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ABSTRACT

The succession-driven reed bed habitat hosts a unique flora and fauna including several endangered invertebrate species. Reed beds can be managed through commercial winter harvest, with implications for reed bed conservation. However, the effects of winter harvest on the invertebrate community are not well understood and vary across studies and taxonomic levels. The aim of this study was to investigate the effects of reed harvest on invertebrate communities. Ground-dwelling and aerial invertebrates were continuously sampled for 10 weeks in the largest coherent reed bed of Scandinavia in order to assess how time since last reed harvest (0, 3, and 25-years) influences invertebrate biomass, biodiversity and community structure across taxonomic levels. Biomass was measured and all specimens were sorted to order level, and Coleoptera was even sorted to species level. The invertebrate community showed distinct compositional differences across the three reed bed ages. Furthermore, biomass of both aerial and ground-dwelling invertebrates was highest in the age-0 reed bed and lowest in the age-25 reed bed. Generally, biodiversity showed an opposite trend with the highest richness and diversity in the age-25 reed bed. We conclude that it is possible to ensure high insect biomass and diversity by creating a mosaic of reed bed of different ages through small-scale harvest in the largest coherent reed bed in Scandinavia. The youngest red beds support a high invertebrate biomass whereas the oldest reed beds support a high biodiversity. Collectively, this elevate our understanding of reed harvest and the effects it has on the invertebrate communities, and might aid in future reed bed management and restoration.

1. Introduction

During the 20th century, 60–90% of the natural wetland area in Europe, including reed beds, has disappeared partly due to exploitation and human management including drainage and land reclamation (Cížková et al., 2013; Gigante et al., 2013), with large consequences for their role in supporting biodiversity (Li et al., 2018). In Europe, reed beds are important wetland habitats to both humans and wildlife as they provide thatching materials, act as water treatment systems (Holland et al., 1990; Hawke and José, 1996; Costanza et al., 1997), and serve as biological hotspots (Hawke and José, 1996; Bogusch et al., 2020).

The reed bed is a succession-driven habitat representing the stage between open water and woodland, dominated by the competitive,

cosmopolitan species, *Phragmites australis* (Hawke and José, 1996). Early successional reed beds are characterized by a high water table, low litter depth and no scrub growth, whereas late successional reed beds have a higher litter layer, low water coverage, higher plant species richness and contains scrub-growth (Hardman et al., 2012). Eventually, late successional reed beds dry out due to litter accumulation and revert into other habitat types (Hawke and José, 1996). Reed beds are important wildlife habitats that host a high number of invertebrate species, are biodiversity hotspots for wasps and bees, and host several invertebrate species of conservation concern (Hawke and José, 1996; Hardman et al., 2012; Bogusch et al., 2020). In addition, reed bed invertebrates provide food for numerous bird species, including several reed bed passerines as well as the Eurasian bittern *Botaurus stellaris* (Paracuellos, 1997; Schmidt

et al., 2005; Polak, 2016). The insect abundance is therefore of tremendous importance for the insectivorous birds (Møller, 2019).

Reed beds are managed by several methods, including grazing, burning and harvest (Hawke and José, 1996) with commercial reed winter harvest being common in Europe (Decleer, 1990; Hawke and José, 1996). Harvest removes reed biomass, which slows the litter accumulating rate and cause alterations to the plant community, decrease scrub growth and increase the water level (Cowie et al., 1992; van der Sluis et al., 2013; Andersen et al., 2021). These alterations make the reed bed similar to a reed bed in an early successional stage, even though differences might exist between harvested reed beds and young successional reed beds (Hardman et al., 2012).

Winter harvested reed can be a valuable product that is suitable as high-quality roughage for ruminants and as thatching material, among other uses (Köbbing et al., 2013; Tanaka et al., 2016). At the same time, experts deem winter harvest the most suitable management strategy to preserve ecosystem services, enable reed utilisation and preserve biodiversity (Karstens et al., 2019). Nonetheless, previous studies have shown that the disturbance caused by reed harvest and other management methods affect the invertebrate community composition and abundance, but the response of various taxonomic groups to reed harvest are contradictory, and studies have mainly compared managed to unmanaged reed beds (Ditlhogo et al., 1992; Schmidt et al., 2005; Valkama et al., 2008). For example, Araneae biomass and richness were not affected by harvest according to Decleer (1990), whereas Schmidt et al. (2005) found reed harvest to have a negative effect on Araneae as well as Coleoptera abundance. Contrary to this, Görn et al. (2014) found winter harvest to positively affect carabid coleopterans compared to unmanaged controls. Moreover, a meta-analysis study showed that harvest decreased invertebrate abundances when repeated over several consecutive years (Valkama et al., 2008). Results also suggest that the successional stage of the reed bed, which is partly reset by harvest, was important for moths and flies (Hardman et al., 2012). However, the successional stage, which could explain differences across studies, is rarely considered when studying the effects of reed management (Decleer, 1990; Schmidt et al., 2005; Görn et al., 2014). Together, this highlights the need for an approach where the age of the reed bed is taken into consideration.

The current study investigate whether commercial winter harvest and time since last harvest affects the invertebrate community. We assessed how reed beds with different ages differ in flying and ground-dwelling invertebrate biomass, community composition and diversity. Rather than comparing managed to unmanaged reed beds, we compared the invertebrate community across reed beds with three different ages: age-0 (newly harvested for commercial use), age-3 and age-25, with the age symbolizing time since last harvest. Biomass was estimated throughout the study period, which allowed us to estimate temporal changes. We hypothesized that harvest would either decrease or have no effect on invertebrate biomass (Ditlhogo et al., 1992; Schmidt et al., 2005; Valkama et al., 2008). We investigated the invertebrate community composition and diversity across the three different reed bed ages at the order level for all specimens collected, and for Coleoptera also at family, genus and species level, as we expected that the effect of reed bed age could differ across taxonomic levels. By studying responses at different taxonomic levels, we were able to evaluate whether data at low taxonomic resolution were sufficient to assess the effects of reed bed age. Coleoptera were chosen as they are good bioindicators of anthropogenic disturbances and habitat alterations (Rainio and Niemelä, 2003), whereas both ground or aerial species of invertebrates have been found as main prey items of e.g. passerine birds (Poulin and Lefebvre, 2002; Schmidt et al., 2005; Trnka et al., 2014). Finally, as previous studies have shown that both invertebrates targeted by surface traps (Decleer, 1990; Schmidt et al., 2005) and flight interception traps (Hardman et al., 2012) are affected by reed management, we sampled both flying and ground-dwelling invertebrates in our study.

2. Methods

2.1. Study site

The study took place in Vejlerne, Denmark (57°04′N, 9°03′E) during the summer (June 25th to August 29th, weeks 26–35) of 2018. Vejlerne, a Birds- and Habitat Directive site protected under the Ramsar convention, contain the largest coherent reed bed of Scandinavia (2000 ha) (Ramsar Convention Secretariat, 2013). This sampling period was chosen as this is when invertebrates are most abundant (Thomsen et al., 2016).

2.2. Study design

Commercial reed winter harvest has taken place since 1979 in Vejlerne. Different areas have been harvested throughout the years resulting in a mosaic of reed beds with different ages. In the year of the study, approximately 70 ha were harvested. Three areas with different ages were located: age-0 (last harvested in 2018), age-3 (last harvested in 2015), and age-25 (last harvested in 1993) (Fig. 1). The age-0 reed bed had a vegetation dominated by common reed *Phragmites australis,* but with patches of forbs requiring open conditions (Andersen et al., 2021). The age-3 reed bed was the most homogenous and consisted mainly of common reed while the age-25 reed bed was dominated by common reed, but with patches of scrub (*Salix* spp.). These trends in vegetation are consistent across Vejlerne. To infer the importance of reed bed age on biomass, richness and diversity we used a space for time substitution (Pickett, 1989).

Flight interception traps (cross vane window traps) were used to sample flying invertebrates (Bouget et al., 2008; Anderson et al., 2013), whereas pitfall traps were used to target ground-dwelling invertebrates (Kotze et al., 2011; Anderson et al., 2013).

In each reed bed age, twelve flight interception traps were placed randomly at different sites using QGIS (QGIS Development Team, 2016), ensuring a within-treatment minimum distance between traps of 100 m. Samples were thus seen as independent of each other and the unit of replication were thus sites. The flight interception traps were built following Nageleisen and Bouget (2009), but with the following modifications making them suitable for placement in the reed bed: each flight interception trap consisted of two transparent, perpendicular panels measuring 50×80 cm, where the panels were placed on top of a black barrel Ø50 cm. The black barrel was placed on top of a wooden frame with the top of the black barrel being 150 cm above ground.

In each reed bed age, pitfall traps were placed randomly at 10 sites sufficiently dry to allow the trap to be placed. At each site, we placed five pitfall traps in a straight line with 5 m between individual traps, hereafter referred to as a pitfall station. The minimum distance of 80 m between pitfall stations (sites) secured each trap a non-overlapping catchment area of at least 1600 m^2, which is considerably larger than the home range of most invertebrates (Traugott, 2002; Matyukhin and Gongalskii, 2007). Samples were thus considered independent of each other and the unit of replication were therefore the pitfall stations (sites). Because of the high water table in the reed beds, pitfall traps were constructed with two plastic cups (Ø8.5 cm), one taller than the other, and with concrete in the gap between them preventing them from floating away. An odourless solution of detergent, salt, and water was added to all traps to ensure preservation of caught invertebrates (Koivula et al., 2003). Flight interception traps were emptied every week, while pitfall stations were emptied bi-weekly (Duelli et al., 1999). No invertebrates were sampled in the pitfall stations in the age-0 reed bed in week 35 due to flooding of the traps following a rainfall. After emptying the traps, specimens were kept in 70% ethanol solution and stored at 5 °C in the laboratory before taxonomical sorting.
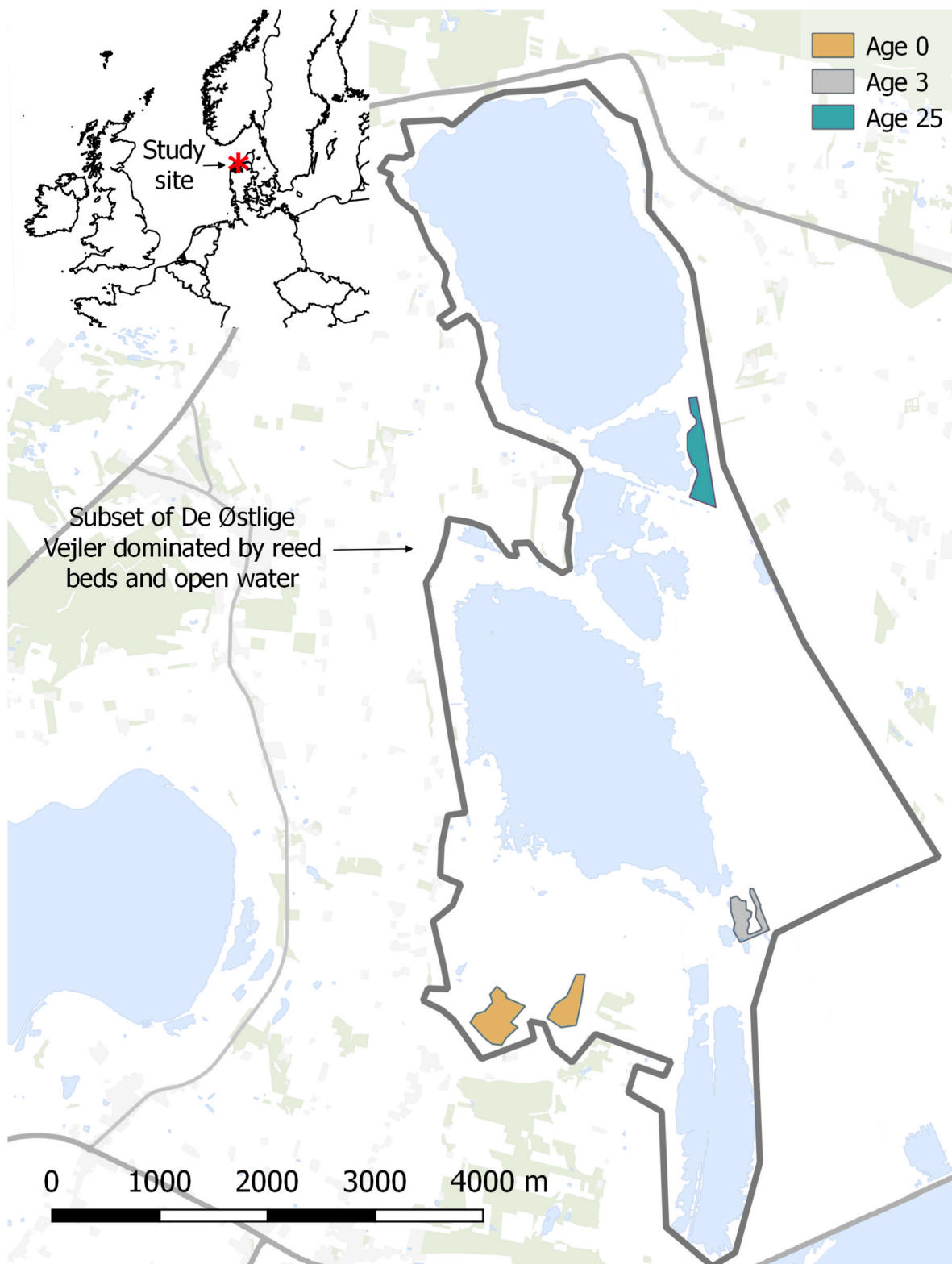
Fig. 1. Map depicting the reed bed ages within *De Østlige Vejler*, Denmark.

2.3. Biomass estimates

The entire biomass of all invertebrate orders in an alcohol-wet state was estimated for each flight interception trap and pitfall station sample using a slightly modified method of Hallmann et al. (2017). The alcohol content was held constant at 70% for 24 h, and the wet biomass placed in sieve with a mesh size of 0.2 mm. The biomass was measured on a

RADWAG PS 4500/C/2 (0.01g precision scale). The content of two traps were each measured ten times to estimate the potential measurement error and we found that the final weight fluctuated by less than 2%. Subsequently, the biomass of Coleoptera from the pitfall stations was also estimated separately.

The biomass from flight interception traps, pitfall stations and Coleoptera were analysed separately. We built generalized linear mixed

models (GLMM) to determine whether biomass differed between areas with different reed bed ages and across sampling time using the *lme4* package v1.1-21 (Bates et al., 2015) for R. As each trap (site) was sampled repeatedly across time, we incorporated trap/trapping station as a random factor in order to take account for the repeated measures. Time was incorporated as a categorical factor. The package *MASS* v7.3–51.1 (Venables and Ripley, 2002) revealed that the log-normal distribution showed the best fit to the data; hence, a log link was incorporated in the model. If the GLMM was significant, we used least square means to determine which reed bed ages that differed significantly from each other (Searle et al., 1980).

2.4. Invertebrate diversity

The content of flight interception traps collected in week 31 and pitfall stations collected in weeks 30–31 were sorted to the order level following Whiting (2014). Coleoptera specimens caught in the pitfall stations (weeks 30–31) were sorted to lowest possible taxonomic level (Lindroth and Bangsholt, 1985; Lindroth, 1986; Hansen, 1987; Holmen, 1987; Nilsson and Holmen, 1995).

We calculated the diversity using Hill numbers of order q for the rarefied richness (q = 0), the exponential Shannon entropy (q = 1), hereafter called the Shannon diversity and the inverse Simpson concentration (q = 2), hereafter called the Simpson diversity (Jost, 2006; Chao et al., 2014) using iNEXT v.2.0.20 (Hsieh et al., 2016). The calculations were conducted for order level data for the flight interception traps and pitfall stations, and family, genus and species level for Coleoptera. The use of Hill numbers in diversity measurements results in unified and intuitive diversity measures (Jost, 2006). Advantages of using Hill numbers include that the estimates have doubling qualities (a diversity of 2x is twice as high as a diversity of x) and that the results are expressed in effective number of species (Chao et al., 2014). Furthermore, it considers the effect of sampling effort by applying a rarefaction process to standardize the sample size prior to calculating the diversity (Chao et al., 2014). We used the rarefaction to obtain equal sample sizes across traps by rarefying all sample sizes to two times the smallest sample size (when a sample was smaller than two times the minimum abundance, it was extrapolated; when a sample size exceeded twice the minimum abundance, it was interpolated). Rarefaction ensures that the species diversity is compatible between different habitats despite differences in the abundances of the original samples.

We used GLMs to determine whether the rarefied species richness, Shannon diversity and Simpson diversity differed significantly between reed bed ages. We used quantile-quantile plots to check the distribution, and the Gaussian distribution showed the best fit (Venables and Ripley, 2002). If significant, we used least square means to determine which reed bed ages differed significantly from each other (Searle et al., 1980). Additionally, we used the Hill numbers to draw diversity profiles, as diversity profiles are suitable for evaluating the evenness of a system (Chao et al., 2014).

2.5. Invertebrate community composition

Based on the data subset from weeks 30 and 30–31, distance-based Redundancy Analyses (dbRDA) (Legendre and Legendre, 2012) were conducted using the package *vegan v2.5–4* (Oksanen et al., 2017) to visualize the relationship between reed bed age and the invertebrate community. We conducted dbRDA's with centring, scaling and trap identity listed as strata. Using rank correlations between dissimilarity indices and gradient separation (Faith et al., 1987), we found Bray Curtis to be the best distance measure across invertebrates caught in flight interception and pitfall stations. Following the dbRDA, permutation tests with 500 permutations were run to assess the significance of the models, axes and reed bed age and adjusted partial R^2 was used to quantify the explained variation (Legendre and Legendre, 2012). To account for general trends, orders/families/genus/species that occurred

with a mean abundance of less than 5 individuals across all traps within a given reed bed age were excluded from the dbRDA (McCune and Grace, 2002).

To test whether invertebrate communities differed between reed bed ages within flight interception traps (order) and pitfall stations (order and Coleoptera: family, genus, species level), we used a Chi square test. If significant, a post hoc chi square test with Bonferroni correction following Beasley and Schumacker (1995) was used to determine which invertebrate orders were statistically linked to each reed bed age.

All data analyses were conducted in R version 33.0 (R Core Team, 2017).

3. Results

3.1. Biomass

We found that invertebrate biomass fluctuated over time (Fig. 2a, c) and that the mean biomass was highest in the newly harvested reed bed (Fig. 2b, d). The biomass from the flight interception traps was significantly affected by reed bed age, sampling week and the interaction between age and week (Fig. 2a, Table 1). For example, we found that the biomass in the age-0 habitat was significantly higher in week 34 compared to each of the other sampling weeks (Fig. 2a) ($p < 0.01$ in all cases). The biomass of flying invertebrates was significantly higher in the age-0 habitat compared to age-25 in week 29 ($p < 0.05$), week 30 ($p < 0.01$), and week 34 ($p < 0.01$), but no difference was found in week 27, 28, or 33 ($p > 0.05$) (Fig. 2a). In week 30, the biomass was significantly higher in the age-3 treatment group compared to age-25 ($p < 0.01$). For the ground-dwelling invertebrates, we found that the biomass was significantly higher in age-0 compared to age-25 ($p < 0.001$) and age-3 ($p < 0.001$) in week 30–31 (Fig. 2c). In week 32–33, the biomass was significantly higher age-0 compared to age-3 ($p < 0.001$), where the biomass did not differ significantly between age-0 and age-3 in week 28–29 ($p > 0.05$) (Fig. 2c). For coleoptera (Fig. 2e), the biomass was significantly higher in age-0 ($p < 0.001$) and age-3 ($p < 0.001$) compared to age-25 in week 30–31, whereas it was significantly higher age-0 compared to age-3 ($p < 0.001$) and age-25 ($p < 0.001$) in weeks 32–33. In week 28–29, the biomass of coleoptera was significantly lower for age-25 compared to age-0 ($p < 0.01$) and age-3 ($p < 0.01$) (Fig. 2e).

On average, the age-0 habitat had a biomass that was 19.8% higher than age-3 and 53.7% higher than age-25, and the biomass of the age-3 habitat was 28.3% higher than age-25 (Fig. 2b). The biomass of the pitfall stations was also significantly affected by reed bed age, sampling week, and the interaction between age and week (Fig. 2c; Table 1). The biomass of pitfall stations from the age-0 reed bed was 115.4% higher across sampling weeks than the biomass of pitfall stations from the age-3 and 140.5% higher than age-25 (Fig. 2d). The biomass of the Coleoptera collected in the pitfall stations was significantly affected by reed bed age and there was a significant interaction between reed bed age and week (Fig. 2e and f; Table 1). Overall, the Coleoptera biomass in age-0 was 97.6% higher than age-3 and 258.2% higher than age-25 reed bed, and the biomass in age-3 was 81.3% higher than in age-25 (Fig. 2e and f).

3.2. Invertebrate diversity

A total of 4.2×10^4 invertebrate specimens from the flight traps were sorted to order level. Nineteen invertebrate orders were present and ten of them occurred at least five times on average per trap (Fig. S1). From the pitfall stations, 8.2×10^4 invertebrates were sorted to order level. Sixteen orders were present in the pitfall stations and 11 of them occurred at least five times on average per trap (Fig. S2). A total of 9.0×10^3 Coleoptera from the pitfall stations were determined to the lowest possible taxonomic level with 92 species identified (full species list in Table S1). Most species occurred at a low abundance and only ten species of Coleoptera occurred with an average abundance of at least five individuals per pitfall station per habitat (Fig. S3). The most abundant
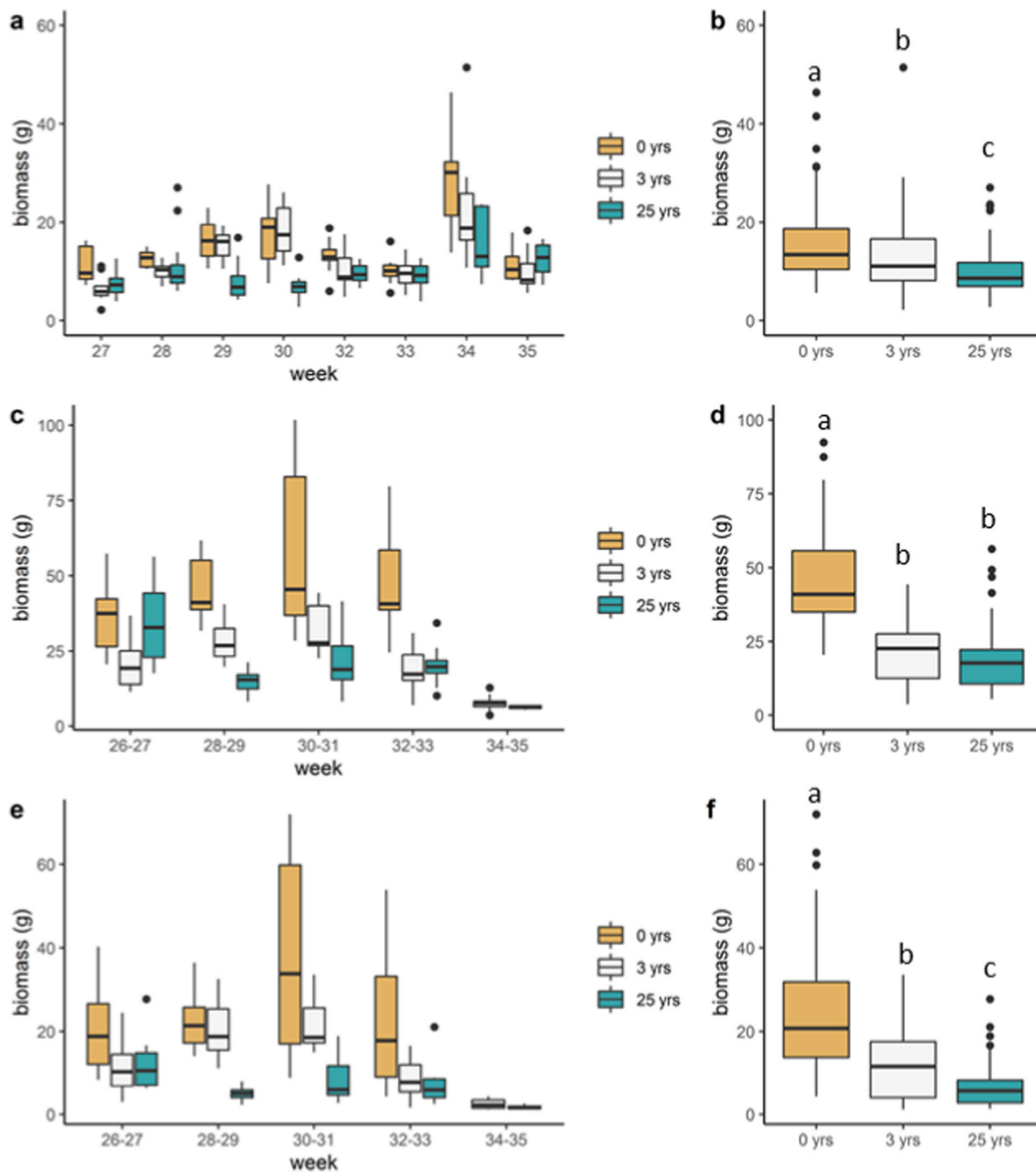
Fig. 2. Boxplot of invertebrate biomass: The biomass of the invertebrates captured in the flight interception traps (a, b), in the pitfall stations (c, d) and for the coleoptera (e, f). While a, c and e show the biomass on a weekly basis, b, d and f depict the average weekly biomass.

Table 1
Results of the generalized linear mixed models on invertebrate biomass for each trap type.

	Reed age	Week	Interaction
Flight interception trap	$p < 0.001$[a] (F = 28.33)	$p < 0.001$[b] (F = 23.12)	$p < 0.001$[c] (F = 4.62)
Pitfall, total	$p < 0.001$[d] (F = 72.75)	$p < 0.001$[e] (F = 11.18)	$p < 0.001$[f] (F = 4.38)
Pitfall, Coleoptera	$p < 0.001$[g] (F = 29.78)	$p < 0.01$[h] (F = 4.63)	$p < 0.001$[i] (F = 2.90)

[a] df = 2, [b] df = 7, [c] f = 14, [d] df = 2, [e] df = 4, [f] df = 7, [g] df = 2, [h] df = 3, [i] df = 6.

Coleoptera families were Carabidae and Staphylinidae.

The rarefied species richness did not differ at the order level for invertebrates caught in the flight interception traps, but was significantly lower in the age-3 reed bed compared to both the age-0 (18.6% higher) and age-25 reed bed (25.7% higher) for pitfall stations (Fig. 3, Table S2). For Coleoptera, the richness was significantly higher in age-25 compared to the age-0 and age-3 reed beds at the genus and species level, while no difference was observed at the family level (Fig. 3). At genus level, species richness was 76.2% higher in age-25 compared to age-0 and 42.1% higher in age-25 compared to age-3, while at species level, the age-25 species richness was 51.5% and 63.5% higher than age-0 and age-3, respectively.

Neither Shannon nor Simpson diversity differed significantly between reed bed ages for invertebrate orders caught in the flight
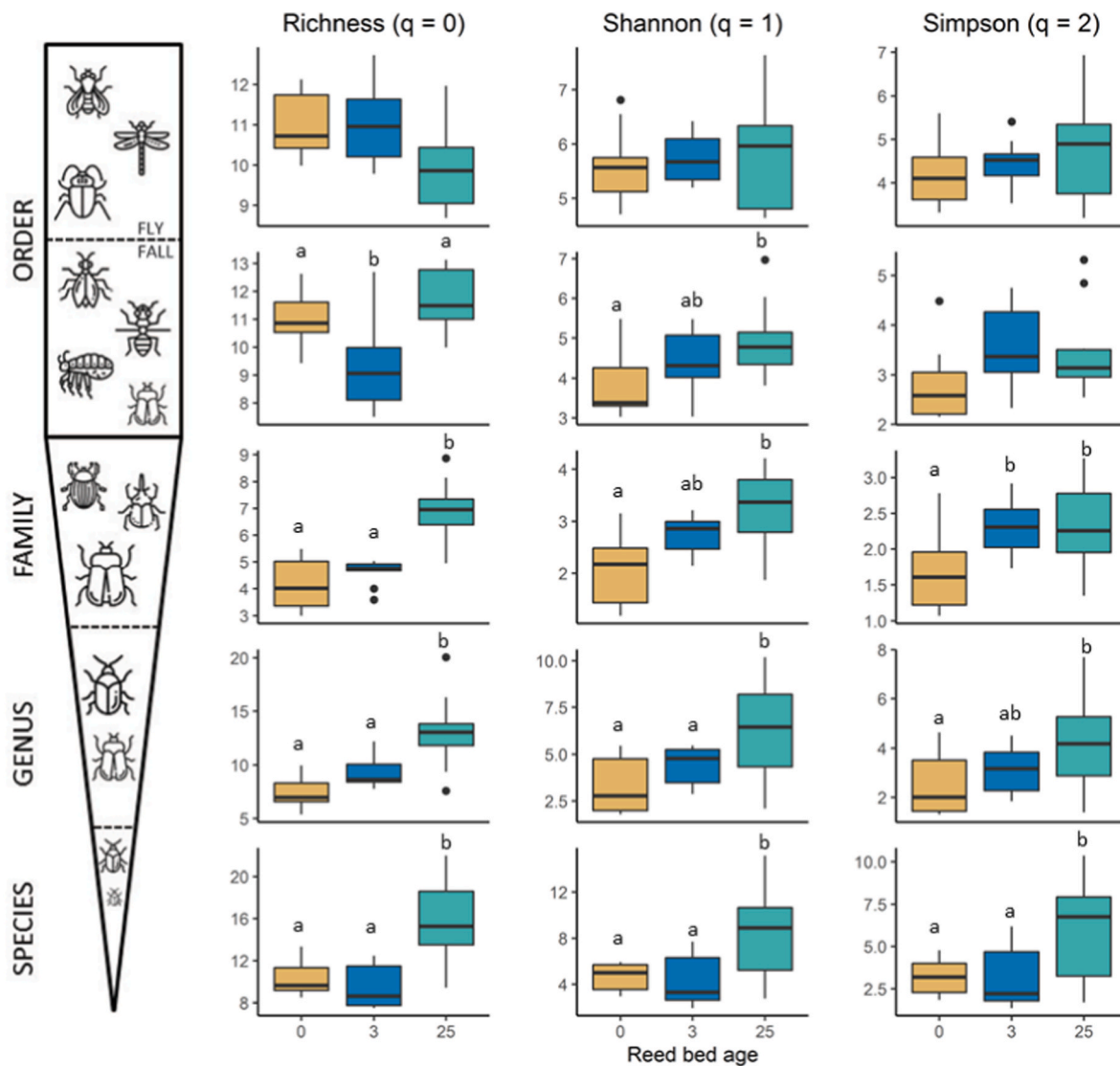
Fig. 3. Boxplot of the invertebrate diversity: The rarefied species richness (q = 0), Shannon diversity (q = 1) and Simpson diversity (q = 2) for (from the top) order level invertebrates in the flight interception traps, order level invertebrates from the pit fall traps, Coleoptera family, Coleoptera genus and Coleoptera at the species level. Invertebrate images from flaticon.com, artists Freepik and Eucalyp.

interception traps (Fig. 3, Table S2). For the pitfall stations, the Shannon diversity at order level was 28.9% higher in the age-25 reed bed compared to the age-0 (Fig. 3).

For Coleoptera, across all taxonomic levels, the Shannon and Simpson diversities were always significantly higher in age-25 compared to age-0 (Fig. 3, Table S2). At the family level, the Shannon diversity for example was 57.7% higher in age-25 compared to age-0 (Fig. 3). The Shannon diversity at genus level was 92.4% higher in age-25 compared to age-0 and 44.8% higher in age-25 compared to age-3. At the species level, the Shannon diversity at age-25 was 80.5% and 99.5% higher than in age-0 and age-3, respectively.

Visual inspection of the diversity profiles showed, regardless of reed bed age or taxonomic level, that the communities were moderately to highly uneven (Fig. S4).
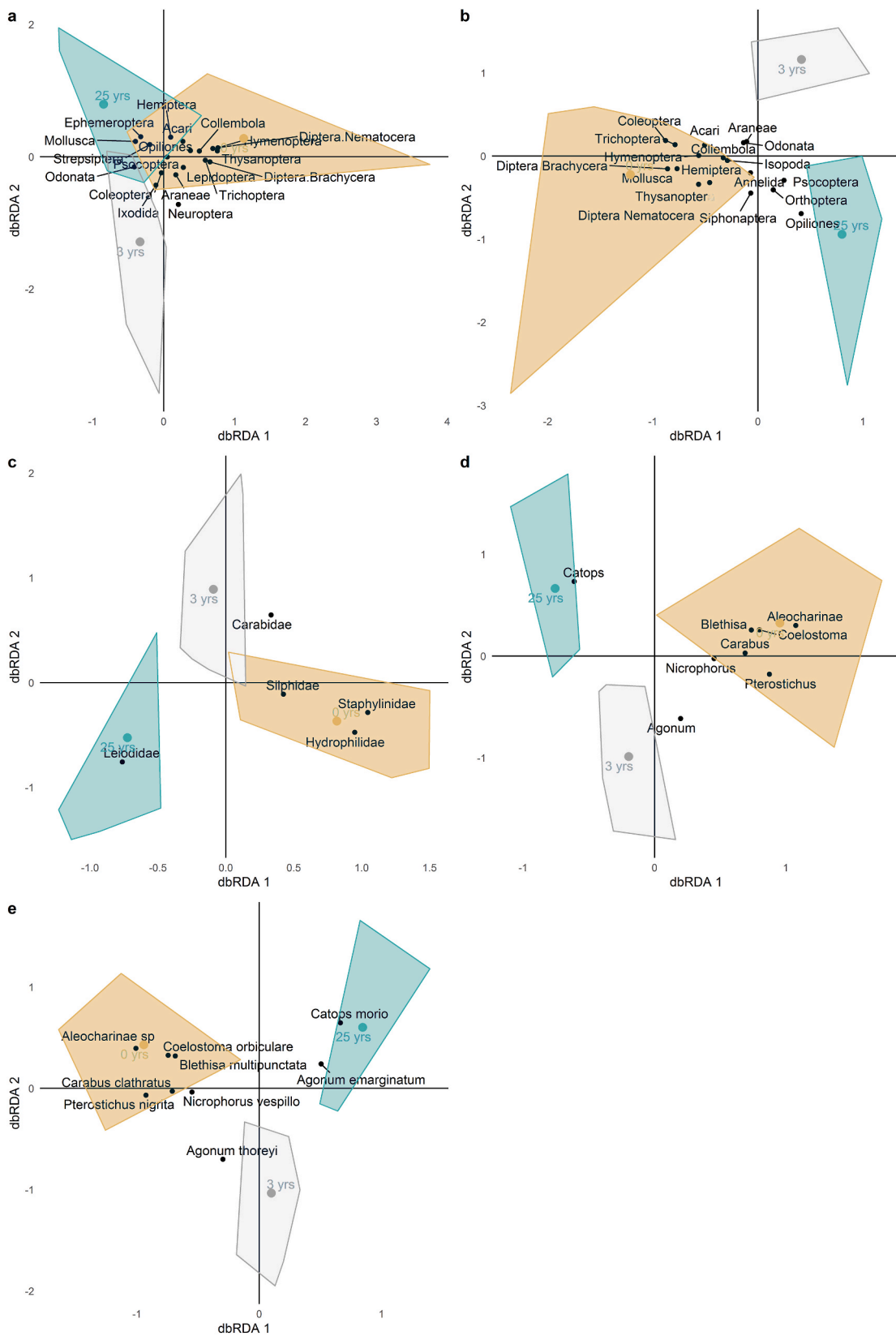
3.3. Invertebrate community composition

The dbRDAs were used to plot the multidimensional relationship between the reed bed ages and invertebrate communities at order level (flight interception traps (Fig. 4a) and pitfall stations (Fig. 4b)), family (Fig. 4c), genus (Fig. 4d) and species level (Fig. 4e). The dbRDAs analysis

indicated a significant effect of reed bed age on invertebrate communities regardless of the taxonomic level of investigation, meaning that no matter what taxonomic resolution we examined, the reed bed ages differed in community composition (Table 2, Fig. 4). Most variation across reed bed age could be explained at the species level for Coleoptera ($R^2 = 36.15$) (Table 2; Fig. 4c–e) and least variation were explained using order level data from the flight interception traps ($R^2 = 19.18$) (Fig. 4a; Table 2).

For the flight traps, order-composition was significantly affected by reed bed ages (chi-squared = 367.2, df = 36, $p < 0.001$). For example, the abundance of Brachycera (suborder within Diptera) was negatively associated with the age-0 and positively associated with the age-3 and Coleoptera associated negatively with the age-0 and positively with the age-3 and age-25 reed bed (Table S3). More order specific responses can be seen in Fig. S1 and Table S2.

The composition at order level differed between the three reed bed ages for the ground-dwelling invertebrates (chi-squared = 534.9, df = 38, $p < 0.001$). For example, for the pitfall stations, Aranea correlated negatively with the age-0 reed bed but positively with the age-3 and age-25 reed beds (Table S4). Both Collembola and Opiliones associated negatively with the age-0 reed bed, and Opiliones associated positively

Fig. 4. The invertebrate community composition at each reed bed age. The figure shows the results of the constrained dbRDA for the invertebrate abundance at the flight interception trap order level (a), pitfall station order level (b), pitfall station family level (Coleoptera) (c), pitfall station genus level (Coleoptera) (d) and pitfall station species level (Coleoptera) (e). The polygons represent the outer position of plots for each reed bed age with the reed bed age positioned as the centroid. Invertebrate orders/families/genus/species occurring with a minimum of 5 individuals/trap in at least one reed bed age were included.

Table 2
Result of the constrained dbRDA for each trap type and taxonomic level. The overall significance of each model (permutation test with 500 permutations) and the R^2 of the constrained dbRDA are listed. For each axis, the percent variation explained and significance value are noted.

Trap	Taxonomic level	Permutation test *p*-value	R^2	Axis 1	Axis 2
Flight trap	Order	0.001	19.18	73.35% (p < 0.001)	26.65% (p < 0.05)
Pitfall trap	Order	0.001	26.21	74.74% (p < 0.001)	25.53% (p < 0.01)
Pitfall trap	Family (Coleoptera)	0.001	34.65	68.68% (p < 0.001)	31.32% (p < 0.01)
Pitfall trap	Genus (Coleoptera)	0.001	35.23	78.20% (p < 0.001)	21.80% (p < 0.01)
Pitfall trap	Species (Coleoptera)	0.001	36.15	77.05% (p < 0.001)	22.95% (p < 0.01)

with the age-25 reed bed. More order specific responses can be seen in Fig. S2 and Table S3.

Similarly, the Coleoptera composition differed significantly between reed bed ages at the family level (chi-squared = 156.9, df = 18, p < 0.001). Family specific responses for Coleoptera can be found in Table S4.

4. Discussion

4.1. Invertebrate biomass and reed bed age

Contrary to our expectations, we found that the biomass of both aerial invertebrates and ground-dwelling invertebrates increased significantly following reed winter harvest and decreased with time since last harvest. Other studies have found that reed bed management decrease or have no effect on invertebrate abundance (Ditlhogo et al., 1992; Schmidt et al., 2005; Valkama et al., 2008). However, these studies investigated winter harvest at a large scale. Interestingly, our results agree with findings from wetlands dominated by monocultures of cattail *Typha* spp., where small-scale removal of plant biomass increased the abundance of invertebrates (Ball and Nudds, 1989). Moreover, disturbances that opens the habitat, including the introduction of beavers in wetlands (Nummi, 1989; Nummi et al., 2021), hay cropping in savannahs (Zalik and Strong, 2008) and timber harvest (Duguay et al., 2000), all increase the invertebrate biomass in accordance with our findings. Davis and Bidwell (2008) showed that several management techniques, including moving, had the potential to increase the invertebrate biomass of wetlands. Reed bed stripping, an intrusive management method that opens up the reed bed and slows down succession by removing the top organic layer, also resulted in an increased abundance in Diptera: Chironomidae compared to unmanaged reed stands (Lods-Crozet and Castella, 2009). The response to reed harvest is likely scale dependent and our results support previous findings that harvest of a small fraction of a reed bed benefit invertebrate abundance (Burgess and Evans, 1989; Trnka et al., 2014) as opposed to large scale harvest (Schmidt et al., 2005).

4.2. Invertebrate diversity and reed bed age

We found the highest species richness and Shannon diversity in the age-25 reed bed, a pattern most apparent at the genus and species levels but also detectable at the order level (pit fall traps). Diversity is highly influenced by habitat heterogeneity (Astorga et al., 2014) and undisturbed habitats with a high heterogeneity and high plant species richness tend to have a high insect diversity (Eggleton et al., 1996; Uchida et al., 2015). In late summer, habitat heterogeneity (the between-plot dissimilarity in plant species composition within each reed bed age) of the reed beds in Vejlerne was highest in age-0, lowest in age-3 and intermediary in age-25 (Andersen et al., 2021), which could partly

explain the observed patterns in invertebrate diversity and evenness.

Current global scale declines in invertebrate numbers (Hallmann et al., 2017; Møller, 2019; Arzel et al., 2020; van Klink et al., 2020) have implications for the invertebrate diversity (Forister et al., 2019; Wagner, 2020). Biodiversity is vital for ecosystem functioning and tend to increase ecosystem stability and productivity, and enhance decomposition, pollination and seed dispersal (Tilman et al., 2014; Isbell et al., 2018; Wong et al., 2019). It is therefore important to consider management strategies that maintain both high invertebrate biomass and diversity. Our results suggest that by securing reed beds of multiple ages, it is possible to maintain various invertebrate communities, areas of higher abundance and areas of higher diversity, and suggest that future studies examine if these finding apply in other locations.

It is important to note that reed winter harvest not only has implications for invertebrates, but that a reed bed mosaic also will increase the plant diversity at a landscape level (Andersen et al., 2021). Management that results in a reed bed mosaic also has positive implications for amphibians (Mester et al., 2015) and reptiles (Luiselli et al., 2020). Additionally, winter harvest can have a financial perspective by providing high quality fodder for ruminants (Tanaka et al., 2016), and it may limit nitrogen eutrophication of the reed bed and surrounding aquatic environments as reed stem removal result in a considerable nitrogen removal (Wang et al., 2021).

Abundance is an important parameter when calculating diversity indices. By using Hill numbers and rarefaction processes, we accounted for differences in abundance when calculating the rarefied species richness while upholding relative abundances of species (Chao et al., 2014).

4.3. Community composition

Natural resource management has the potential to mitigate climate change and preserve biodiversity (Aryal et al., 2019; Ćosić-Flajsig et al., 2020; Javadinejad et al., 2020). In this study, we found that both management and time since last management created distinct invertebrate community and thus favoured various orders, families and species. This corresponds with results from beaver wetlands, where different invertebrate communities can be found in wetlands in various successional stages (Bush et al., 2019; Nummi et al., 2021). As the invertebrate fauna is linked to the height and structure of the vegetation (Morris, 1967), the immediate change in the microclimate and habitat structure of the reed bed following reed management (Ditlhogo et al., 1992) may explain the changed community composition. For example, Hemipterans are mostly herbivorous and have diverse trophic requirements making them sensitive to changes in habitat structure and floral composition (Moir and Brennan, 2007), potentially explaining why their relative abundance were highest in the undisturbed age-25 reed bed. Opiliones are omnivores that are sensitive to disturbance (Stašiov et al., 2020), potentially explaining why they were positively associated with the age-25 reed bed.

Various Coleoptera families were associated with each reed bed age. Staphylinid beetle abundance responded positively to reed management in our study, though other studies highlight that alternative management methods such as summer harvest and grazing are better suited for Staphylinid management than winter harvest (Hoffmann et al., 2016). Görn et al. (2014) found reed winter harvest beneficial to Carabidae, whereas we found that Carabidae abundance increased with time since harvest. Overall, this highlights that responses to management are family-specific and depend on the age of the unmanaged stands.

We recorded two red listed species (Wind and Pihl, 2010). *Dytiscus circumcinctus* was found once in age-25, whereas *Carabus clathratus* was most abundant in age-0 (Fig. S5). *Carabus clathratus* hunts in wet habitats (Lindroth and Bangsholt, 1985); consequently, its low abundance in the old successional age-25 reed bed could be explained by years of accumulated litter making the habitat drier. Therefore, *C. clathratus* would likely decline in abundance if harvest stopped and natural

succession took its course.

4.4. Taxonomic sufficiency

Order level data may in some cases be sufficient to indicate how various environmental factors affect the invertebrate community (Hewlett, 2000; Schipper et al., 2010), whereas data at a finer taxonomic resolution is better to differentiate between different habitat types (Verdonschot, 2006; Smith et al., 2007). We found that regardless of taxonomic resolution there was a clear effect of reed bed age on the invertebrate community. However, differences between the species richness and Shannon diversity across reed bed ages were most evident at the family, genus, and species level. Several studies have found family-specific effects of reed management (Decleer, 1990; Ditlhogo et al., 1992; Lods-Crozet and Castella, 2009; Knoblauch and Gander, 2020), and our Coleoptera data support the idea that both family, genus and species-specific responses can occur. In conclusion, data at the order level was sufficient to determine overall differences in taxonomic composition, but that data at species or genus level were required for to establish differences in diversity across reed bed ages.

4.5. Methodological considerations and future studies

Classical experiments are not well-suited to ecological studies at larger spatial scales. For example, it is difficult to manipulate or replicate over large spatial scales and to maintain a manipulation for long periods (Hargrove and Pickering, 1992). Vejlerne provide a unique setting for testing manipulation at a large scale, by allowing placement of multiple sites across a large area (minimum of 80 m between sampling sites). Restricting the experiment to a few sites is spatial pseudo-replication, since the inference space will be larger than the area covered by replicates (Hurlbert, 1984). In the present study we were not able to employ a fully randomized design, but were able to maximize distance between sites/stations (from 80 m to 975 m between sites) compared to reed beds with different ages (from 1600 m to 4600 m between habitats). This naturally raises the question: what constitutes a reasonable or adequate replication? As pointed out by Hargrove and Pickering (1992) the answer to this question is not absolute, but is subject to interpretation of the factors believed important with regard to the measurements being made. It cannot be ruled out that treatments were confounded by sampling site, but given the home range of most invertebrates (Traugott, 2002; Matyukhin and Gongalskii, 2007) and extensive sampling effort with large distances between stations/sampling sites (and reduced distance between reed bed ages) we believe that the design is appropriate for the question. Further, edge effects are neglectable in our study (Davies and Gray, 2015). We were, however, unable account for the effect of reed harvest patch size. Other studies have found that patch size can affect the outcome of reed harvest (Trnka et al., 2014). We thus suggest that future studies should, if possible, in combination address the effects of reed bed age, patch size and edge. Together these factors may have important implications for management of reed beds.

5. Conclusions

Overall, our results show that commercial small-scale reed harvest is compatible with sustaining a high invertebrate abundance and diversity in the largest coherent reed bed of Scandinavia. By maintaining both new and old patches of reed, it is possible to affect invertebrate composition and possible enhance biomass and diversity. Small-scale commercial harvest can ensure a high invertebrate biomass in managed patches, while preserving a high biodiversity in unmanaged areas. By preserving several reed bed ages, managers can maintain a high biomass and invertebrate diversity at the landscape level. We therefore suggest that, in the present study system, while some reed patches should remain unmanaged, other parts can be harvested at varying intervals creating a mosaic of reed bed ages. We also propose

that future studies addressing effects of reed harvest on invertebrate biomass and diversity should incorporate reed age and that more studies across local, regional, and global scales are needed.

Credit author statement

Line Holm Andersen: Conceptualization, Methodology, Data curation, Visualization, Writing – original draft, Petri Nummi: Writing - review and editing, Supervision, Jeppe Rafn: Data Curation, Cecilie Majgaard Skak Frederiksen: Data Curation, Mads Prengel Kristjansen: Data Curation, Torben Linding Lauridsen: Funding acquisition, Writing - review and editing, Kristian Trøjelsgaard: Conceptualization, Funding acquisition, Writing - review and editing, Cino Pertoldi: Supervision, Conceptualization, Funding acquisition, Writing - review and editing, Dan Bruhn: Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing - review and editing, Simon Bahrndorff: Supervision, Conceptualization, Funding acquisition, Writing - review and editing.

Author contributions statement

LHA, KT, CP, DB and SB came up with the idea for the study. LHA, JR, CMSF and MPK collected the data in the field. JR identified all Coleoptera specimens. LHA identified invertebrates at the order level and did the biomass estimates. LHA wrote a first draft of the manuscript in collaboration with SB and PN. All authors commented on the results and manuscript prior to submission.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2021.113637.

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