by using PC-ORD 5.0 (MjM Software Design, Gleneden Beach, OR, US; Dufrêne and Legendre, 1997).

3. Results

3.1. Habitat characteristics

The cover of the three plant indicator species for habitat productivity significantly differed between nutrient-rich restored bogs and nutrient-poor restored bogs/the control (Table 1). *Juncus effusus* had a higher cover in nutrient-rich restored bogs and, in contrast, both *Eriophorum* species had a higher cover in the two other bog types. All other biotic, and also all abiotic parameters, did not differ between the three bog types.

3.2. Dragonfly species richness and abundance

In total, we collected 14,042 exuviae from 33 plots (Zygoptera: $n = 10,488$; Anisoptera: $n = 3554$), comprising a total of 29 autochthonous dragonfly species; among them were nine target species (raised-bog species: $n = 4$; transition-bog species: $n = 5$; Table A3). The most frequent species was *Lestes sponsa*, occurring in all except one of the plots (constancy: 97%). *Leucorrhinia rubicunda*, *Sympetrum danae* and *Enallagma cyathigerum* were also common, being detected in more than three quarters of the plots. The latter species was also the most abundant species, accounting for more than one third of all found exuviae.

The species richness and abundance of all species did not differ between the three bog types (Fig. 1a and b). In contrast, the species richness and abundance of raised-bog species were higher for the control plots than the nutrient-poor plots, which were in turn higher than the nutrient-rich restored bogs (Fig. 1c and d). While, for the abundance, the difference was significant among all three bog types, the species richness only differed significantly between the control and nutrient-rich restored bogs. For transition-bog species, the pattern was exactly the opposite: both the species richness and abundance were lower for the control plots than the nutrient-poor plots, which were in turn lower than the nutrient-rich restored bogs (Fig. 1e and f).

3.3. Response of dragonfly species to environmental conditions

For two of the three bog types, the ISA identified indicator species (Table 2): *Aeshna subarctica*, *Coenagrion lunulatum*, *Leucorrhinia dubia* and *L. rubicunda* were characteristic of the control and *Aeshna mixta*, *Anax imperator*, *Ceriagrion tenellum*, *Coenagrion puella*, *Lestes virens*, *Leucorrhinia pectoralis*, *Sympetrum sanguineum*, *Sympetrum striolatum* and *Sympetrum vulgatum* were characteristic of the nutrient-rich restored bogs. In contrast, for nutrient-poor restored bogs, the ISA failed to detect any indicator species.

The GLMM analysis revealed that three environmental variables especially affected the raised-bog species: (i) the cover of *E. vaginatum*, which was negatively correlated with the pH value (see Table A2); (ii) the loss of water surface extent and (iii) the cover of *Sphagnum* mosses (Table 3a and b). The cover of *E. vaginatum* and *Sphagnum* mosses had a positive effect on species richness and abundance of raised bog species, while the loss of the water surface extent over the course of the summer (=strong water level fluctuation) had a negative effect. Additionally, the abundance of raised-bog species decreased with the increasing cover of other vascular plants (Table 3b). A high cover of other vascular plants also had negative effects on the species richness and abundance of transition-bog species (Table 3c and d). Moreover, the species richness of transition-bog species was positively influenced by an increasing cover of *J. effusus* (Table 3c), which was positively correlated with the pH value (see Table A2).

The plot age of the nutrient-poor restored bogs had no effect on the species richness of raised-bog species (Fig. 2). However, the species richness of transition-bog species significantly decreased with the plot age of the nutrient-rich restored bogs.

4. Discussion

4.1. Diversity and abundance patterns in control versus restored bogs

Our study demonstrated that restored bogs are important habitats for dragonfly conservation. Both types of restored bogs were as diverse in their overall species richness as the control plots. These findings are in accordance with the results of other restoration studies (e.g., D'Amico et al., 2004; Samways and Sharratt, 2010; Modiba et al., 2017). Restored habitats are usually occupied within a short time period by several species across different taxonomic groups (Mazerolle et al., 2006; Elo et al., 2015; Noreika et al., 2015). However, the species

Table 1
Mean values (± SE) of the abiotic and biotic environmental parameters for the three bog types. Sample size: control (n = 12), nutrient-poor (n = 12) and nutrient-rich restored bog (n = 9). Differences between bog types were tested using a GLMM with a negative binomial error structure. Different letters indicate significant differences (α = 0.05).

Parameter	Control	Restored bog		P
		Nutrient-poor	Nutrient-rich	
Abiotic parameters				
Maximum water surface extent (ha)	0.3 ± 0.1	1.4 ± 0.5	1.1 ± 0.4	0.06
Loss of water surface extent (%)	24.6 ± 8.4	44.5 ± 10.7	33.9 ± 14.3	0.62
pH	3.9 ± 0.04	3.9 ± 0.04	4.4 ± 0.13	0.17
Electrolytic conductivity (μS/cm)	73.3 ± 3.4	89.1 ± 6.5	82.5 ± 11.2	0.38
Biotic parameters (% cover)				
Sphagnum mosses (submerged or floating)	44.3 ± 4.5	46.4 ± 5.6	29.2 ± 10.6	0.32
Eriophorum angustifolium	6.9 ± 2.0[a]	7.3 ± 3.5[a]	0.1 ± 0.1[b]	0.0047
Eriophorum vaginatum	18.3 ± 3.3[a]	14.3 ± 2.6[a]	0.2 ± 0.1[b]	< 0.001
Juncus effusus	0.9 ± 0.6[a]	0.4 ± 0.4[a]	28.3 ± 4.9[b]	< 0.001
Other vascular plants	42.9 ± 3.9	47.1 ± 5.5	33.3 ± 4.9	0.13

composition of the restored habitats often differs from that of the control (van Duinen et al., 2003; Mazerolle et al., 2006; Samways and Sharratt, 2010; Taillefer and Wheeler, 2012; Remm and Sushko, 2018). In our case, this was especially true for the nutrient-rich restored bogs. Due to the more mesotrophic conditions, they were occupied by a specific dragonfly assemblage – quite different from that of the oligotrophic rural peat cuts (control). Consequently, overall species richness and abundance is often a poor predictor of restoration success (cf. van Duinen et al., 2003; Modiba et al., 2017).

However, the patterns become much clearer when considering target species. In line with van Duinen et al. (2003) and Mazerolle et al. (2006), the highly specialized raised-bog species preferred the control, the most natural bog pools in our study area. In contrast, they were almost completely absent from the nutrient-rich restored bogs. The nutrient-poor restored bogs had an intermediate position – in between the other two bog types. Our GLMM analysis revealed that a high cover of *E. vaginatum* – a substitute for a low nutrient level and low pH – determined the occurrence of the raised-bog species. These species are well adapted to the extreme environmental conditions of raised bogs (Spitzer and Danks, 2006; van Kleef et al., 2012). Additionally, most larvae of raised-bog species are semivoltine and, consequently, do not tolerate strong water level fluctuation, and especially desiccation (Beadle et al., 2015; Brown et al., 2016). In contrast, a high cover of submerged or floating peat mosses favored raised-bog species. This finding is in line with previous studies. Submerged and floating peat mosses provide shelter and foraging habitats for the larvae, as well as favorable egg-laying substrates for the adults (e.g., Henrikson, 1993; Sternberg and Buchwald, 2000; Hannigan and Kelly-Quinn, 2012).

For transition-bog species, the pattern was exactly the opposite: they preferred nutrient-rich restored bogs and rarely occurred in the oligotrophic control. A strong relationship between their species richness and the nutrient level of the habitat was also revealed by the GLMM analysis. The higher the nutrient availability, indicated by the *J. effusus* cover, the more transition-bog species occurred. We explain this not only with the nutrient availability, which is connected with a larger amount of prey (Fincke et al., 1997), but especially with the relatively moderate pH within the bog pools dominated by *J. effusus*. Acidic conditions (low pH) limit the viability of numerous dragonfly species (Honkanen et al., 2011; Simaika and Samways, 2011). In addition, rushes are an important oviposition substrate for some species, such as *L. virens* (Sternberg and Buchwald, 1999). A further predictor of species richness and abundance of the transition-bog species was the cover of other vascular plants. At first sight, the relationship is difficult to interpret. A high cover of vascular plants can possibly have negative impacts on the water temperature by shading the water body and, therefore, may hinder successful larval development. Many transition-bog species, such as *C. tenellum*, *L. virens*, *L. pectoralis* and *S. danae*, have very thermophilic larvae (Sternberg and Buchwald, 1999, 2000). However, a high cover of vascular plants may also be considered an indicator of a disturbed hydrology of the bogs, as this variable corresponds mainly with the cover of *Molinia caerulea* (cf. Section 2.3). The grass avoids waterlogged habitats (Grime et al., 2007) and is characteristic of degraded bogs (Swindles et al., 2016). Most of the transition-bog species depend on permanent water bodies; only *S. danae* and L. *virens* are able to survive temporary desiccation (Sternberg and Buchwald, 1999, 2000).

4.2. Factors affecting the recolonization of bog dragonfly species

A successful recolonization by target species after a restoration measure depends on a complex of different factors. One important driver is the age of the restored habitat (e.g., van Duinen et al., 2003). It usually takes several years until the abiotic and biotic habitat characteristics allow for colonization by characteristic species (Mazerolle et al., 2006; Watts et al., 2008; Taillefer and Wheeler, 2012). Additionally, the distance of the restored habitat to potential source populations, the patch occupancy of the target species in the region and their mobility are also crucial (Kadoya et al., 2008; Bonifait and Villard, 2010; Beadle et al., 2015). Consequently, the recolonization lag by target species varies – often between 2 and 15 years (Stanczak and Keiper, 2004; Mazerolle et al., 2006; Watts et al., 2008; Taillefer and Wheeler, 2012; Elo et al., 2015). However, in some species or taxonomic groups, it takes much longer – this is especially true for some plant species (Haapalehto et al., 2011; Pouliot et al., 2012) and animal species with very low mobility (Stanczak and Keiper, 2004). In our study, we detected no differences in the species richness of raised-bog species between the control and nutrient-poor restored bogs. Hence, the time period from the conduction of the restoration measures to our investigation (at least 8 years) was sufficient for successful recolonization. This finding may be attributed to the relatively high mobility of dragonflies and the good connectivity of the restored habitats; all were located within more or less large peatlands (range: 376 to 16,098 ha; cf. Section 2.2), which still harbor a large variety of typical raised-bog species (cf. Elo et al., 2015). However, the abundance was still lower than in the control. We assume that, despite a more or less favorable habitat structure, the trophic network was still incomplete (cf. Mazerolle et al., 2006). Dragonflies need – due to their predatory mode of life – a high amount of aquatic invertebrates and, therefore, are considered indicators of elevated food availability (Brown et al., 2016).

In contrast to raised-bog species, in our study, the transition-bog species responded to the age of the restored plots. However, contrary to expectations, the relationship between age and species richness was negative. This pattern might be explained by the preference of the thermophilic larvae of transition-bog species for early succession stages

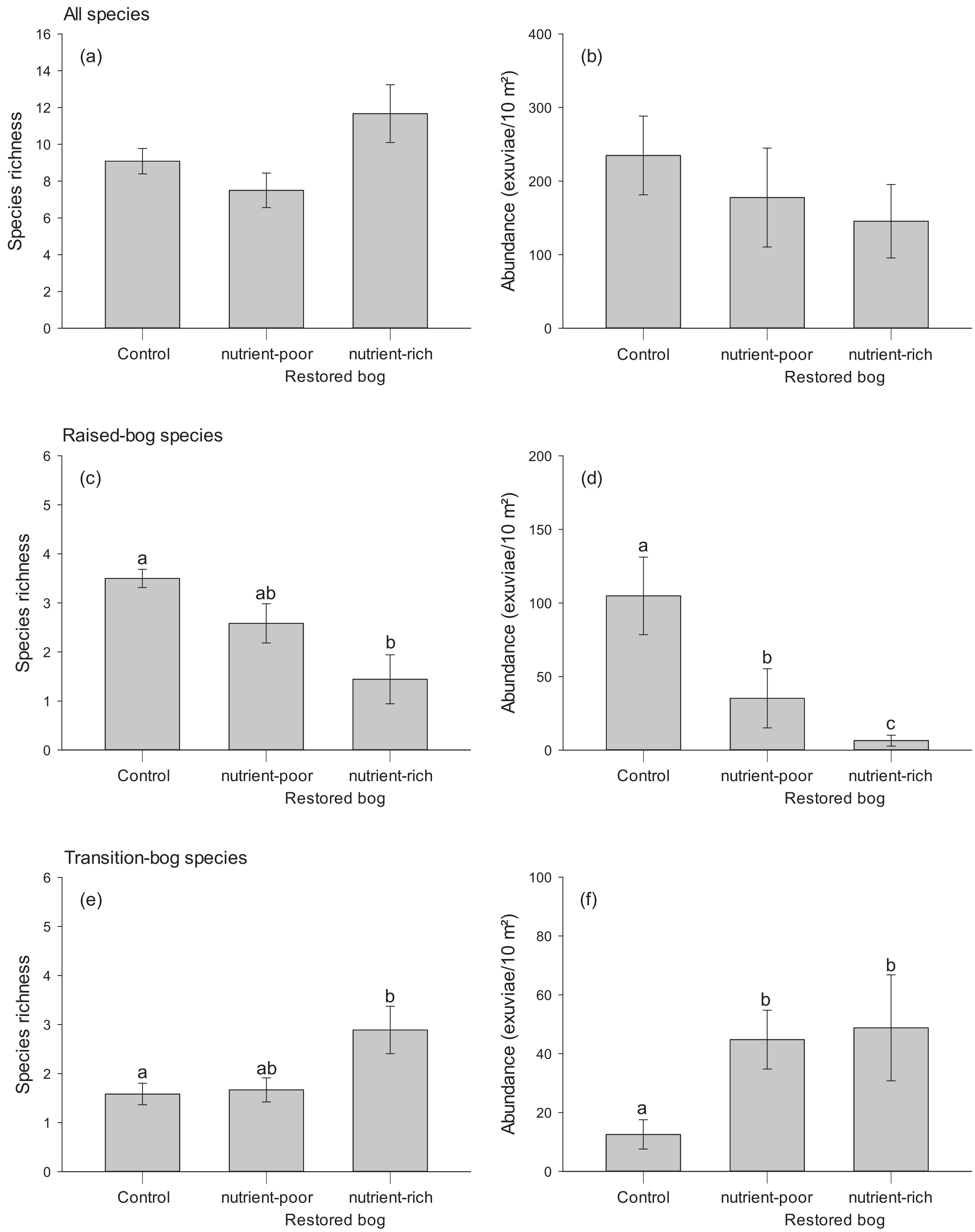

Fig. 1. Mean values (± SE) of species richness and abundance (exuviae/10 m^2) of all (a and b), raised-bog (c and d) and transition-bog species (e and f) for the three studied bog types (control, nutrient-poor and nutrient-rich restored bog; for details, see Section 2.2). Differences between bog types were tested for all response variables using a GLMM with a Poisson or negative binomial error structure and *subarea* as a random factor (for details, see Section 2.5). Different letters indicate differences between the bog types ($P < 0.05$).

(low cover of other vascular plants, Section 4.1). With ongoing succession, vegetation cover increases, especially in the nutrient-rich restored bogs, with adverse effects through shading on this group of dragonflies.

5. Conclusions

The restoration of peatlands is not only an important contribution to global climate protection, but also of great significance for the conservation of biodiversity (Andersen et al., 2017). Our study illustrated that the control plots (rural peat cuts) – as the most natural bog pools in the study area – represent valuable refuges for rare raised-bog dragonfly species. All raised-bog species of the study area were able to recolonize at least some of the nutrient-poor restored bogs. Although the abundance in the nutrient-poor restored bogs were lower than in the control, the establishment of raised-bog species can be evaluated as a partial

Table 2
Dragonfly indicator species of the control, nutrient-poor and nutrient-rich restored bogs (results of ISA, Dufrêne and Legendre, 1997). Species are sorted by IV for the bog type. All species with significant indicator values are shown. IV = indicator value, ra = relative abundance, rf = relative frequency. Grey shaded values: indicator species for this bog type. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Species	P	Control			Restored bog					
					Nutrient-poor			Nutrient-rich		
		IV	ra	rf	IV	ra	rf	IV	ra	rf
Leucorrhinia dubia	***	**75**	74	100	.	23	67	.	2	44
Leucorrhinia rubicunda	*	**61**	61	100	.	28	83	.	11	56
Aeshna subarctica	**	**59**	71	83	.	26	67	.	4	22
Coenagrion lunulatum	*	**54**	81	67	.	18	42	.	1	22
Lestes virens	***	.	0	8	.	0	8	**78**	100	78
Coenagrion puella	***	.	1	17	.	1	17	**66**	98	67
Sympetrum sanguineum	***	.	0	0	.	0	0	**56**	100	56
Anax imperator	***	.	15	8	.	0	0	**47**	85	56
Aeshna mixta	***	.	0	0	.	0	0	**44**	100	44
Sympetrum striolatum	***	.	2	8	.	0	0	**44**	98	44
Ceriagrion tenellum	*	.	5	33	.	38	25	**44**	56	78
Leucorrhinia pectoralis	*	.	0	0	.	0	0	**33**	100	33
Sympetrum vulgatum	*	.	0	0	.	0	0	**33**	100	33

success of the restoration measures (cf. Gorham and Rochefort, 2003).

However, the situation was different for the nutrient-rich restored bogs. Due to the high nutrient content – caused by the former agricultural use – the characteristic dragonfly fauna of raised bogs will hardly be able to recolonize the nutrient-rich restored bogs – even in the long term. Consequently, land-use history has a strong effect on restoration success. Nevertheless, the nutrient-rich restored bogs also have a high nature conservation value as their habitat characteristics are comparable with those of the mesotrophic lagg zone of raised bogs. Due to large-scale drainage in the course of peat extraction, this zone has often been vanished in raised bogs (van Kleef et al., 2012). The nutrient-rich restored bogs, thus, represent an important secondary habitat (Dolný and Harabiš, 2012; Howie and van Meerveld, 2018; Remm and Sushko, 2018), especially for transition-bog species. In conclusion, the conducted restoration measures created a network of small oligo- to mesotrophic water bodies, which fosters the aquatic macroinvertebrate diversity in bogs (cf. Verberk et al., 2006; Hannigan and Kelly-Quinn, 2012).

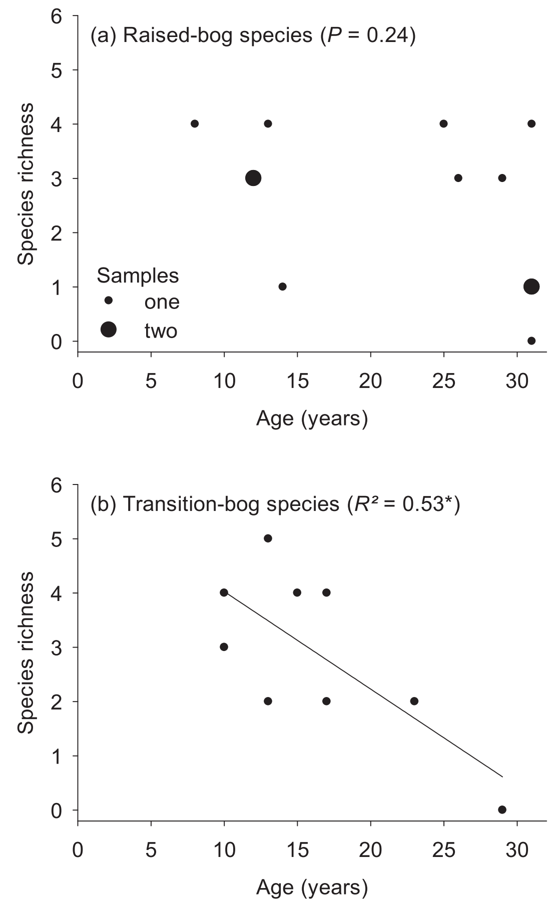

Fig. 2. Relationship between the species richness of raised-bog (a) and transition-bog species (b), with the plot age as the predictor variable. Sample sizes: nutrient-poor restored bogs for raised-bog species ($n = 12$), nutrient-rich restored bogs for transition-bog species ($n = 9$). The significance and model accuracy were tested using a univariate GLM with a Gaussian or Poisson error structure, respectively. Significance level for panel b is indicated as follows: *$P < 0.05$; $y = f(x) = -0.18x + 5.82$.

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Table 3
Synthesis models: Influence of several environmental parameters (predictor variables, Table A2) on the species richness and abundance of the target species (negative binomial error structure) for a and b: raised-bog species; c and d: transition-bog species. Model-averaged coefficients (conditional average) were derived from the top-ranked generalized linear mixed-effects models (ΔAICc < 3). Only significant predictors are shown. Statistical significances are indicated as follows: n.s. = not significant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Parameter	Estimate	SE	Z	P	Parameter	Estimate	SE	Z	P
Raised-bog species									
(a) Species richness					(b) Abundance				
(Intercept)	1.28	0.403	3.03	**	(Intercept)	0.77	0.434	1.69	n.s.
Eriophorum vaginatum	0.04	0.010	3.40	***	*Eriophorum vaginatum*	0.05	0.009	5.11	***
Water surface loss	−0.01	0.003	−2.97	**	Water-surface loss	−0.01	0.004	−3.56	***
Sphagnum mosses	0.02	0.007	2.34	*	*Sphagnum* mosses	0.02	0.006	2.71	**
					Other vascular plants	−0.02	0.008	−2.18	*
Transition-bog species									
(c) Species richness					(d) Abundance				
(Intercept)	2.15	0.395	5.22	***	(Intercept)	2.43	0.292	8.00	***
Other vascular plants	−0.02	0.009	−2.33	*	Other vascular plants	−0.02	0.005	−2.94	**
Juncus effusus	0.03	0.009	3.23	**					

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.06.032.

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