The effect of peatland drainage and restoration on Odonata species richness and abundance

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Abstract

Restoration aims at reversing the trend of habitat degradation, the major threat to biodiversity. In Finland, over the half of the original peatland area has been drained and during recent years restoration of some of the drained peatlands have been accomplished. Short-term effects of the restoration on peatland hydrology, chemistry and vegetation are promising but little is known how other species groups in addition to vascular plants and bryophytes respond to restoration efforts. We studied how abundance and species richness of Odonata (dragonflies and damselflies) respond to restoration by sampling larvae in three sites (restored, drained, pristine) in 12 different study areas. We sampled Odonata larvae before restoration (n = 12), during the first (n = 10) and the third (n = 7) year after restoration and used generalized linear mixed models to analyze the effect of restoration. Before restoration drained sites had lower abundance and species richness than drained sites. During the third year after restoration both abundance and species richness had risen in restored sites. Adults of pre-selected indicator species were detected more often in restored sites than in drained sites. Our results show that Odonatas suffer from drainage but seem to benefit from peatland restoration and are able to colonize newly formed water pools relatively rapidly.

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Introduction

Degradation of natural habitats has become a major threat to biodiversity, questioning the survival of a vast number of species (Pimm and Raven 2000; Sala et al. 2000; Foley et al. 2005). In addition to impoverishment of environment, the loss of species may compromise our own well-being as degradation of habitats may hamper ecosystem function (Hooper et al. 2012), resulting even in ecosystem collapse (MacDougall et al. 2013). In order to halt the loss of biodiversity and ecosystem services international targets have been set not only for slowing down the rate of degradation but also for restoring already degraded ecosystems (CBD 2010). In general, ecological restoration aims at reversing the degradation by partial or complete restoration of the original structure and function of the ecosystem (Dobson et al. 1997).

Ecosystems with an urgent need for restoration are peatlands which have been, and still are, a subject for different human impacts, such as forestry, peat extraction and agriculture (Strack 2008). Peatlands cover approximately 3 % of the Earth's surface from which a majority, nearly 90 %, is found from the northern hemisphere (Strack 2008). Alone in Finland peatlands have been extensively drained, mainly for forestry purposes: over half of the original peatland area (altogether 4.7 million hectares) is currently drained (Finnish Forest Research Institute, 2013). This drastic diminishing of the natural peatland area has resulted in 223 species confined to peatlands classified as threatened (Rassi et al. 2010).

Drainage leads to major and rapid changes in the hydrology and chemistry of peatland. Water level drops immediately by 20 - 60 cm (Laine and Vanha-Majamaa 1992; Haapalehto et al. 2011; Haapalehto et al. 2014) resulting in complex changes in the amount and availability of different nutrients (Laiho et al. 1999; Haapalehto et al. 2011; Haapalehto et al. 2014), and in decrease of peat pH (Laine et al. 1995; but see Haapalehto et al. 2014). Consequently, these changes in abiotic conditions have their impact on the vegetation: peatland species confined to wet conditions are replaced by peatland species inhabiting hummocks and species colonizing from the nearby forests (Laine et al. 1995). Peatland restoration aims at reversing these changes by damming or filling in the ditches with peat and by removing the trees grown after drainage (Hedberg et al. 2012). Although studies concerning the long-term effects of these restoration efforts are still scarce [but see Haapalehto et al. (2011)] reported short-term effects occurring within a few years after restoration are promising: a rapid rise of the water-table and subsequent changes in peat chemistry (Jauhiainen et al. 2002; Laine et al. 2011; Haapalehto et al. 2011; Haapalehto et al. 2014), and also vegetation community seems to start recovering (Mälson et al. 2008; Haapalehto et al. 2011; Hedberg et al. 2012). However, little is known how other species groups in addition to vascular plants and bryophytes respond to restoration of drained peatlands.

Here we studied whether Odonata (dragonflies and damselflies) abundance and species richness respond to peatland restoration. Odonatas are widely used as bioindicators of different freshwater systems as they are sensitive to both local abiotic conditions and surrounding terrestrial landscape (Sahlén and Ekestubbe 2001; Butler and deMaynadier 2008; Oertli 2008; Bonifait and Villard 2010; Silva et al. 2010; Simaika and Samways 2011; Kutcher and Bried 2014). Particularly, Odonata have been used already in several restoration monitoring studies (D'Amico et al. 2004; Kadoya et al. 2008; Mabry and Dettman 2010; Magoba and Samways 2010). In Finland, there are altogether 55 species of Odonata and a handful of these species are restricted to peatlands (e.g. *Somatochlora arctica* and

S. alpestris) (Karjalainen 2010). In addition, peatlands are habitats also for generalists occupying almost any kind of waters, such as *Sympetrum danae* and *Libellulla quadrimaculata* (Karjalainen 2010).

Materials & Methods

Study sites and sampling of larvae

The study contained 12 areas (mire complexes) representing geographic variation from 60°52' N to 64°19' N and from 21°59' E to 26°43' E. From each area there were 3 sites: i) a pristine site, ii) a drained site, and iii) a drained site which was restored after the first observation. Drainage for forestry was accomplished by the state several decades ago, during 1960s and 1970s. All of the 12 areas were sampled for Odonata during June 2010, before the restoration (two areas were sampled twice before restoration). Odonata were sampled as larvae since it confirms the actual breeding of the species and excludes vagrants, in contrast to adults (Raebel et al. 2010). Moreover, sampling of the larvae is not dependent on the weather conditions. From each site three samples with a water-net were taken, each sample representing 2 strong net sweeps. In drained sites samples were taken from ditches and in pristine sites from bog pools.

Restorations of different sites were accomplished in different times between November 2010 and March 2014. After the restoration each area was visited at first year (end of May - June) after restoration (n = 10) and/or at the third year after restoration (n = 7). In drained sites the samples were taken from the same ditches and in pristine sites from the same bog pools as before. In the restored sites samples were taken from the newly formed water pools, and sampling at the first year after restoration was conducted to confirm that there are no larvae (as adult Odonata wouldn't have time to lay the eggs). Hence, the larvae possible found at the third year after restoration are due to new colonizations. Larvae were preserved in 70 % alcohol and determined to species according to Norling and Sahlén (1997). Specimens which were not identified to species level due to their small size were excluded from the analyses. These specimens represented mainly *Leucorrhinia dubia* and *L. rubicunda* species as distinguishing between the two species is dubious in very small larvae.

Indicator species

Presence and number of adults of four mire-dwelling Odonata (*Aeshna caerulea*, *Coenagrion johanssoni*, *Leucorrhinia albifrons* and *Libellula quadrimaculata*) were monitored by transect censuses at the same project sites and at the same time with bird line censuses (see report on monitoring of birds).

Statistical methods

The study set-up represents a nested structure where sites having different treatments are situated within study areas and are not thus independent observations (Zuur et al. 2009). Moreover, each site was sampled more than once and these observations are not independent either. Thus, we used generalized linear mixed models using Poisson distribution (log link) from the package 'nlme4' (Bates et al. 2014) in R (R Core Team 2014). Abundance and species richness of a site were set as response variables and fixed effects were treatment (restored, drained, pristine), year (before restoration, the first year after restoration, the third year after restoration) and their interaction term denoting the possible effect of restoration. Area and site were added as random factors, and the random effect ‘site’ was nested within the random effect of ‘area’. Abundance and species richness from the three samples within the site were pooled to achieve site level data. For the two areas visited twice before restoration mean number of individuals and species were used. No individuals (and consequently no species) were found from the restored sites during the first year after restoration. This violated model assumptions and caused inflated standard errors for the parameter in question. Thus, we reran the analyses using only the sites sampled before restoration and the third year after restoration (n = 7) (Table S1 in Supporting Information).

Increased sampling of individuals results in increased number of species (Gotelli and Colwell 2001). Thus, in addition to the real differences in species richness different raw species richness values may occur solely because different number of individuals have been collected, which may in turn reflect important differences in, for instance, resource availability or environmental conditions, but also differences in sampling effort or conditions in sampling (Gotelli and Colwell 2001). Thus, comparing raw species richness counts are meaningful only when sampling curves have reached a clear asymptote i.e. all species from the community has been sampled. When this is not the case, rarefaction curves can be used. We created individual-based rarefaction curves i.e. species accumulation curves (SACs) for each site by randomly drawing individuals from the observed species pool 100 times and plotted the mean of these random draws against the number of individuals drawn. We used these curves to detect whether the curves i) have reached asymptotes, and (ii) whether there are systematic differences among restored, drained and pristine sites within an area. Even though the data is relatively well replicated the number of observations for each treatment is nevertheless so small that analyzing community differences is not reliable and thus such analyses have not been conducted.

Results

We found altogether 515 individual larvae representing 13 species (Table 1). The number of individuals found from a site ranged from zero to 52 (mean = 5.9), and species richness from zero to five (mean = 1.1, when at least one individual was found: mean = 2.3). Before restoration both abundance and species richness was higher in pristine sites than in drained sites (Table 2). When considering also the first and the third year after restoration interaction of treatment and year was statistically significant for both abundance and species richness: abundance and species richness of restored sites increases in the third year after restoration (Table 3, Figs 1&2). These results were consistent when using only the areas visited during the third year after restoration (Table S1). The effect was due to three of the seven sites visited with relatively high species richness (4-5 species) whilst no individuals was found from the rest of the sites.

Inspecting SACs showed that where more than one species was found, SACs did not tend to reach an asymptote (Fig. S1). Moreover, there was variation between the curves between the years in some sites (e.g. Fig. S1d&g). Thus, the sampling could not be taken as exhaustive. In cases where an asymptote seems to be reached (e.g. Fig. S1i,j&f) the samples represent *Leucorrhinia dubia* which is commonly found in high abundance among the *Sphagnum* mosses. Comparing SACs among restored, drained and pristine sites was hindered by the fact that no individuals were found in many of the restored and drained sites. However, in the restored sites where individuals were found SACs lay above the curves of pristine sites suggesting that more species with the same number of individuals was found from the restored sites (Fig. S1a,c&l).

The number of individuals of indicator species overall was higher in restored sites than in drained sites and in many cases also higher than in pristine sites but there were too few observations to be able to run any statistical analyses on the data or make valid conclusions about the effect of restoration (see Table 1).

Table 1. Number of indicator Odonata observations. In each of the year columns there is number of individual observation over the summer for A.caerulae-C.johanssoni-L.albifrons-L.quadrimaculata respectively. Number of observations was so low that statistical analyses were not feasible.

Area	Treatment	2010 pre-restoration	2011	2012	2013	2014	Total
Kansanneva	Restored	0-0-0-1				0-0-0-0	0-0-0-1
	Drained	6-0-0-0				0-0-0-2	6-0-0-2
	Pristine	3-0-0-0				0-0-0-0	3-0-0-0
Oudonrimmit	Restored	6-0-0-0				0-0-0-9	6-0-0-9
	Drained	0-0-0-0				0-0-0-0	0-0-0-0
	Pristine	27-0-0-7				1-0-0-27	28-0-0-34
Pitkäsneva	Restored	0-0-0-6				0-0-0-2	0-0-0-8
	Drained	3-0-0-0				0-0-0-0	3-0-0-0
	Pristine	0-0-0-1				0-0-0-1	0-0-0-2
Pitkäsuo	Restored	0-0-0-0				0-0-0-2	0-0-0-2
	Drained	0-0-0-0				0-0-0-1	0-0-0-1
	Pristine	0-0-0-0				0-0-0-2	0-0-0-2
Kukilankeidas	Restored	0-0-0-0		0-0-0-0	0-0-0-31	7-0-0-2	7-0-0-33
	Drained	0-0-0-0		0-0-0-0	0-0-0-1	0-0-0-0	0-0-0-1
	Pristine	0-0-0-0		0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0
Haapakeidas	Restored						
	Drained						
	Pristine						
Lauhanvuori	Restored	0-0-0-0			1-0-0-28	4-2-0-4	5-2-32
	Drained	0-0-0-0			0-0-0-0	0-0-0-0	0-0-0-0
	Pristine	0-0-0-0			1-0-0-2	4-0-0-5	5-0-0-7
Kauhaneva	Restored	0-0-0-0				0-0-0-5	0-0-0-5
	Drained	0-0-0-0				0-0-0-0	0-0-0-0
	Pristine	0-0-0-0				0-0-0-1	0-0-0-1
Pirjatanneva	Restored	0-0-0-0	0-1-0-0	0-0-0-4	0-0-0-17	0-0-0-5	0-1-0-23
	Drained	0-0-0-0	1-0-0-0	0-0-0-0	0-0-0-1	0-0-0-0	1-0-0-1
	Pristine	0-0-0-0	0-0-0-0	0-0-0-0	2-0-0-7	2-0-0-3	4-0-0-10
Pilvineva	Restored	0-0-0-0					0-0-0-0
	Drained	0-0-0-0					0-0-0-0
	Pristine	0-0-0-0					0-0-0-0
Pohjoisneva	Restored	0-0-0-0	1-0-0-0	1-0-0-3	4-0-0-89	1-0-0-1	7-0-0-93
	Drained	0-0-0-0	0-0-0-0	0-0-0-0	12-0-0-19	0-0-0-0	12-0-0-9
	Pristine	0-0-0-0	0-0-0-0	0-0-0-0	5-0-0-4	0-0-0-0	5-0-0-4
Pyhähäkki	Restored	0-0-0-0		0-0-0-0	3-0-0-2	4-0-0-0	7-0-0-2
	Drained	0-0-0-0		0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0
	Pristine	0-0-0-0		0-0-0-0	3-0-0-1	1-0-0-0	4-0-0-1
Total number of observations		**45-0-0-15**	**2-1-0-0**	**1-0-0-4**	**31-0-0-201**	**24-2-0-72**	**103-3-0-297**

Discussion

Our results showed that Odonata clearly suffered from peatland drainage as both abundance and species richness of Odonata were lower in drained than in pristine sites. The reason for lower abundance and species richness in drained sites may be due to multiple factors: peatland drainage may change either the larval habitat or the surrounding landscape, and the effect may be direct or indirect *via* their prey. The simplest and the most probable cause for lower Odonata abundance in drained sites is the reduction of the available breeding habitat. Adult Odonata find suitable habitat by visual cues (Wildermuth 1998; Corbet 2004). Thus, transformation from bog pools (with a cover ranging from several square meters to more than a hectare) to a ditch with an approximately meter wide water surface may significantly diminish the changes for finding the site or simply reduce its attractiveness. Moreover, due to their small size drifts are also susceptible for drying and they may also sustain smaller amount of other invertebrates, lowering the amount of prey for Odonata.

Drainage also changes water quality which may affect Odonatas, either directly or indirectly *via* decreasing their prey. Particularly, drainage may result in decrease of pH (Laine et al. 1995). Indeed, pH has been shown to be an important factor affecting Odonata community composition (Johansson and Brodin 2003) but the suggested reason has been an indirect effect due to fish predation (Eriksson et al. 1980; Bendell and McNicol 1987). However, fish are unlikely to occur in bog pools. Although Odonata in general are relatively tolerant to low pH it may affect survival of some species (Corbet 2004). In addition to water quality drainage results in inevitable changes in vegetation patterns (Laine et al. 1995; Haapalehto et al. 2011). This may affect Odonatas as they use vegetation for multiple purposes (Buchwald 1992), and a positive relationship between Odonata and plant species richness have been found at multiple spatial scales (Sahlén 1999; Keil et al. 2008; Honkanen et al. 2011). However, the fact that in some sites Odonata species respond rapidly to restoration acts suggests that vegetation patterns are not at least the main reason for diminished abundance in drained sites as vegetation responds to restoration are generally slower (Mälson et al. 2008; Haapalehto et al. 2011; Hedberg et al. 2012).

As expected, during the first summer after restoration no larvae were found from the restored sites. This confirms that the increased abundance and species richness during the third year after restoration are due to new colonizations. Thus, Odonata are able to rapidly colonize the newly formed pools and seem to benefit from peatland restoration. However, increase of abundance and species richness was found only in three of the seven sites. By contrast, no individuals were found in the rest of the sites. This may be because of adults have not been able to find the pools. This is unlikely because although landscape structure influences the movements of Odonata (Jonsen and Taylor 2000) the study set-up included a pristine site in the same mire complex acting as a source pool. The other possible reasons for no individuals found are that either the adult do not find the newly formed pools suitable for egg laying or larvae may be in so low abundance that they were not detected. Either way, this means that the pools were relatively unattractive which may reflect the variation in hydrological and nutrient regimes due to unavoidable differences in restoration acts.

Odonata larvae were found in very low abundances from the studied peatlands. As the number of species increases with increasing number of individuals (Gotelli and Colwell 2001) and species accumulation curves representing this relationship failed to reach asymptotes, the sampling was not exhaustive enough to reveal the true Odonata species richness of the study sites. Thus, in order to have a better estimate of absolute species richness of the sites, sampling should have been enhanced. However, our main results are about the relative species richness and abundance among the pristine, drained and restored sites and for this comparison the sampling is robust enough.

Even if statistical testing of indicator species data was not feasible, the higher number of observations on the indicator species from restored sites than drained sites also suggests that the adults of Odonata species are searching for food and suitable sites for laying eggs more often and more actively in restored sites than drained sites.

To conclude, Odonata showed decreased abundance and species richness in drained peatlands compared to pristine ones. Thus, drainage cause changes in hydrological and nutrient regimes in peatlands that have consequences not only to vegetation but also to other species groups. As the Odonata are top predators in many bog pools, their diminishing may cause cascading effects in other water invertebrates also. Fortunately, our results also showed that peatland restoration have potential to lead a relatively rapid recovery of Odonata abundance and species richness.

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Supporting information

Table S1 Results of generalized linear mixed models using only the areas sampled during the third year after restoration
Fig. S1 Species accumulation curves

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Table 1 Odonata species found and their mean number of individuals in different occupied sites (note that the number of sampled areas differs, before: n = 12; the first year after restoration: n = 10; the third year after restoration: n = 7)

	Restored			Drained			Pristine		
	before	1. year after	3. year after	before	1. year after	3. year after	before	1. year after	3. year after
Lestes sponsa (Hansemann, 1823)							2 (1)	2.5 (2)	3.7 (3)
Coenagrion hastulatum (Charpentier, 1825)			2 (1)				1.5 (2)	2.3 (3)	9 (2)
Coenagrion johanssoni (Wallengren, 1894)							6.5 (2)		
Enallagma cyathigerum (Charpentier, 1840)								2 (1)	
Aeshna juncea (Linnaeus, 1758)			1 (1)				2 (3)	1.3 (3)	1 (1)
Aeshna subarctica (Walker, 1908)			1 (1)			1 (1)	2.8 (5)	1 (1)	3 (1)
Somatochlora alpestris (Selys, 1840)			1 (1)	1 (1)					
Somatochlora arctica (Zetterstedt, 1840)	5.5 (4)			7.3 (3)	13(1)	2.5 (2)	13 (1)		
Somatochlora metallica (Vander Linden, 1825)	1 (1)		2 (1)						
Libellula quadrimaculata (Linnaeus, 1758)			3.3 (3)				1.3 (3)	1 (1)	
Sympetrum danae (Sulzer, 1776)			1 (1)					1 (1)	8 (1)
Leucorrhinia dubia (Vander Linden, 1825)	8 (1)		2 (3)	1(1)	1(1)	10 (1)	16.8 (11)	8.9 (8)	9.6 (5)
Leucorrhinia rubicunda (Linnaeus, 1758)			5 (2)				1 (1)	1 (2)	1 (3)

Table 2 Fixed effects part of generalized linear mixed models for abundance (a) and species richness (b) for all areas (n = 12) before restoration. Pristine sites are used as baselines, and treatment(D) = drained sites, treatment(R) = restored sites. Random variables = study area, study site; number of observations = 36, residual degrees of freedom = 31

		Estimate	SE	z	*P*
a)	Intercept	**2.57**	**0.40**	**6.35**	**<0.001**
	treatment(D)	**-3.17**	**0.64**	**-4.98**	**<0.001**
	treatment(R)	**-2.90**	**0.61**	**-4.74**	**<0.001**
b)	Intercept	**0.88**	**0.19**	**4.75**	**<0.001**
	treatment(D)	**-1.98**	**0.53**	**-3.71**	**<0.001**
	treatment(R)	**-1.58**	**0.45**	**-3.51**	**<0.001**

Table 3 Fixed effects part (year, treatment, and their interaction term) of generalized linear mixed models for abundance (a) and species richness (b) for all areas (n = 12). Before restoration and pristine sites are used as baselines. Year(1)= first year after restoration, year(3) = third year after restoration, treatment(D) = drained sites, treatment(R) = restored sites. Random variables = study area, study site; number of observations = 87, residual degrees of freedom = 76

		Estimate	SE	z	*P*
a)	Intercept	-0.77	0.62	-1.25	0.211
	year(1)	-18.53	1998.18	-0.01	0.993
	year(3)	**2.01**	**0.47**	**4.31**	**<0.001**
	treatment(D)	-0.57	0.82	-0.70	0.485
	treatment(R)	**3.38**	**0.71**	**4.79**	**<0.001**
	year(1):treatment(D)	18.05	1998.18	0.01	0.993
	year(3):treatment(D)	-1.14	0.62	-1.85	0.064
	year(1):treatment(R)	17.81	1998.18	0.01	0.993
	year(3):treatment(R)	**-1.96**	**0.49**	**-4.02**	**<0.001**
b)	Intercept	-0.83	0.45	-1.85	0.064
	year(1)	-19.15	248.36	-0.08	0.939
	year(3)	**1.40**	**0.50**	**2.78**	**0.006**
	treatment(D)	-0.41	0.66	-0.62	0.539
	treatment(R)	**1.62**	**0.48**	**3.39**	**0.001**
	year(1):treatment(D)	18.64	248.36	0.08	0.940
	year(3):treatment(D)	-0.88	0.87	-1.01	0.311
	year(1):treatment(R)	19.10	248.36	0.08	0.939
	year(3):treatment(R)	**-1.49**	**0.59**	**-2.51**	**0.012**

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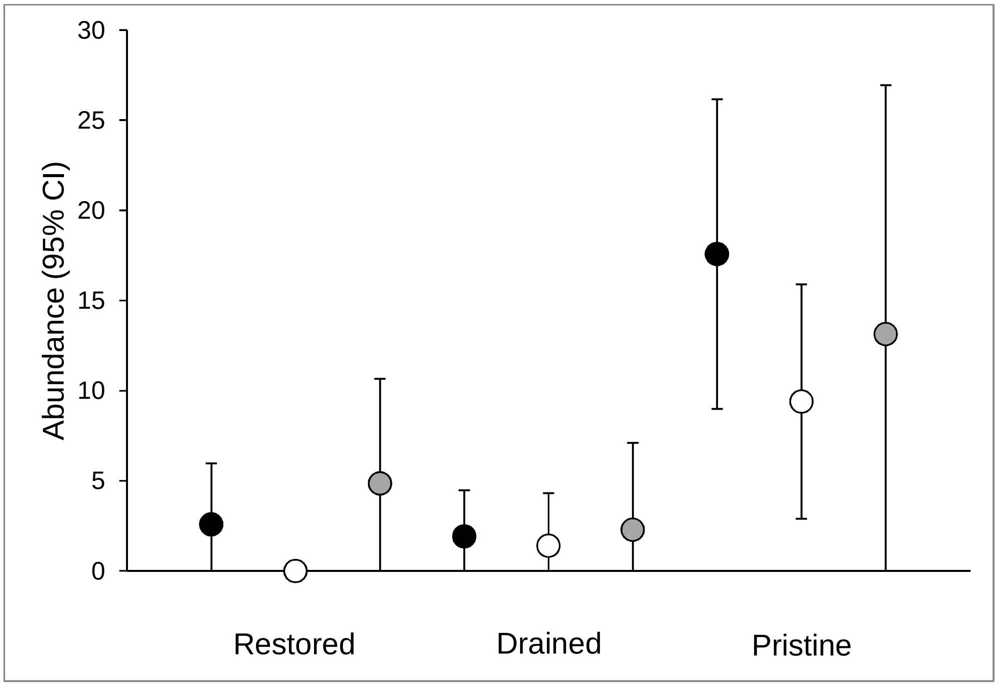

Fig. 1 Abundance of Odonata (mean and respective 95% Confidence Intervals) in restored, drained and pristine sites before restoration (black dots, *n* = 12), first year after restoration (white dots, *n* = 10) and third year after restoration (grey dots, *n* = 7)

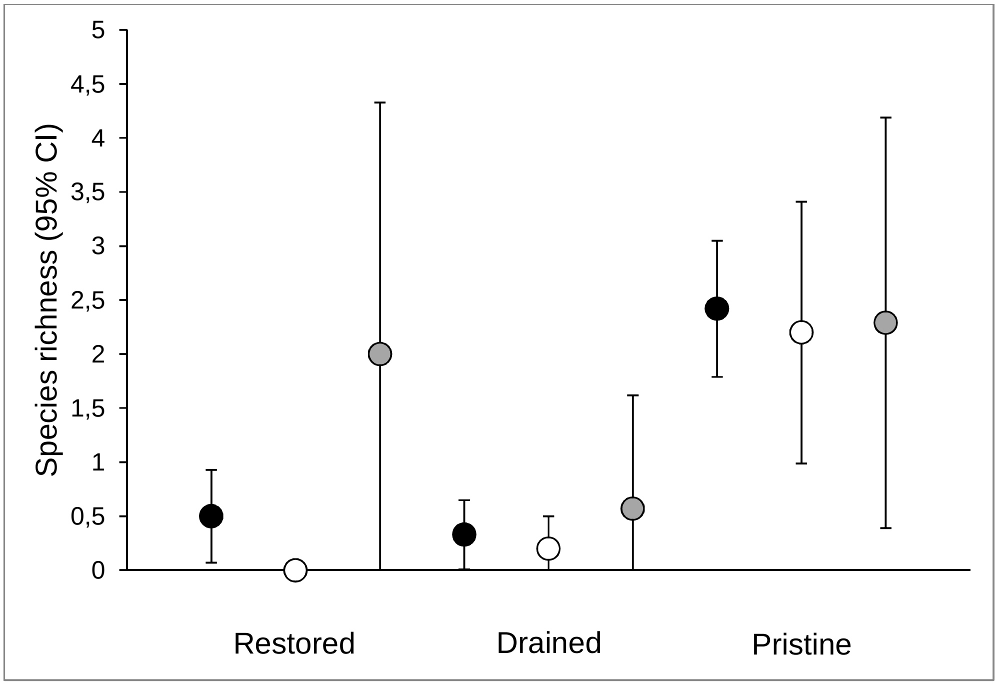

Fig. 2 Number of Odonata species (mean and respective 95% Confidence Intervals) in restored, drained and pristine sites before restoration (black dots, *n* = 12), first year after restoration (white dots, *n* = 10) and third year after restoration (grey dots, *n* = 7)

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Table S1 Fixed effects part (year, treatment, and their interaction term) of generalized linear mixed models for abundance (a) and species richness (b) for areas sampled during the third year after restoration (*n* = 7). Before restoration and pristine sites are used as baselines. Year(3) = third year after restoration, treatment(D) = drained sites, treatment(R) = restored sites. Random variables = study area, study site; number of observations = 42, residual degrees of freedom = 34

		Estimate	SE	z	*P*
a)	Intercept	**2.39**	**0.52**	**4.61**	**<0.001**
	year(3)	0.02	0.15	0.15	0.882
	treatment(D)	**-3.15**	**0.84**	**-3.73**	**<0.001**
	treatment(R)	**-4.17**	**0.94**	**-4.43**	**<0.001**
	year(3):treatment(D)	0.45	0.43	1.04	0.297
	year(3):treatment(R)	**2.41**	**0.62**	**3.88**	**<0.001**
b)	Intercept	**0.82**	**0.33**	**2.49**	**0.013**
	year(3)	-0.12	0.34	-0.34	0.732
	treatment(D)	**-1.84**	**0.67**	**-2.76**	**0.006**
	treatment(R)	**-2.26**	**0.78**	**-2.88**	**0.004**
	year(3):treatment(D)	0.41	0.84	0.48	0.628
	year(3):treatment(R)	**2.06**	**0.83**	**2.49**	**0.013**

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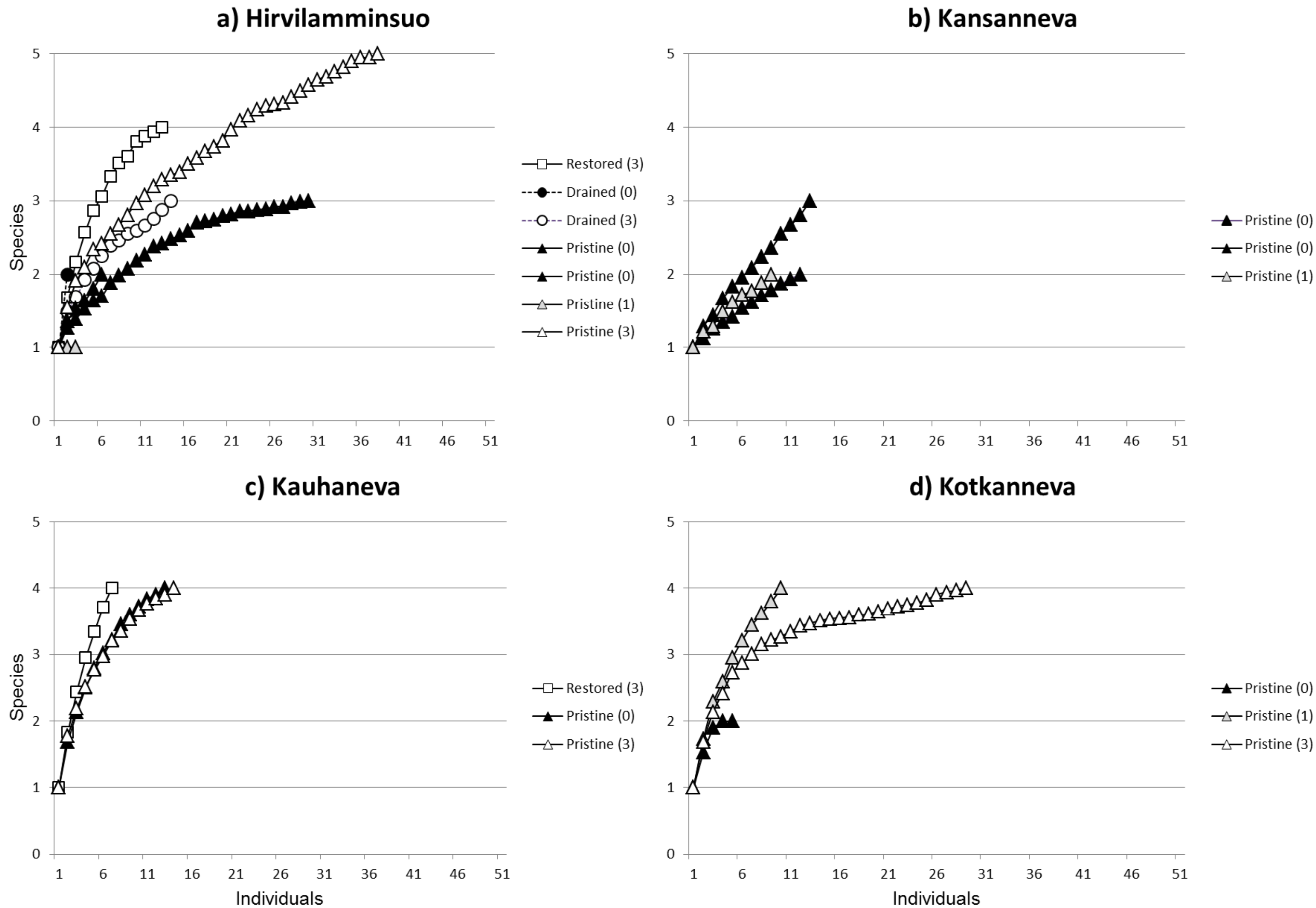
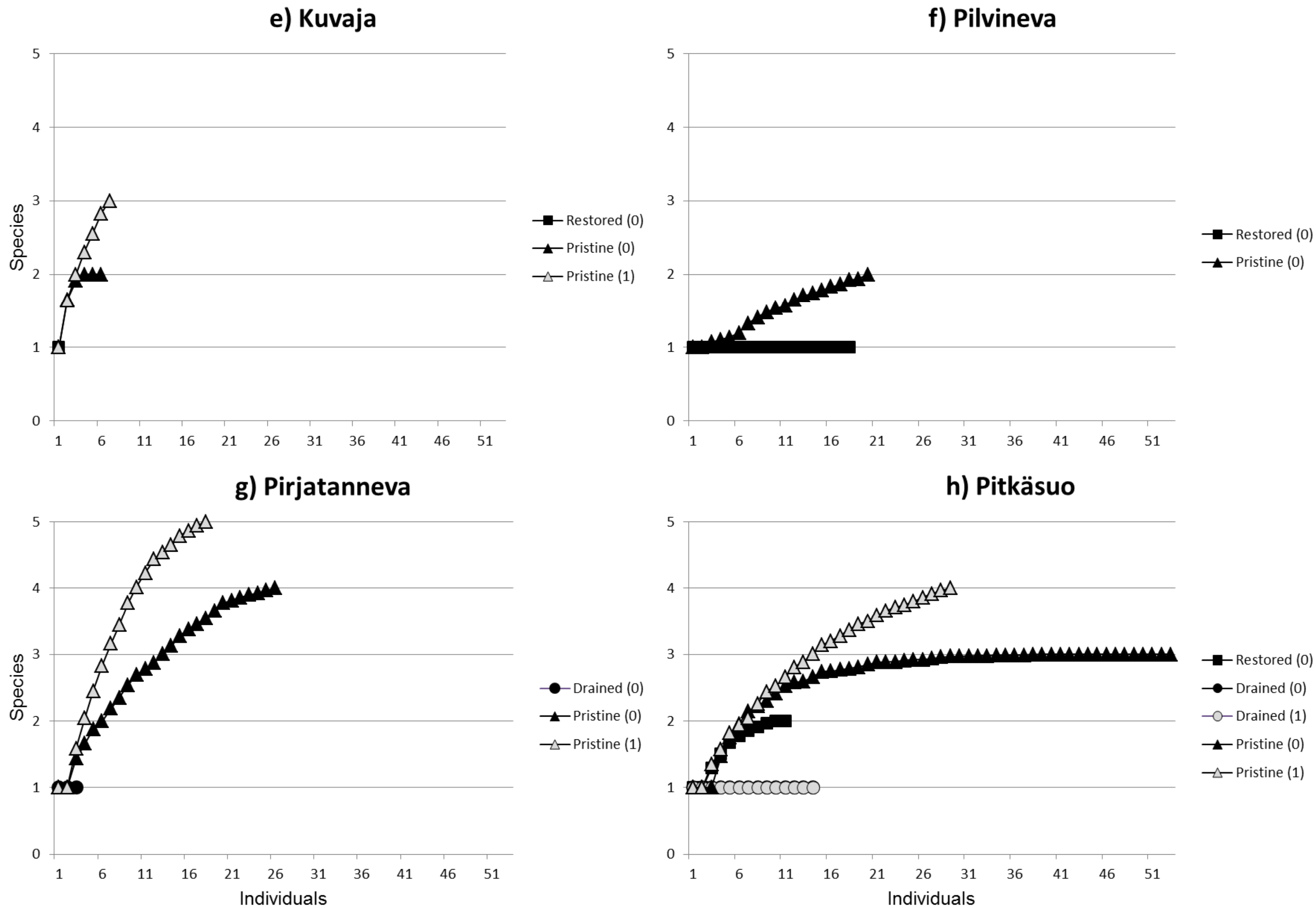

a) Hirvilamminsuo
b) Kansanneva
c) Kauhaneva
d) Kotkanneva
Species
Individuals
Restored (3)
Drained (0)
Drained (3)
Pristine (0)
Pristine (0)
Pristine (1)
Pristine (3)
Pristine (0)
Pristine (0)
Pristine (1)
Restored (3)
Pristine (0)
Pristine (3)
Pristine (0)
Pristine (1)
Pristine (3)


e) Kuvaja
f) Pilvineva
g) Pirjatanneva
h) Pitkäsuo
Species
Individuals
0
1
2
3
4
5
1
6
11
16
21
26
31
36
41
46
51
Restored (0)
Drained (0)
Drained (1)
Pristine (0)
Pristine (1)

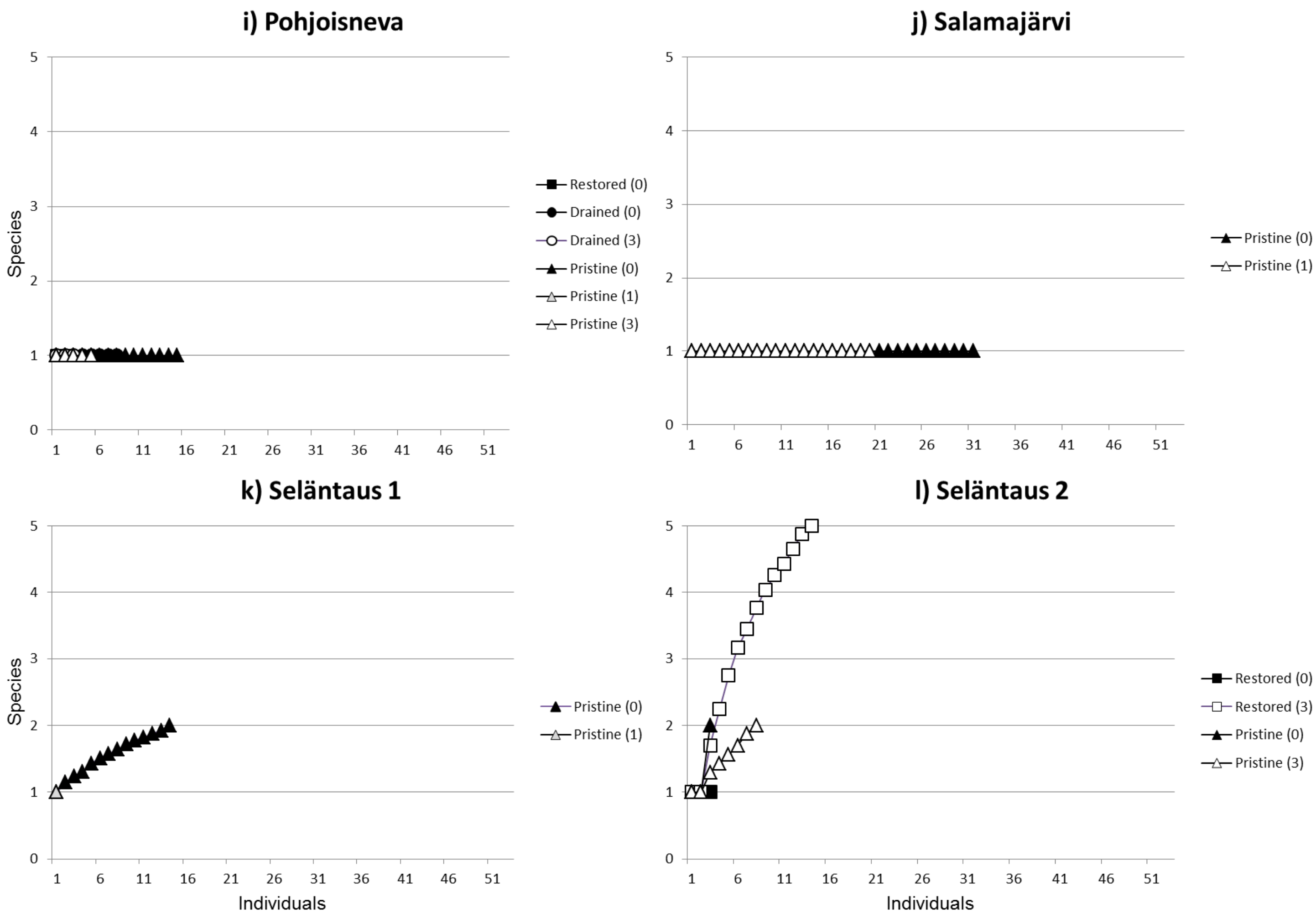


Fig. S1 Species accumulation curves in different study areas (a-l) representing all samplings from which any individuals were found