



Impacts of artificial drainage on amphibian breeding sites in hemiboreal forests

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ABSTRACT

Artificial drainage is widely used to increase timber production and improve its quality in northern boreal and temperate forests, but its impact on biodiversity remains largely unexplored. Amphibians are particularly dependent on forest wetland qualities to complete their complex life cycles. We explored the supply of water bodies, their occupancy by amphibians, and persistence during the larval period comparatively in drained and natural forest plots in two years in Estonia. The water bodies in drained plots were more abundant but less diverse and of generally lower quality than in natural plots; however, the drainage ditches were favoured by newts. In the dry spring of 2009, water bodies were used more frequently in natural than in drained plots, while in the typical spring of 2010, several natural depressions appeared in drained plots and the frequency of use of water bodies did not differ between natural and drained plots. However, most natural depressions used for breeding in drained plots dried out before tadpole metamorphosis; such drying was not observed in natural plots. Thus, by profoundly changing natural hydrology, intensive large-scale forest drainage reduces the variety of water bodies and the quantity and quality of amphibian breeding sites. Moreover, we suspect that, at least in some years, temporary water bodies in drained areas function as ecological traps for amphibians. We suggest that, where possible, intact wet-forest areas with remaining natural hydrology should stay undrained. In areas already drained, breeding sites for amphibians can be provided by creating depression-like enlargements to some ditches.

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1. Introduction

During the 20th century, half of the world's wetlands were lost, largely because of artificial drainage for increased agricultural production (OECD, 1996). Draining reduces wetland diversity, increases fluctuations in hydrological regime and rapidly lowers water levels (Babbitt and Tanner, 2000).

Mechanical large-scale draining, creating a dense network of open ditches, has also been carried out for silvicultural purposes – to reduce waterlogging and promote tree growth in forested wetlands and semi-open mires where precipitation exceeds the transpiration. By the early 1990s, more than 15 million hectares wetlands had been drained for forestry, with over 90% in Fennoscandia, Russia and the Baltic States (Paavilainen and Päivänen, 1995). By leading excess surface water away via ditches, forest drainage decreases the duration of seasonal floods, improves soil aeration and avoids nutrient flow from the soil. While that improves tree growth and the quantity and quality of timber produced (Peltomaa, 2007), it by definition also affects the natural quality of aquatic ecosystems (Ramberg, 1976; Lundin, 1994). Such impacts on freshwater environments have been described in many

studies (e.g. Vuori et al., 1998; Prévost et al., 1999). Regarding faunal responses, there are several studies on soil mesofauna (e.g. Markkula, 1986; Silvan et al., 2000; Laiho et al., 2001) and stream biota (Vuori and Joensuu, 1996; Vuori et al., 1998; Bond and Downes, 2003; Louhi et al., 2010), but only a few on vertebrates (Jutila et al., 1998; Ludwig et al., 2008).

Amphibians are a taxonomic group of global conservation concern (Stuart et al., 2004), which also plays an important role in the structure and functioning of forest ecosystems: they contribute significantly to the biomass of forest fauna (Burton and Likens, 1975; Wyman, 1998), provide essential food supply for predators (Blaustein and Wake, 1995), and are among keystone predators of invertebrates (Davic and Welsh, 2004; DuRant and Hopkins, 2008). Thus amphibian population declines can have serious impacts on other organisms and whole ecosystems (Blaustein et al., 1994). Loss of freshwater bodies generally reduces amphibian productivity and abundance via the number and density of breeding sites (Semlitsch, 2000; Rannap et al., 2007). Yet, the extent of forest drainage impacts on amphibians remains unexplored (Elmberg, 1993).

In this study we explore the impact of forest drainage on amphibian populations in Estonia, hemiboreal Europe, where ca. 25% of forest land has been historically drained and most of those drainage systems continue functioning (Torim and Sults, 2005). Our aim is to compare artificially drained and natural forest areas

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in terms of (1) the supply and characteristics of small water bodies available, (2) use of the water bodies for breeding by amphibians, (3) water-level changes during the larval development and (4) amphibian abundance and diversity.

2. Materials and methods

2.1. Study area and sampling design

The study was conducted in 2009–2010 in three South Estonian areas (125,600 ha each; between 27°1'E, 57°44' N and 25°18' E, 58°29' N; Fig. 1). The areas had a varied hilly relief that rises over 200 m above the surrounding plains, and broadly similar forest composition and cover (Valk and Eilart, 1974). On the map of each of the three areas, we placed a 700 × 700 m cell grid and pre-selected (using the Estonian Basic Map and aerial photos) all the 49-ha cells having relatively uniform forest areas according to the following criteria: (i) ≥80% forest cover and no recent large-scale logging or clear-cutting visible on aerial photos, and (ii) broadly similar forest types, according to the Estonian Forest Registry data (49 ha inevitably supports site-type mosaics, of which the most frequent mixtures of *Oxalis*, *Aegopodium* and *Filipendula* were chosen). When several adjacent cells met the criteria, one was selected randomly. Among those plots, 18 plots of two contrasting types were sampled (three plots of each type in each area; Fig. 1): nine plots having a dense network of artificial drainage ditches (typically, ca. 4 km per plot; created mainly in the

1970s–1980s, but still functioning; hereafter 'drained plots') and nine plots having mostly natural hydrology (no ditches depicted on the Basic Map; at least 1 km of rivers/streams per plot; hereafter 'natural plots'). The ditches in the drained plots were all vegetated with different grasses and often had young willows (*Salix* sp.) or grey alders (*Alnus incana*) on their banks, indicating that the banks had been cleared by cutting ca. 5–15 years ago. During the fieldwork, a total of five old ditches were found in natural plots (probably hand-dug before the 1920s, now partly overgrown with forest and not depicted on maps any more). We did not observe any recent ditch renewing or other type of forest management practices in the study plots.

Patterns of winter and spring precipitation, which affect breeding conditions of amphibians, differed between the years (Fig. 2). The precipitation in April and May formed only 30–36% of the long-term average in 2009, but 95–115% in 2010 when the mean amount of precipitation was three (35–50 mm in Viljandi county) to four (37–59 mm in Valga county) times higher than in 2009 (17–16 mm and 8–16 mm respectively; data from the Estonian Meteorological and Hydrological Institute).

2.2. Fieldwork

In each year (2009 and 2010) every plot was explored twice. The first visit was carried out in the beginning of amphibian breeding season in late April or early May, when the night temperatures had been over zero (+3–4 °C) for at least 4–5 days. Each plot was

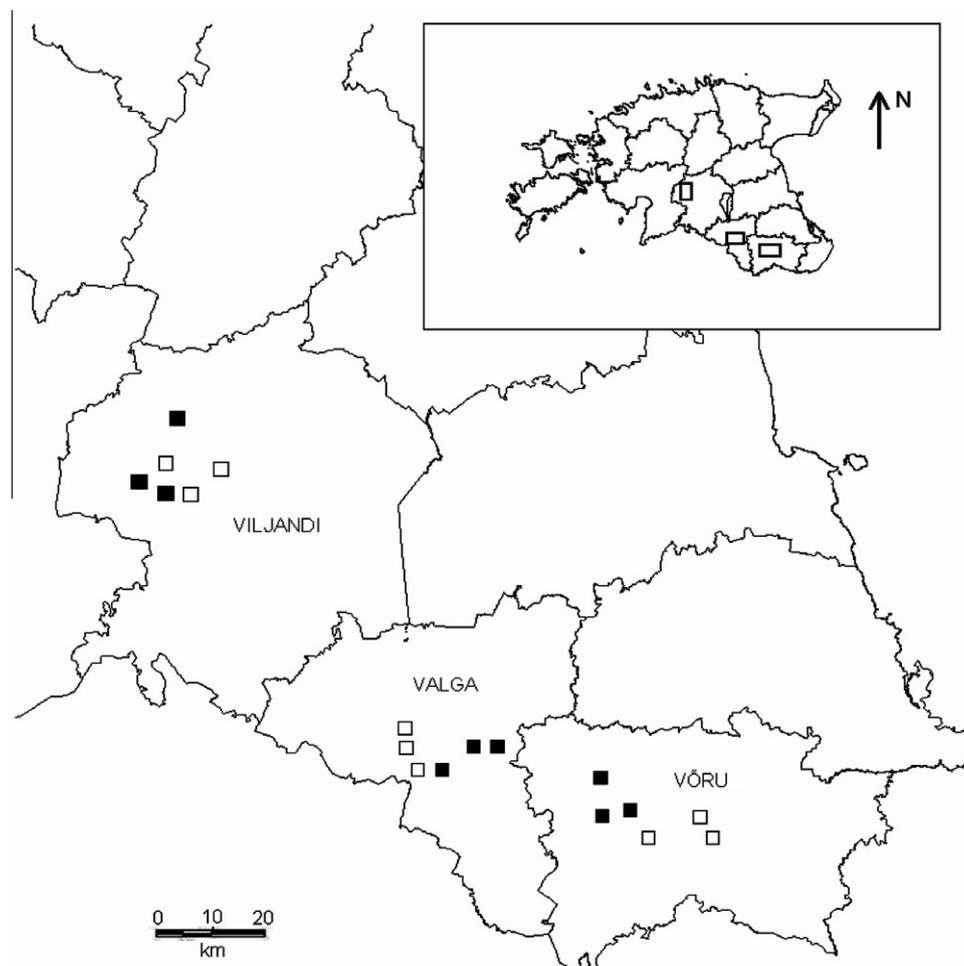


Fig. 1. Map of study areas in three Estonian counties; filled squares (■) represent drained and hollow squares (□) natural plots.

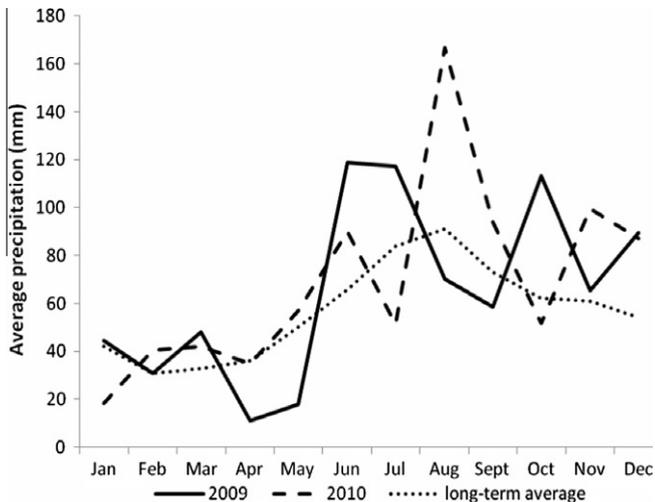


Fig. 2. The average precipitation in the study area in 2009 and 2010 with the long-term average (1961–1990). Data from Estonian Meteorological and Hydrological Institute.

thoroughly searched for all water bodies at least 5 cm deep and at least 10 m² in area. For each such water body, 11 characteristics were described. Categorical variables included water-body type, sediment type, water transparency/colour, water flow and surrounding land cover type. Continuous variables included the length and width of the water body, maximum water depth, mean inclination of slopes, proportion of area under submerged vegetation and in shade.

Amphibians' eggs were searched for in all aquatic habitats found in the plots. Each water body was investigated for a maximum of 20 min. Newts' eggs, anuran clutches, egg strings and larvae were counted and the species was determined. Dip-netting was also used to detect breeding sites when tadpoles had already hatched. In ditches and streams, 10 dip-net sweeps were made per 50 m. In water-filled depressions, ponds and other types of wetlands 10–30 dip-net sweeps were made, depending on the size of water body, covering all aquatic micro-habitats. The dip-netting also provided data on the presence of predators of amphibian eggs and tadpoles (leeches, dragonfly larvae, and fish). Given the difficulties in distinguishing the clutches and tadpoles of the pool frog (*Rana lessonae*) and the edible frog (*R. kl. esculenta*), those species were collectively treated as "green frogs" (*R. esculenta* complex).

In order to detect and describe changes in breeding sites during larval period, all breeding sites were revisited in early June (before the metamorphosis of larvae). The maximum water depth of each water body was measured. Dip-net sampling was used to capture larval amphibians (those caught were counted and identified) and newt eggs were sought from aquatic vegetation.

2.3. Data analysis

Statistical analyses were carried out using the Statistica 7 software. Characteristics of the water bodies and amphibian breeding sites in drained and natural plots were compared using conventional parametric (*t*-test) and nonparametric tests (Mann–Whitney *U*-test). Repeated measures ANOVA was used for simultaneous comparisons between years or visiting times (a repeated measure) and treatments (a categorical factor). Kolmogorov–Smirnov test was used to assess distribution normality.

To explain amphibian performance at the water-body scale, we used generalised linear modelling (GLZ) approaches. First, amphibian species richness was related to habitat characteristics using Poisson distribution and log link function. That model was built

according to the procedure of Hosmer and Lemeshow (1989): (i) univariate analyses for each of the eight independent variables; (ii) preliminary multivariate models, which included the potentially important variables from the univariate analyses, (iii) omission of non-significant and/or redundant variables from the multivariate model considering their biological meaning and large differences in univariate significance levels. In the first two steps, α was set at <0.15 (to retain the variables that could gain significance while in combination with other variables); in the final step, $\alpha < 0.05$ was used. Secondly, a logistic regression model was built to evaluate whether the incidence of amphibian breeding success (established as presence of larvae in breeding sites during the second visit) differs between years and plot types (natural vs. drained). Factor significance was estimated using likelihood-ratio tests.

3. Results

3.1. The water bodies

There were a total of 129 water bodies in the study plots in 2010 (the more typical spring; Fig. 2) compared to 92 water bodies in the dry spring 2009. However, the increase in the spring of 2010 was not significant at the plot scale (repeated-measures ANOVA: $F_{1,16} = 0.8$; $p = 0.39$). In both years water bodies tended to be more abundant in drained plots (14.1 ± 4.5 water-bodies km⁻¹ in 2009; 18.4 ± 4.0 in 2010) than in natural plots (6.8 ± 4.5 and 10.9 ± 2.3 , respectively; $F_{1,16} = 4.5$; $p = 0.05$).

Ditches predominated in drained plots, while depressions were the most frequent water-body type in natural plots (Table 1a). Yet, in 2009 only 3% of water bodies had running water in drained plots and 9% in natural plots (in 2010, 8% and 5%, respectively). Water bodies in natural plots were on average deeper than those in drained plots (Fig. 3a; *t*-tests for log-transformed values; in 2009: $t_{90} = 5.3$, $p < 0.001$; in 2010: $t_{125} = 6.3$, $p < 0.001$), but their slopes were less steep than in drained plots (Fig. 3b; Mann–Whitney *U*-test; in 2009: $U = 474$, $n = 92$, $p < 0.001$; in 2010: $U = 876$, $n = 129$, $p < 0.001$). In natural plots, water bodies were frequently surrounded by natural wet grasslands along streams/rivers or in forest (47% in 2009; 50% in 2010); while in drained areas the banks were typically forested or the water bodies were situated along forest roads/rides (95% in both years).

3.2. Amphibian breeding sites, diversity and abundance

Amphibians bred in 27 water bodies in 2009 and in 50 water bodies in 2010 (Table 1a). In drained plots, 23% of all water bodies available were used in 2009 and 39% in 2010; in natural plots 43% and 38%, respectively (Table 1a). Ditches were the main breeding waters in drained plots (about one third were used for breeding) but, when water-filled depressions became available in spring 2010, the latter were relatively more often used for breeding there (notably by *Rana temporaria*; Table 1). Depressions were also highly favoured for breeding in natural plots where they were common (Table 1a) and deeper on average than the depressions in drained plots (*t*-test for log-transformed values: $t_{33} = 2.6$, $p = 0.01$).

Altogether six species (including the green-frog complex) of amphibians were recorded, with up to three species per breeding site in each year and plot type. At the water-body scale, amphibian species richness was positively associated with water depth and submerged vegetation cover in both years (Table 2). In 2010 also water-body type contributed: depressions and ditches were preferred, rivers/streams avoided (Table 2).

Table 1

(a) Abundance of water bodies by type and their frequency of use as breeding sites by amphibians; (b) amphibian species and number in their breeding localities in 9 natural and 9 drained study plots in 2009 and 2010.

Area	Type	(a) Water bodies				(b) Amphibian species and no. of their breeding localities ^b	
		No. of water bodies		% used for breeding ^a		2009	2010
	Year:	2009	2010	2009	2010	2009	2010
Natural	Ditch	4	5	(0)%	(0)%	–	–
	Stream/river	7	8	29%	25%	2 BB	2 BB
	Flooded area	8	15	38%	27%	1 RA, 1 RE, 1 RT	1 BB, 1 RA, 2 RT
	Depression	11	20	73%	65%	1 LV, 3 RA, 6 RT	1 BB, 7 RA, 2 RE, 9 RT
Drained	Ditch	56	65	25%	37%	1 BB, 7 LV, 2 RA, 2 RE, 9 RT, 2 TC	7 LV, 13 RA, 14 RT, 1 TC
	Stream/river	1	1	(0)%	(0)%	–	–
	Depression	5	15	0%	53%	–	1 RA, 8 RT
Total n		92	129	27	50		

^a Frequencies based on <5 observations in brackets.

^b BB, *Bufo bufo*; LV, *Lissotriton vulgaris*; RA, *R. arvalis*; RE, *R. esculenta* complex; RT, *Rana temporaria*; TC, *Triturus cristatus*.

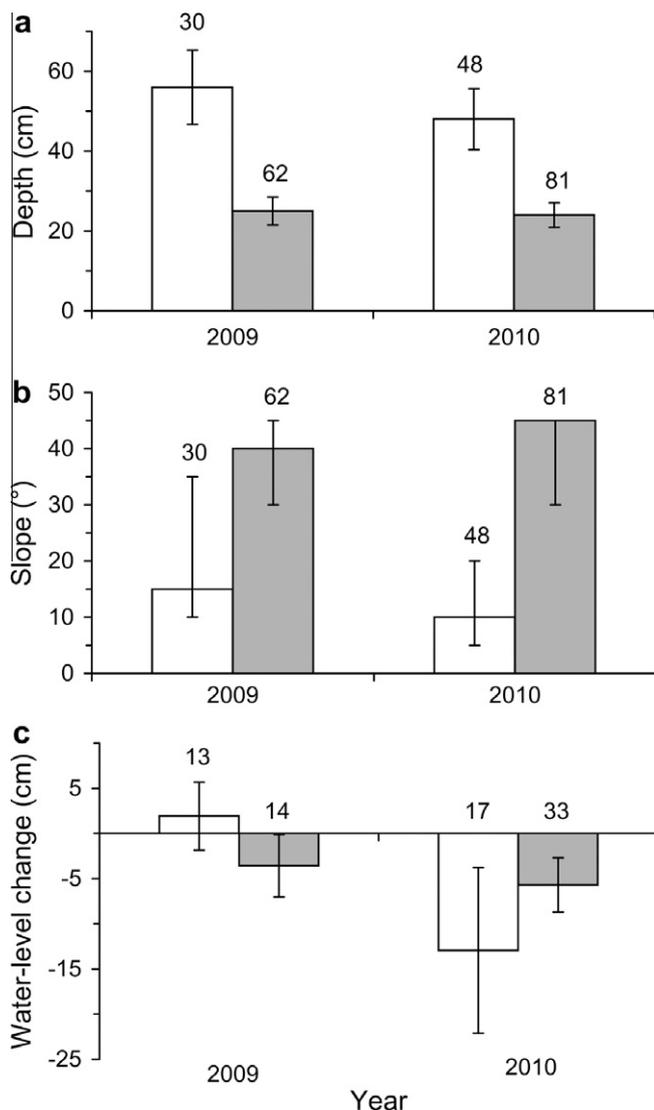


Fig. 3. Water-body characteristics in natural (white bars) and drained plots (grey bars) in 2009 and 2010: (a) mean maximum depth ($\pm 95\%$ CI); (b) median slope of the bank (\pm quartiles); (c) mean ($\pm 95\%$ CI) water-level reduction between late April and early May and early June. The numbers above bars denote sample size (No. of water bodies) and part (c) includes four water bodies that dried out completely.

Among species, the common frog (*R. temporaria*) and the moor frog (*R. arvalis*) were most abundant both in drained and in natural plots (Table 1b). The smooth newt (*Lissotriton vulgaris*) was

Table 2

Generalized linear models (Poisson distribution; log link) explaining the species richness of amphibians via water-body characteristics in 2009 and 2010.

Variable	Coefficient \pm SE	Log-likelihood	χ^2	p
<i>Year 2009 (n = 92) Model log-likelihood -102.8; p < 0.001</i>				
Submerged vegetation	0.011 \pm 0.003	-109	12.4	<0.001
Maximum depth	0.011 \pm 0.004	-106.2	6.8	0.009
<i>Year 2010 (n = 129) Model log-likelihood -154.1; p < 0.001</i>				
Submerged vegetation	0.007 \pm 0.003	-156.5	4.8	0.028
Maximum depth	0.017 \pm 0.004	-160.9	13.8	<0.001
Type of water body		-164.1	20.1	<0.001
Ditch	0.703 \pm 0.231			
Depression	0.668 \pm 0.209			
River or stream	-0.262 \pm 0.375			

confined to ditches in drained plots (14 of 15 occurrences), preferring deeper ditches (Mann–Whitney *U*-test for presence; in 2009: $U = 48.0$, $n = 56$, $p = 0.001$; in 2010: $U = 87.0$, $n = 65$, $p = 0.004$). The crested newt (*Triturus cristatus*) also used ditches, but it was found in each year only in one drained plot. The common toad (*Bufo bufo*) and green frogs were more frequent in natural areas where they bred in depressions (green frogs) and floods of rivers and streams (common toad).

Total abundance of amphibian larvae found per water body was significantly higher in natural than in drained plots in 2009, but not in 2010 (Fig. 4; for 2009: $U = 718.5$, $p = 0.02$; for 2010: $U = 1789$, $p = 0.36$). By early June, five (38%) breeding sites in natural plots and six (43%) in drained plots did not have any larvae in 2009, while in 2010 larvae were not found in one (5%) breeding site in natural plots and in ten (32%) sites in drained plots. At the water-body scale, the incidence of successful breeding differed between years (multifactor logistic regression: $\chi^2_1 = 5.4$, $p = 0.020$; greater losses in 2009), but also tended to be higher in natural plots ($\chi^2_1 = 2.9$, $p = 0.087$). The year \times plot type interaction was not significant ($\chi^2_1 = 1.9$, $p = 0.16$). There was no relationship between the incidence of amphibian breeding success and their predators (fish; predatory invertebrates) in the 77 water-bodies studied (Chi-square test: $\chi^2_1 = 0.26$, $p = 0.61$), and the incidence of predators did not differ between the plot types ($\chi^2_1 = 0.41$, $p = 0.52$).

3.3. Water-level reduction during larval development

Seasonal reduction in water levels (between the two visits) depended on plot type and year (Fig. 3c). In the 27 water-bodies re-checked in 2009, the reduction was only observed in drained plots (repeated measures ANOVA; time \times plot type interaction: $F_{1,25} = 4.4$, $p = 0.046$; main effect of time: $F_{1,25} = 0.4$, $p = 0.53$). In the 50 water-bodies followed in 2010, water-level reductions took place in both types of plots (main effect of time: $F_{1,48} = 22.2$,

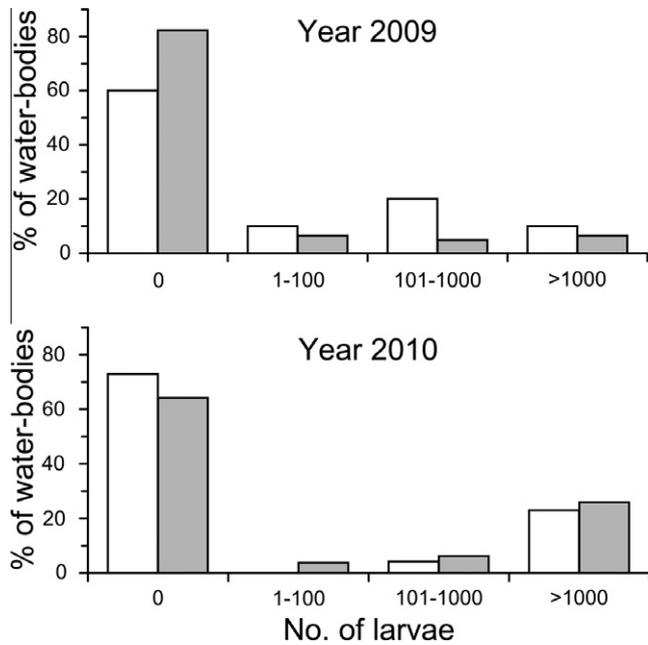


Fig. 4. Distribution of water bodies according to the abundance of amphibian larvae in natural (white bars) and drained plots (grey bars) in 2009 ($n = 92$) and in 2010 ($n = 129$).

$p < 0.001$; time \times plot type interaction: $F_{1,48} = 3.4$, $p = 0.073$). Complete drying of breeding waters before tadpole metamorphosis was also observed in drained plots only where 7% of all ditches dried out by June 2009, and five depressions (62%) of eight used for breeding dried out by June 2010. In 2009, complete drying of breeding sites was probably even more frequent than recorded (and likely took place also in natural plots) because of an extremely dry period from April to mid May. That may have remained partly unnoticed because of refilling during the rainfalls in late May and early June (Fig. 2).

4. Discussion

Our study demonstrated that, by creating a network of open ditches, forest drainage can increase the overall number of small water bodies, but their diversity and quality will be reduced. In particular, most likely because of a more rapid runoff, water-bodies in drained plots are more prone to drying out by early summer, and natural depressions (a water-body type dominant in natural plots and preferred by some amphibians) are nearly absent.

4.1. Amphibian breeding sites

The supply of water-bodies in drained vs. natural plots differed by three major features (diversity, water depth, and slopes of the bank), which all affect amphibian performance.

Regarding diversity, the majority of water bodies in natural plots were natural depressions and floods, while in drained plots ditches (created to drain the areas) were overwhelmingly dominant. Since amphibians preferred natural depressions for breeding (especially *Rana* species; see also Griffiths, 1997) draining obviously reduces the breeding site supply for them. A likely reason is that the hydroperiods of water-filled depressions are particularly suitable for amphibians. On the one hand, such water-bodies are typically temporary, depending on their depth as the water balance is controlled primarily by precipitation, evaporation and ground-water exchange (Brooks and Hayashi, 2002). That attracts predation-sensitive amphibians (such as the common frog; see

Laurila and Aho, 1997; Loman, 2002) because such water bodies lack fish and have fewer predatory invertebrates (Griffiths, 1997; Herzon and Helenius, 2008). On the other hand, natural depressions still have longer hydroperiods and slower drying rates than anthropogenic water bodies in forests (DiMauro and Hunter, 2002).

Both these aspects were illustrated in the drained plots in the typical spring of 2010. Differently from the pattern in 2009, the frequent appearance of water-filled depressions in spring 2010 equalised the initial occupancy of water bodies by amphibians with that observed in natural plots. However, most of those natural depressions used for breeding in drained plots dried out before tadpole metamorphosis, while such drying was not observed in natural plots. In addition to differences in runoff rates, a reason could be that depressions in natural study plots were significantly deeper. Therefore, we suggest that artificially drained areas may sometimes function as ecological traps – attractive, but poor-quality habitats – for amphibians. Previously, DiMauro and Hunter (2002) have demonstrated that artificial water bodies in industrial forests can also function as ecological traps for amphibians for similar reasons. Apparently, in human-modified environments formerly reliable cues of habitat selection may no longer correlate with survival and reproductive success and, as a result, such maladaptive behaviour can lead to population declines (Schlaepfer et al., 2002; Battin, 2004).

Ditches were the most numerous water-body types in our study plots, but only one third of them were used for breeding by amphibians. Their low quality for anurans has been demonstrated earlier by Wederkinch (1988), who observed that larvae of the agile frog (*Rana dalmatina*) did not reach metamorphosis in forest ditches in Denmark. Several effects may contribute to that; for instance, the increased acidity of water and the amount of suspended solids, which reduce water oxygen level during their decomposition (Paavilainen and Päivänen, 1995). Nevertheless, our study demonstrated that drainage ditches can provide breeding habitat particularly for newts in deeper ditches. Deeper ditches may be permanent or persist longer than natural depressions (Brooks and Hayashi, 2002), being thus favoured by newts that are more aquatic and have longer breeding seasons (Dolmen, 1983; Griffiths, 1997) than the common toad or *Rana* species. The avoidance of shallow water bodies by newts has been noticed also in other parts of their range (Schoorl and Zuiderwijk, 1981; Denoël and Ficetola, 2007). In addition, amphibians could use ditches for moving between different landscapes (Mazerolle, 2004) or for hibernation (Elmberg, 2008).

Water bodies in natural plots were larger, having remarkably shallower slopes and deeper water than water bodies in drained plots. Two latter characteristics were positively associated with amphibian species richness in our study. While deeper water bodies persist longer, shallow slopes enable shallow littoral zones of submerged vegetation to develop. The latter provide suitable egg laying, foraging and refuge sites for amphibians and their larvae (Porej and Hetherington, 2005). Water depth may be particularly important for amphibian breeding success in dry years, such as in 2009 in our study.

4.2. Management implications

We conclude that intensive large-scale forest drainage profoundly changes natural hydrology of the area, reducing the variety of water bodies and diminishing their quality (depth and persistence) for amphibian breeding. Because vast areas of wet forest have been already drained artificially in boreal and temperate zones, we highlight the importance of those wet-forest areas, which are still intact in terms of natural hydrology in these regions. Large-scale draining should be avoided in such areas (see also Sjöberg and Ericson, 1997) because of many ecosystem services

they provide (Kimmel and Mander, 2010), including various biodiversity considerations (Wiklander et al., 1992; Nilsson, 1997). In addition to amphibians, negative effects of intensive forest drainage (especially via habitat changes) have been demonstrated for many other taxa (Jutila et al., 1998; Vuori et al., 1998; Ludwig et al., 2008; Louhi et al., 2010).

In landscapes already drained, three approaches could be considered. First, it is important to understand the dynamics and nature values of both aquatic and terrestrial communities in small undrained forest patches. The crucial questions are the rates of drainage-induced change, and the effects of the patch size and forest type on such changes. This approach could ultimately help to distinguish critical sites for protection and restoration. Secondly, considering the requirements of amphibians, some existing ditches should be modified to include depression-like enlargements in heavily drained landscapes managed for timber. Such enlargements should be large enough to promote extended hydroperiods and have shallow margins that favour the formation of submerged vegetation, which is positively associated with amphibian species richness (Porej and Hetherington, 2005). Increasing the variety of water bodies in an area enables also to increase the number of alternative breeding sites for amphibians, which has a positive effect on their survival (Petranka et al., 2003; Rannap et al., 2009). Thirdly, blocking outlets of ditches should be considered for restoring natural hydrology in protected areas, especially in areas where drained wet forests form a part of coherent wetland complex.

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