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Temporary and small waterbodies in human-impacted forests: an assessment in Estonia

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Temporary freshwater bodies are important as wildlife habitats and in biomass cycling, but their quantity and characteristics in relation to forest management are poorly documented. We surveyed small waterbodies in Estonian forest landscapes, along randomly placed transects in forests and non-forested fens. The area of natural puddles and floods varied by nearly two orders of magnitude among habitat types. The main effect of drainage and clear cutting was the conversion of waterbody types: natural ones were partly replaced by ditches and wheel-rut puddles, respectively. Using the common brown frog and the moor frog as indicator species revealed that anthropogenic changes are not necessarily detrimental: the frogs preferred to breed in anthropogenic waterbodies in open areas (i.e., clear cuts). Mitigation of forestry effects on the biota of temporary waterbodies should combine restoration (allowing flooding in selected areas; restoring streams) and compensatory measures (excavating ponds; retaining wheel-rut puddles in key sites).

Introduction

Temporary freshwater bodies (TWBs) are an integral part of natural landscapes where they provide diverse and distinct habitats for aquatic and semi-aquatic organisms. In dry seasons, TWBs function as terrestrial ecosystems and, in wet seasons, as aquatic ecosystems that lack species requiring permanent waters. In forests, such waterbodies are heterotrophic systems dominated by protists and bacteria in terms of both species richness and abundance (Carrino-Kykeraff and Swanson 2008), but they can also host diverse and partly specific biota of other taxon groups (Colburn 2004, Deil 2005, Stoks and McPeek 2006). Additionally, TWBs are significant biomass transformers and temporary reciprocal subsistence partners for terrestrial ecosystems (Nakano and Murukami 2001, Progar and Moldenke 2002, Kraus and Vonesh 2012). The main factors that influence the biota of TWBs are hydroperiod, temperature, turbidity, flow velocity, bottom substrate, canopy closure, debris input, and the availability of oxygen and other dissolved substances (Williams 1987, Lamouroux *et al*. 2004, Williams 2005).

Due to their large shoreline-to-area ratio TWBs are closely connected to their surroundings, and their locations are mainly determined by landscape factors (topographic and edaphic conditions). Such waterbodies often emerge year after year in the same depressions where the soil has low permeability and they may be formed by a number of processes, ranging from geologi-

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cal events to temporary trails of large animals. TWBs are frequently aggregated (Brooks *et al.* 1998), isolated (Tiner 2003) or, in the case of floods of lakes and rivers, partly connected with permanent waterbodies (Amoros and Bornette 2002). In contrast to those factors determining the locations of TWBs, their quantity and persistence depend mostly on fluctuating climatic conditions — discrepancy between precipitation and evapotranspiration, winter snowpack — and the resulting soil ground- and floodwater levels (Winter *et al.* 2001, Brooks 2004, Colburn 2004, Brooks 2005). Because the hydrological settings of wetlands vary considerably, accurate prediction of water quantity based on universal simple functions is impossible (Winter *et al.* 2001). However, the quantity and habitat quality of TWBs can be estimated at a point in time or, broadly, for a longer period affected by a set of factors depending on the length of the period. For example, more than a half of water depth variation in vernal pools at a given moment is explained by precipitation and evapotranspiration during previous days (Brooks 2004). The remaining variation is related to pool characteristics, of which the volume in combination with shoreline-to-area ratio is the most significant (Millar 1971, Brooks and Hayashi 2002).

Despite their functional significance, TWBs have seldom been included in forest ecosystem research and monitoring, particularly at the landscape scale. Previous studies were focused on a few areas or waterbody types, such as vernal pools in North America (e.g. Brooks *et al.* 1998, Van Meter *et al.* 2008, Reif *et al.* 2009). Specifically, little attention has been paid to large-scale human impacts on TWBs in managed forest landscapes, although such landscapes are increasingly dominant in most forested regions of the world.

In this paper, we describe temporary and small permanent waterbodies in a north-European lowland region heavily influenced by centuries-long forest management — notably artificial drainage (ditching) and clear cutting based silviculture. We focus on the effects of ditching, which has been extensively used to increase timber yield and accessibility (Paavilainen and Päivänen 1995). Although previous studies explored the habitat value of waterbodies situated downstream of drainage objects (Jutila *et al.* 1998, Vuori *et al.* 1998), the aquatic habitats within forest drainage networks have remained almost unexplored (but *see* Suislepp *et al.* 2011). Ditching generally shortens the hydroperiod of natural lentic TWBs (Suislepp *et al.* 2011) and dredges and straightens natural streams. Along with the changing forest structure (Minkkinen *et al.* 1999, Remm *et al.* 2013), additional long-term changes are expected given shifts in temperature regimes and base substrate. Structure-mediated processes are also introduced by clear cutting, which abruptly promotes warmer, deeper, and less permanent waterbodies than under forest cover (Nilsson and Svensson 1995, Kolka *et al.* 2011). The overall negative effect of forest management on TWBs is not self-evident, however, since human activities can create new, small waterbodies. Wildlife can benefit from intentionally created ditches (e.g. Simon and Travis 2011) and peat-digging pools (Verdonschot *et al.* 2011), but also from such "side effects" as wheel-rut puddles (Armitage *et al.* 2012) or waterbodies dammed behind ditch mounds and road embankments (Burroni *et al.* 2011). The expected result in managed forests is a partial replacement of natural TWBs by anthropogenic waterbodies, but the extent of that process and its consequences on habitat quality in real landscapes are poorly known.

The aim of this study was to describe the landscape-scale quantity and quality of small and temporary waterbodies as habitats and to assess the effect of forest management on them. To this end, we studied the abundance and characteristics of different types of small and temporary waterbodies on randomly placed transects across Estonian forest and mire landscapes. This approach bridges the previous large-scale mapping (e.g. Van Meter *et al.* 2008) and small scale descriptive surveys (e.g. Brooks and Hayashi 2002). We assessed the extent of replacement of natural TWBs with artificial ones in drained areas, and we examined whether the effect of clear cutting could depend on soil moisture. We expect that the TWB-promoting effect of clear cutting (due to decreased transpiration and interception by canopy cover) is weaker on drier soils that lack soil water. We then exemplify the integrative effects of forest management on habitat quality of TWBs using the common brown frog (*Rana temporaria*) and the moor frog (*R. arvalis*), which are typical amphibian species in hemiboreal forests (Suislepp *et al*. 2011), as indicator species. Amphibians are characteristic inhabitants of TWBs (Bedford *et al*. 2001), contribute significantly to the biomass of forest fauna (Burton and Likens 1975, Wyman 1998), are food for predators (Blaustein and Wake 1995), and are themselves keystone predators of invertebrates (Davic and Welsh 2004, DuRant and Hopkins 2008). We hypothesized a mixed effect of forest management: that the egg-clusters and tadpoles of the frogs are more frequent in natural waterbodies situated in exposed conditions, such as undrained clear cuts.

Material and methods

Study area and sampling design

Estonia (total area 45 228 km^2) is a low-lying country in the northwestern part of the East European Plain. The mean air temperatures in January and July are –4 °C and +17 °C, respectively. Precipitation (on average 646 mm y^{-1}) exceeds evaporation (400 mm y^{-1}) and the mean duration of snow cover is on average 75–135 days per year. Forests cover 2.2 million ha, of which ca. 40% are 'wet forests' (peatlands and those water locked mineral soil sites that are considered drainage targets; Jürimäe 1966, Lõhmus 1984); drained forest lands encompass 410 000 ha (Adermann 2012). Due to drainage, the share of natural streams among small water courses (catchment size 2–30 km^2) has been reduced to 5% (Rosenvald *et al*. 2014).

In Estonia, forest ditching started in the early 19th century but the majority of artificial drainage systems were constructed between the 1950s and the 1980s. According to one estimate, almost all paludifying forests and 82% of existing peatland forests were drained (Ilomets 2005), although the effects of draining on their current functioning may vary. Drainage of naturally non-forested fens has been similarly extensive but no precise estimates exist in terms of forest land: while the initial aim was often to expand agricultural land (Ilomets 2005), those lands may have been abandoned and afforested later. One regional study has estimated that among the new forests, established after 1940, almost all pine forests and ca. 60% of wet mixed and deciduous forests have been created by mire drainage (Lõhmus and Lõhmus 2005). The remaining non-forested fens (including mixotrophic mires) cover ca. 83 000 ha (Paal and Leibak 2013).

Seventy-five percent of the Estonian forest land is currently managed for timber production, 15% balance timber production with environmental values, and 10% is strictly protected (The Estonian Environment Agency 2013a). The timber production is based on clear cutting (> 95% of the volume of regeneration fellings) and mostly natural regeneration. Because the wettest sites on deep peat have naturally sparse tree cover, such sites are used for timber production only after ditching. Typical cut blocks are small (< 5 ha), and since the late 1990s on average 6% of the growing stock has been left as solitary retention trees on clear cuts (Rosenvald *et al*. 2008).

We sampled waterbodies along randomly placed transects in Estonian forests and non-forested fens, stratified by landscape region. We did not sample open bogs because of our focus on forest management: bogs do not provide economically significant timber yields even after ditching (Paavilainen and Päivänen 1995). The Estonian landscape regions (25 in total) are differentiated based on morphogenetic types of relief, dominant soils, vegetation, movement of waters, and land use (Arold 2005). We preselected the 13 largest and/or most distinct landscape regions and established within each a cluster of transects (ca. 4 × 2 km in cardinal directions; 92 km in total; Fig. 1) centred on a random point. To reduce spatial autocorrelation, the central points of adjacent clusters were at least 15 km apart, and the starting points of the transects 0.5 km from the central point. We omitted the mining areas in northeastern Estonia with restricted public access.

Field methods

We visited most transects once in 2011 or 2012, either between late April and late May

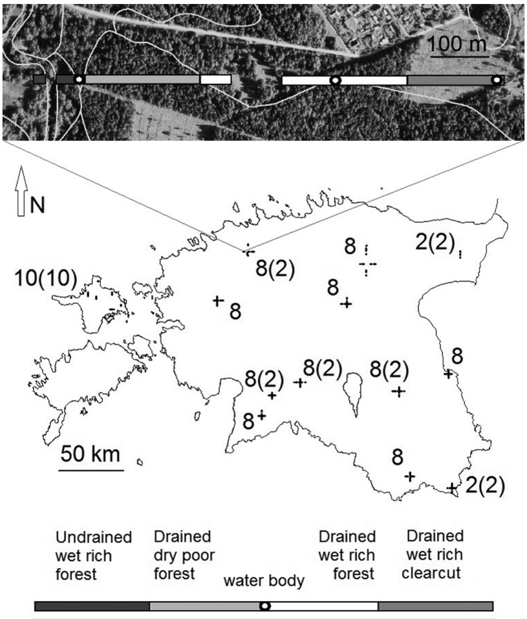

Fig. 1. Locations of the clusters of random study transects in Estonia. The numbers indicate the transect lengths in km (in parentheses are the lengths of transect visited the second time). The upper photo (ortophoto with the borders of soil map polygons) exemplifies how transect areas were divided into habitat types. Note that the transects were established only in forests and fens — a farmstead in the middle, as well as a river and a grassland on the left were omitted.

or between early September and early October, i.e., in wet seasons when the amount of TWBs is relatively large. For those transects, seasonal and spatial differences are not separable in the analyses. To assess the persistence of small waterbodies, a subset of transects (21 km in 7 clusters) was visited both in spring and in autumn of the same year (Fig. 1).

On each transect, we mapped all small waterbodies that had a surface area greater than ca. 25 × 25 cm but were not large enough to be presented on the 1:20 000 base map of Estonia. Of lotic waterbodies we additionally included those that were represented as line-objects on the base map. Thus we excluded permanent waterbodies larger than 200 m^2, and streams and canals wider than 8 m. The width of the field transect was 10 m or, for waterbodies smaller than 3 m^2, 4 m (later extrapolated to 10-m width). While walking along the transect, we delineated the areas significantly affected by drainage, i.e., with artificially and constantly lowered ground-water table, which has caused soil top horizon aeration and continuous peat decomposition. That estimation was based on the vegetation composition reflecting peat decomposition (Paal 1997, Lõhmus 1984, Laiho 1996), distance from ditches and their condition.

For each detected waterbody, we examined several aquatic and terrestrial features of potential importance to biota. (i) We distinguished the following types of waterbodies (*see* also Fig. 2): anthropogenic waterbodies included ditches (lotic; with linear streambed but not necessary flowing at the time of the survey), man-made ponds, and wheel-rut puddles. Natural streams were distinguished from ditches by their natural, meandering streambed. Natural lotic TWBs included depressions created by treefall (pits), other natural depression puddles, and flood areas. In the case of rugged and fragmented floods and tightly aggregated puddles, we compiled one summarising description. (ii) We evaluated the shape of a waterbody by measuring its surface area, depth and shoreline length per area, which has a major effect on hydroperiod. For large wet areas, we estimated the water cover of 3–15 2-metre segments along the transect line, and the shoreline length in 1-m^2 squares next to the line segments. (iii) We measured the following water characteristics: pH, electrical conductivity, temperature (using Lutron meters PH-212, CD-4302, and DO-5510 respectively), and flow velocity. (iv) We visually assessed water colour (brown or clear, revealing the concentration of humic substances), percentage cover of emergent (< 1 m) and submerged vegetation, percentage of the open water shaded either by vegetation or deep slopes, and the bottom substrate. The total number of measurements was 825, excluding the repeated measurements in those transects that were visited twice.

In each vernal waterbody, we checked whether breeding of the moor frog and the common frog occurred. In April and early May we searched for egg clusters. In late May, we used standard dip-netting to find tadpoles (Skei *et al*. 2006): in each waterbody, 10 dip-net sweeps were made covering important microhabitats of those species. In extensively flooded areas and lotic waters, inventories were made

Fig. 2. Examples of temporary waterbodies on the transects: (**a**) a natural flood in drained forest on wet rich soil in October 2012, (**b**) a water-filled treefall pit on undrained clear cut edge on moist rich soil in May 2011, (**c**) a wheel rut puddle in undrained forest on wet poor soil in October 2012, and (**d**) a man-made pond on undrained clear cut on wet rich soil in May 2012. The latter was used by brown frogs for breeding.

within 10 m of the transect. To describe terrestrial habitat of the frogs and to evaluate land-use effects on the characteristics of waterbodies, we assessed the proportions of forest, young forest, clear cuts, open mire, haul roads and strongly anthropogenic areas (fields and larger roads) within 100 m of the waterbody.

Data processing

The main analyses compared the abundance and characteristics of waterbodies among habitat types, with a specific focus on the habitat contrasts reflecting drainage and clear cutting effects. Prior to those analyses, we delineated habitat types on the map of each transect, by combining the national base map, ortophoto, soil map (Reintam *et al*. 2003) and the Forest Register (Fig. 1). We distinguished 18 habitat types as combinations of broad land cover (forest; clear cut; open fen), nutrient content of soil (rich or poor), soil moisture (dry-to-moist or wet), and (considering also our field notes) incidence of significant drainage. Soils classified as 'rich' had fertility comparable to or higher than Gleyic Luvisols, Rendzinas or transitional bog soils shallower than 1 m. By definition, 'open fen' occurred only on undrained wet soils; the dominant woody vegetation had to be < 1.3 m high and provide < 30% canopy cover. Clear cuts included young, regenerated stands with dominant trees < 4 m in height and up to 6 cm in diameter at breast height.

The main response variables analysed for habitat type variation were total open water area (m^2 ha^{-1}), and area and average depth of natural lentic TWBs. For natural lotic waterbodies, we present only summary statistics because we encountered very few natural streams. Because our data were not normally distributed and the sample sizes were rather small, we used Wilcoxon's matched pairs test for a few strictly planned comparisons between pooled habitat types (distinguished only by soil moisture and management factor of interest). The unit of those analyses was a habitat-type contrast within a transect cluster, i.e. all patches of the same habitat type within a transect cluster were pooled. We addressed spatial variation by including only those transect clusters where both habitat types of interest had been sampled (≥ 0.4 ha of dry-to-moist areas or ≥ 0.1 ha of wet areas).

To describe the effects of drainage on individual waterbodies, we compared ditches and natural lentic TWBs as well as natural lentic TWBs on drained and undrained areas. We carried out the comparison within each transect cluster, where at least five waterbodies had been sampled from both types of interest, screening the data by the means of Feature Selection and Variable Screening (FSL) procedure in Statistica 8 software. To reduce variation, we carried out those analyses only for wet, nutrient-rich forests, which are rich in waterbodies and a major drainage target (Paavilainen and Päivänen 1995).

The effect of forest management on the breeding of brown frogs was assessed in two steps. The sampling unit was an individual waterbody visited in spring. First, we screened for variation in the incidence of breeding in relation to potential habitat factors, using univariate logistic regression. We then combined each pre-selected factor with the detected management effects using bivariate logistic regression (likelihood-ratio type 1 tests or type 3 test in case of two management effects) to explore whether these factors explain the management effects. We did not use multifactor models, because of rather small number of breeding sites detected (*see* Results). If the breeding sites were located less than 0.5 km from each other, we included only the one with more egg-clusters/tadpoles to secure spatial independence of observations. In case of waterbodies with no egg-clusters/tadpoles, we excluded those that were shallower than the shallowest waterbody used for breeding.

Results

Distribution of waterbodies on the landscape

We sampled a total of 50 834 m^2 small and temporary waterbodies, including natural snowmelt- and rainwater puddles in topographic depressions, on game trails and in treefall pits; waterbodies dammed behind ditch mounds and road embankments; the floods of lakes and rivers (including those caused by beavers); ditches, man-made excavations (e.g. peat-digging ponds) and wheel-rut puddles (Fig. 2). Their distribution on the landscape varied widely among habitat types. Soil characteristics were apparently the main factor since waterbodies were distinctly scarcer (< 280 m^2 open water per ha) on dry-to-moist and nutrient-poor wet soils than on nutrient-rich wet soils (> 320 m^2 open water per ha; Table 1). In undrained areas, the median area of natural lentic TWBs on wet soils (291 m^2 ha^{-1}; all habitat types pooled) exceeded that on dry-to-moist soils (16 m^2 ha^{-1}) roughly 18 times (Wilcoxon's matched pairs test: $Z = 3.1$, $n = 12$ transect clusters, $p = 0.002$). The maximum contrast between habitat types on undrained dry-to-moist *vs*. wet areas reached almost two orders of magnitude (forests on nutrient-rich dry-to-moist soils *vs*. nutrient-rich fens; Table 1). However, we could not detect significant differences in the overall median water depth either between wet and dry-to-moist areas (Wilcoxon's test: $Z = 0.8$, $n = 8$, $p = 0.40$) or among habitat types in general (Appendix 1; *see* also the next subchapter).

Natural puddles and flooded areas formed the majority of waterbodies almost in all undrained habitat types, except on wet clear cuts where wheel-rut puddles dominated. In five of the eight drained habitat types, ditches were the dominant waterbody type by area. Natural streams and treefall pit puddles were the rarest waterbody types forming only 2.5% and 0.4% of the total open water area, respectively (that share was even smaller on wet soils; Table 1). The mean water depth differed remarkably among the waterbody types: man-made ponds, streams and ditches were at least two times deeper than natural lotic TWBs and wheel-rut puddles (Table 2).

Waterbodies in relation to drainage and clear cutting

There were no significant differences either between drained and undrained areas or between forests and clear cuts in terms of total cover of open water or the mean water depth of natural lentic TWBs (Wilcoxon matched pairs tests: $p > 0.1$). Two planned comparisons for the total

Table 1. Mean area of different types of waterbodies by habitat type on random transects in Estonia. Standard errors are presented for those estimates based on at least three transect clusters where such waterbodies were found.

Habitat type (area (ha); sample size[1])	Area of waterbodies (m^2 ha^{-1})						
	Natural puddles and floods	Treefall pit puddles	Natural streams	Ditches	Wheel rut puddles	Man-made ponds	All water bodies
Forest on dry-to-moist soil (25.2; 12)	80 ± 40	5 ± 4	9 ± 6	18 ± 6	6 ± 3	7 ± 5	125 ± 44
Undrained, nutrient-rich (13.6; 10)	24 ± 11	0	9	3 ± 2	3	9	48 ± 21
Drained, nutrient-rich (2; 4)	29	3	0	32 ± 13	12	6	81 ± 45
Undrained, nutrient-poor (7.9; 8)	177 ± 105	3 ± 1	10	9 ± 5	6 ± 6	0	205 ± 104
Drained, nutrient-poor (1.7; 3)	146	16	0	86 ± 33	14	11	273 ± 193
Clear cut on dry-to-moist soil (10; 9)	94 ± 68	1	0	22 ± 14	15 ± 8	0	131 ± 67
Undrained, nutrient-rich (4.1; 6)	64 ± 50	1	0	3	21 ± 14	0	89 ± 59
Drained, nutrient-rich (0.4; 1)	12	0	0	61	0	0	72
Undrained, nutrient-poor (2; 4)	105 ± 72	0	0	1	5	0	110 ± 74
Drained, nutrient-poor (0.5; 1)	0	0	0	200	0	0	200
Forest on wet soil (44.4; 13)	800 ± 396	3 ± 1	21 ± 10	82 ± 18	17 ± 6	4 ± 3	927 ± 410
Undrained, nutrient-rich (18.3; 13)	1064 ± 498	5 ± 3	37 ± 18	32 ± 7	26 ± 12	2 ± 1	1166 ± 503
Drained, nutrient-rich (19.9; 12)	527 ± 315	3 ± 1	0	176 ± 42	14 ± 5	4	725 ± 348
Undrained, nutrient-poor (3; 6)	148 ± 98	4	0	4	7	0	163 ± 101
Drained, nutrient-poor (3.2; 7)	28	2	0	57 ± 16	1	10	98 ± 31
Clear cut on wet soil (6.9; 11)	212 ± 138	1	0	90 ± 24	226 ± 173	9 ± 5	537 ± 321
Undrained, nutrient-rich (2.2; 10)	125 ± 68	2	0	33 ± 23	151 ± 57	12	323 ± 88
Drained, nutrient-rich (2.9; 9)	333 ± 322	0	0	180 ± 58	424 ± 404	0	944 ± 757
Undrained, nutrient-poor (0.9; 4)	33	0	0	0	49 ± 35	0	81 ± 66
Drained, nutrient-poor (0.9; 3)	133	0	0	34 ± 26	7	0	174 ± 122
Open fen (5.5; 2)	1521	0	0	3	0	0	1524
Nutrient-rich (2.4; 2)	2148	0	0	7	0	0	2155
Nutrient-poor (3.1; 1)	278	0	0	0	0	0	278
Total (92;13)	369 ± 189	2 ± 1	12 ± 4	49 ± 10	27 ± 12	5 ± 3	464 ± 204

[1] Number of transect clusters. Note that, to increase accuracy, the clusters with very small patches of a given biotope were pooled until 0.1 ha (on wet soils) or 0.4 ha (on dry soils) total area was reached.

Table 2. Area-weighted average values of waterbody features by types of waterbodies in random transects in Estonia. Standard errors are presented for those estimates based on at least three transect clusters where such waterbodies were found. *See* Table 1 for sample sizes.

Features of waterbodies	Natural puddles and floods	Treefall pit puddles	Natural streams	Ditches	Wheel rut puddles	Man-made ponds	All water bodies
Depth (cm)	11 ± 2	13 ± 3	34 ± 15	27 ± 7	11 ± 2	35 ± 13	18 ± 3
Electrical conductivity (μS dm^{-1})	28 ± 4	19 ± 4	34 ± 9	42 ± 6	21 ± 3	31 ± 13	31 ± 4
pH	6.4 ± 0.2	5.1 ± 0.4	6.9 ± 0.4	6.8 ± 0.2	6.1 ± 0.3	5.7 ± 0.5	6.5 ± 0.2
Bottom composition (%)							
peat	6 ± 3	22 ± 10	11	25 ± 6	17 ± 8	5 ± 2	11 ± 2
leaves	52 ± 7	36 ± 8	10 ± 7	32 ± 5	25 ± 7	38 ± 13	40 ± 4
thorns	0.9 ± 0.5	1.5 ± 0.3	0.2	1.5 ± 1	0.7 ± 0.2	0.5	1.5 ± 0.9
Sphagnum mosses	4 ± 2	17 ± 10	0	2 ± 1	2 ± 1	20	4 ± 2
grass	20 ± 5	10 ± 4	0	6 ± 2	23 ± 6	21 ± 12	15 ± 4
woody debris	6 ± 2	2 ± 1	8 ± 2	6 ± 1	6 ± 3	7 ± 3	6 ± 1
mineral matter	5 ± 4	12 ± 6	71 ± 18	18 ± 3	19 ± 9	5	16 ± 4
Water color (% of brown)	48 ± 10	70 ± 12	25	35 ± 8	61 ± 10	61 ± 16	41 ± 8
Shoreline length per area (m × m^{-2})	2.4 ± 0.7	3.5 ± 0.4	1.3 ± 0.3	2.1 ± 0.3	4 ± 0.7	0.9 ± 0.1	1.8 ± 0.3
Temperature discrepancy (°C)[1]	0.1 ± 0.2	–1.4	–0.6	0.4 ± 0.5	1.2 ± 0.3	1 ± 0.7	0 ± 0.2
Shading (%)	59 ± 6	69 ± 7	68 ± 6	61 ± 7	48 ± 8	41 ± 9	60 ± 5
Vegetation (< 1 m), cover (%)	8 ± 3	4 ± 3	3 ± 2	7 ± 2	9 ± 3	7 ± 4	7 ± 2
Submerged vegetation, cover (%)	1.2 ± 0.6	0.2	1.9	4.4 ± 2	0.9 ± 0.5	0.3	2.3 ± 0.7
Surroundings within 100 m vicinity (%)							
forest	63 ± 7	87 ± 6	71 ± 11	65 ± 6	58 ± 8	64 ± 9	71 ± 4
young forest	1 ± 1	10 ± 6	1	2 ± 1	4 ± 1	0	2 ± 1
clear cuts	19 ± 8	2 ± 1	0	6 ± 2	32 ± 8	13 ± 8	10 ± 3
open fen	2.3 ± 1.6	0.3	0.2	2 ± 1	0	0.3	2.2 ± 1.5
haul roads	0.6 ± 0.4	0.1	0.5	4.2 ± 1.4	3.8 ± 2	0	1.6 ± 0.5
anthropogenic structures	4.3 ± 2.3	0.1	0	4 ± 1.4	0.1	6.8 ± 4.9	3.2 ± 1.3
Flow velocity (cm s^{-1})	0	0	7 ± 3	2 ± 1	0	0	2 ± 1

[1] The difference between the temperature of individual waterbody and the mean temperature of waters on the transect cluster at the same daytime. The latter depicted degree two polynomial relationship between time since sunrise and temperature discrepancy of the cluster average across daytimes.

cover of natural lentic TWBs on dry-to-moist soils were also not significant.

However, there were obvious changes in the composition of different types of waterbodies on wet soils where ditches became dominant, partly replacing natural TWBs after drainage (Table 1). The total cover of natural lentic TWBs was smaller on drained than on undrained wet sites (median values 32 and 146 m^2 ha^{-1}, respectively; Wilcoxon's test: $Z = 1.8$, $n = 12$, $p = 0.071$). The compositional change can be more pronounced in dry seasons, as ditches were in general more permanent — in six out of seven double-checked transects the area of ditches formed a larger proportion of total water cover in drier season, while natural lentic TWBs were relatively abundant in wetter seasons. On wet clear cuts the area of natural lentic TWBs was smaller than in forests (Wilcoxon's test: $Z = 2.0$, $n = 11$ transect clusters, $p = 0.040$). This effect was due to abundant wheel-rut puddles on wettest clear cuts, except on drained nutrient-poor soils. The abundance of wheel-rut puddles on wet clear cuts exceeded that in similar types of forests consistently ca. six times (5.8–6.8 times in the four types of wet clear cuts; Table 1).

While the main characteristics of natural lentic TWBs were rather similar in undrained and drained wet rich forests (no characteristic was selected as informative in more than three clusters out of seven in FSL at $p < 0.05$), ditches (that dominated in drained sites) were generally deeper and had more peaty sediment than a natural lentic TWB (informative predictors in five out of seven clusters, FSL). However, in the course of time, ditches deteriorate and become shallower as revealed by the observation that in areas currently classified as undrained, (the few old) ditches were on average more than two times shallower than in analogous drained habitats (Appendix 1). Clear cutting had some consistent effects on the features of waterbodies across habitat types (Appendix 2): waterbodies on clear cuts had lower electrical conductivity, more frequently brown water, and more woody debris on their bottom than waterbodies in forests. In addition, waterbodies on wet clear cuts had higher water temperatures as well as lower leaf and exposed peat cover on the bottom than those in forests.

Breeding sites of brown frogs

We recorded breeding of brown frogs in 27 waterbodies out of more than 700 studied. The shallowest breeding water was 8-cm deep. From the 27 waterbodies, we included 21 in the analyses as independent observations. In the univariate likelihood ratio test, two management-related factors were significantly related to the incidence of breeding: the frogs preferred anthropogenic waterbodies (LL = –77.4, $\chi^2 = 6.6$, $n = 371$, $p = 0.01$; Table 3) and clear cuts in the surroundings (LL = –78.1, $\chi^2 = 5.1$, $p = 0.024$); but were rather evenly distributed among drained and undrained areas (LL = –80.6, $\chi^2 = 0.1$, $p = 0.746$). Depth, shoreline length per area, flow existence, proportion of water in shade, submerged vegetation coverage and soil nutrient-richness had suggestive univariate effects ($p < 0.05$). Bivariate logistic models showed that the preference for clear cuts was well explained by less shading and also by a greater proportion of anthropogenic waterbodies (Appendix 3). The significant preference for anthropogenic waterbodies, however, remained independent of other habitat factors.

Discussion

Natural and anthropogenic waterbodies on the landscape

In the studied forestry-impacted landscapes, we found a diverse array of small waterbodies, some of which (such as larger streams and ditches and man-made ponds) were presumably (semi)

Table 3. The frequency of breeding of frogs (*Rana arvalis, R. temporaria*) by waterbody type. Only the waterbodies at least 8 cm deep (minimum of breeding sites) were included.

Type of waterbody	Breeding (%)	*n*
Natural puddles and floodings	3	151
Treefall pit puddles	0	25
Natural streams	0	11
Ditches	8	117
Wheel rut puddles	7	56
Man-made ponds	27	11
Total	6	371

permanent. The total density of lentic small waterbodies on the forest and fen transects (403 m^2 ha^{-1}) was almost equal to the cover of permanent ponds and lakes on the Estonian land area (489 m^2 ha^{-1}; calculated using the data of the base map, including Lake Peipsi), and it varied mostly according to soil type. While it was expectable that small waterbodies are more abundant on wet soils, their area remained relatively small at nutrient poor sites, where *Sphagnum* mosses dominate and reduce the open water coverage. To some extent, this may be affected by our definition of 'wet' soils based on drainage planning (i.e., tree growth conditions), which includes a wider moisture range on nutrient-poor sites (Jürimäe 1966, Lõhmus 1984).

Most of the area of small lentic waterbodies was formed by natural puddles and floods (Table 1), confirming that TWBs may be seasonally extensive and form a significant element of landscape complexity (Calhoun 1999). We recorded most extensive floods near undrained wetland complexes, where water flows still locally override the effect of ditching. Thus, in managed forest landscapes it is important to protect the remaining natural wetlands and to allow natural flooding in other selected sites.

The lack of small natural streams on our study transects can be partly explained by the flat topography of the studied landscapes, but it also reflects the long history of forest management. Somewhat larger water courses are known to be heavily modified by dredging, which has caused an impoverishment of the fish fauna (Rosenvald *et al*. 2014). Our study indicates that such impoverishment pervasively includes very small water courses (not subjected to dredging) and timber harvesting effects (natural streams were absent on clear cuts). Compared with ditches, natural streams had over two times higher water velocity (*see* also Rosenvald *et al*. 2014) as well as harder bottom substrate with more woody debris (Table 2). It is thus very likely that many important functions of natural headwater streams (e.g., Meyer *et al*. 2007) are impaired or lost in modern landscapes, and their restoration — together with flooding regimes — is a priority for landscape planning (Lake *et al*. 2007).

Our results demonstrate that treefall disturbance is only a minor process in creating TWBs in modern forest landscapes. Its role was probably larger in natural conditions: for example, in natural *Oxalis*-type spruce–birch forest up to 25% of the surface area can be covered by pit-and-mound topography generated by uprooted trees (Ulanova 2000). Avoiding treefall is an objective in forests managed for timber and, even if it is not successful, the pits formed are smaller (depending on tree size) and shallower when tree species having shallow rooting (such as spruce) are preferred (e.g., Lõhmus *et al*. 2010). This obviously affects water accumulation, particularly in combination with reduced flooding. However, in managed forests on dry soils treefall pits can still form a large proportion of lentic TWBs, presumably because the depressions created are deep enough to reach ground water level — note that these areas are often dominated by deep-rooting pines, and extensive flooded areas rarely occur there.

The effects of forest management

The main effect of ditching and clear cutting was a substitution of natural small waterbodies with anthropogenic waterbodies. The effects on the total quantity of waterbodies were not significant, at least in wet seasons and years with large amount of snow (as were the study years; EMHI 2012, The Estonian Environment Agency 2013b), but they deserve further studies over longer time frames and at sites with known management history. For example, the apparently large natural variability in waterbody abundance reduces test power, and our coarse categorization of the moisture gradient may hide some differences between "drained" and "undrained" sites. It is likely, however, that management actually induces contrasting effects. Thus, the area of open water may even increase after drainage, when water from wet soil discharges to ditches that are deeper than natural depressions (cf. Suislepp *et al*. 2011). Clear cutting could further enhance that process in wet forests where the water table typically raises due to decreased interception and transpiration (Dube and Plamondon 1995). However, neither of those net effects was supported by our study, possibly because of a severe simultaneous loss of floods and natural streams. Other processes reducing the theoretical management-caused increase in open water remain speculative but they include (i) fast overgrowing of the TWBs by *Sphagnum* mosses in clear cuts, and (ii) increased evaporation after clear cutting on dark-coloured organic soils (Lockaby *et al*. 1994).

The two main types of artificial waterbodies created by forest management were ditches and wheel-rut puddles. Ditches clearly differed from natural lentic TWBs: the peat was frequently exposed in ditches, which were also deeper and in general more persistent. All these are important features for biota (Colburn 2004). Moreover, ditches are connected to river networks and thus more accessible for fish (Hohausova *et al*. 2010, Rosenvald *et al*. 2014), which may reduce their suitability for predation-prone species. The water characteristics of ditches vary depending on whether they have been dug to the mineral layer under the peat, and the composition of that layer (Ramberg 1981, Saarinen *et al*. 2013).

Our results confirmed that heavy forestry vehicles create depressions especially in peaty soils (Nugent *et al*. 2003) and, in the Estonian clear cutting-based seminatural forestry, they are mostly formed in clear cuts. We can roughly estimate that the subsequent disappearance of wheel-rut puddles takes place at a rate of ca. 4% annually. This estimate is based on the detected six-fold difference in their abundance in clear cuts *vs*. forests, the average age of clear cuts and forests in Estonia (Adermann 2012), and assuming similar formation processes during the machine -based management era since the 1950s. Wheel-rut puddles can contribute to macroinvertebrate diversity (Armitage *et al*. 2012) and even serve as refuge habitats for threatened disturbance-dependent large branchiopods (Gołdyn *et al*. 2012). More generally, such puddles may be used by species that naturally inhabit treefall pit puddles (Semlitsch *et al*. 2009) because catastrophic windthrows can create similar open areas with puddles in pristine forests (Ulanova 2000). Indeed, several characteristics of treefall and wheel-rut puddles were similar in our study: both had frequently peat on the bottom, and they were small and tightly connected to the land as evidenced by their shoreline length per area (Table 2). Furthermore, when wheel-rut puddles become vegetated in time, they start to resemble the puddles of open mires in respect to bottom substrate and depth (but water characteristics stay different because of the soil differences). To summarize, wheel-rut puddles appeared to be considerably more 'natural' substitute waterbodies for the lentic TWBs lost by forest management than were ditches for natural streams (*see* also Rosenvald *et al*. 2014) or to lentic TWBs.

Breeding sites of brown frogs in modern forest landscapes

Our analyses confirmed that at least some frog species inhabiting small waterbodies can readily use the anthropogenic waterbodies in managed forest landscapes. In fact, brown frogs preferred to breed in anthropogenic waterbodies, especially in isolated pond-like excavations (Fig. 2d), which were deeper than natural TWBs. Such anthropogenic depressions may also hold water better during critical periods, particularly when their bottom consists of water-resistant deposits (e.g., excavated ditches and ponds) or is compressed (e.g., wheel-rut puddles; Ampoorter *et al*. 2012). However, Suislepp *et al*. (2011) found in Estonia that if natural depressions are available at drained sites, both the common brown frog and the moor frog prefer these to ditches (53% of depressions and 37% of ditches were used for breeding). Combining those findings, it appears that high-quality natural waterbodies are scarce and only form a small fraction of natural TWBs in modern Estonian forest and fen landscapes, while their average quality is already below that of anthropogenic sites.

Our results indicated that sun exposure was a major cause why the frogs preferred clear cuts. Similar results have been reported from West Virgina, where amphibians frequently use those man-made ponds on clear cuts that are deep enough to hold water until tadpoles complete their metamorphosis (Barry *et al*. 2008). Unfortunately, we could not follow the development of the frogs and thus it remained unknown, in which waterbodies the tadpoles reached metamorphosis. The general implication is still that, at least for the habitat quality of brown frogs, excavating of ponds and retaining deeper wheel-rut puddles in open areas (especially in sites that are kept open, such as under power lines) could successfully and on a larger scale complement local attempts to restore natural hydrology.

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Appendix 1. Area-weighted mean depth of different types of waterbodies by habitat type in random transects in Estonia. Standard errors are presented for those estimates based on at least three transect clusters where such waterbodies were found. *See* Table 1 for sample sizes.

Habitat type	Depth of waterbodies (cm)						
	Natural puddles and floods	Treefall pit puddles	Natural streams	Ditches	Wheel rut puddles	Man-made ponds	All water bodies
Forest on dry-to-moist soil	16 ± 5	10 ± 3	17 ± 6	15 ± 3	8 ± 2	74 ± 29	18 ± 4
Undrained, nutrient-rich	11 ± 4	7	13	7 ± 1	8	60	16 ± 6
Drained, nutrient-rich	8	6		12 ± 3	12	130	14 ± 5
Undrained, nutrient-poor	21 ± 7	11 ± 4	25	11 ± 4	7 ± 4		17 ± 5
Drained, nutrient-poor	8	7		15 ± 5	7	33	10 ± 2
Clear cut on dry-to- moist soil	15 ± 8	14		13 ± 6	8 ± 3		14 ± 5
Undrained, nutrient-rich	17 ± 12	14		7	10 ± 4		17 ± 8
Drained, nutrient-rich	4	3		11			10
Undrained, nutrient-poor	9 ± 2			4	4		9 ± 2
Drained, nutrient-poor				14			14
Forest on wet soil	11 ± 2	14 ± 3	34 ± 18	29 ± 7	10 ± 2	12 ± 4	16 ± 3
Undrained, nutrient-rich	12 ± 3	12 ± 3	16 ± 4	23 ± 7	11 ± 2	17 ± 9	13 ± 2
Drained, nutrient-rich	11 ± 2	13 ± 2		34 ± 9	10 ± 1	18	23 ± 5
Undrained, nutrient-poor	11 ± 1	10		6	14		10 ± 1
Drained, nutrient-poor	10	10		21 ± 7	7	11	17 ± 6
Clear cut on wet soil	10 ± 1	26		18 ± 5	9 ± 1	61 ± 23	14 ± 3
Undrained, nutrient-rich	8 ± 1	26		6 ± 1	9 ± 1	81	12 ± 4
Drained, nutrient-rich	9 ± 2			20 ± 6	10 ± 2	20	15 ± 3
Undrained, nutrient-poor	6				10 ± 1		10 ± 1
Drained, nutrient-poor	11			16 ± 7	8		16 ± 6
Open fen	9			40			9
Nutrient-rich	9			40			9
Nutrient-poor	12						12
Total	11 ± 2	13 ± 3	34 ± 15	27 ± 7	11 ± 2	35 ± 13	18 ± 3

Appendix 2. Area-weighted average values of waterbody features by habitat type (UD = undrained, D = drained, F = forest, C = clear cut, O = open fen, d-to-m = dry-to-moist) in random transects in Estonia. Standard errors are presented for those estimates based on at least three transect clusters where such habitat types were found. *See* Table 1 for sample sizes.

Habitat type	Electrical conductivity (μS dm^{-1})	pH	Bottom composition (%)							Water color (% of brown)	Shoreline length per area (m × m^{-2})	Temperature discrepancy (°C)[1]	Shading (%)	Vegetation (< 1 m) coverage (%)	Submerged vegetation coverage (%)
			peat	leaves	thorns	*Sphagnum* mosses	grass	woody debris	mineral matter						
UD d-to-m rich F	26 ± 4	6.3 ± 0.6	1.5	47 ± 13	0.8 ± 0.5	0	23 ± 14	6 ± 1	16 ± 8	26 ± 17	1.9 ± 0.6	–0.78	56 ± 9	4 ± 2	0.8 ± 0.7
D d-to-m rich F	48 ± 15	6.9 ± 0.2	1.6	54 ± 15	0.1	0	2	12 ± 6	30 ± 13	35 ± 22	4.7 ± 1.6	1.16 ± 0.7	70 ± 11	5 ± 3	0
UD d-to-m poor F	22 ± 4	6.3 ± 0.8	6.5 ± 6	46 ± 11	0.6 ± 0.5	15 ± 11	4 ± 3	6 ± 2	19 ± 12	40 ± 14	2.3 ± 0.9	0.38 ± 0.7	52 ± 11	10 ± 3	1.3
D d-to-m poor F	31 ± 12	6.1 ± 0.7	0.4	54 ± 14	2.3	4	4	4 ± 2	27 ± 21	57 ± 22	2.8 ± 0.9	–0.09	76 ± 6	4 ± 2	0
UD d-to-m rich C	26 ± 8	5.9 ± 0.4	2.2	30 ± 11	0	1	50 ± 17	1 ± 0	13 ± 6	37 ± 17	8.4 ± 5.8	2.37 ± 1.5	40 ± 14	15 ± 9	4.7
D d-to-m rich C	26 ± 0	6.6	12.3	75	0.2	0	0	4	9	73	2.9	0.84	92	8	0
UD d-to-m poor C	13 ± 1	4.7	4.4 ± 0	37	0.5 ± 0	37 ± 26	18	3	0 ± 0	84 ± 15	2.8 ± 1	–0.45	53 ± 22	4	0
D d-to-m poor C	14 ± 0	6.3	1.6	60	2.3	0	1	13	19	19	2.7	–0.99	72	0	0
UD wet rich F	35 ± 9	6.6 ± 0.2	11 ± 6	42 ± 6	0.7 ± 0.2	3 ± 2	14 ± 5	8 ± 3	17 ± 7	42 ± 8	1.9 ± 0.4	–0.3 ± 0.3	61 ± 6	8 ± 3	3.8 ± 2.7
D wet rich F	39 ± 6	6.6 ± 0.2	23 ± 6	45 ± 6	1.8 ± 1.3	1 ± 1	9 ± 2	6 ± 1	13 ± 4	35 ± 11	1.8 ± 0.3	0.2 ± 0.3	62 ± 7	5 ± 1	3 ± 1
UD wet poor F	18 ± 5	4.8 ± 0.5	7.8 ± 5	51 ± 13	2.1 ± 1	19 ± 10	14 ± 7	4 ± 2	0	89 ± 9	5 ± 1.9	–0.59	75 ± 9	5 ± 2	3.7 ± 2.4
D wet poor F	22 ± 7	5 ± 0.6	14.5 ± 6	46 ± 12	1 ± 0.5	26 ± 15	8 ± 3	4 ± 1	0	70 ± 17	2.4 ± 0.6	0.99 ± 0.6	62 ± 11	11 ± 5	4.9
UD wet rich C	29 ± 5	6.2 ± 0.4	2.5 ± 1	20 ± 7	0.2	4 ± 4	35 ± 10	5 ± 3	16 ± 7	51 ± 13	3.1 ± 0.7	1.3 ± 0.7	48 ± 8	14 ± 5	0.6 ± 0.4
D wet rich C	31 ± 8	6.4 ± 0.3	18.4 ± 9	16 ± 4	0.4 ± 0.2	1	24 ± 9	7 ± 3	33 ± 14	46 ± 14	3.1 ± 0.7	0.58 ± 0.9	51 ± 12	9 ± 3	7.4 ± 4.8
UD wet poor C	17 ± 4	5.1 ± 0.6	0.6	38 ± 25	0	28	32 ± 24	0	0	90 ± 8	6 ± 2.7	4.57 ± 3.1	49 ± 19	6	2.3
D wet poor C	16 ± 3	4.6 ± 0.6	11.3	13 ± 4	0.9 ± 0.6	46 ± 21	2 ± 1	1	24	93 ± 7	1.9 ± 0.2	1.32 ± 0.6	53 ± 20	3	0.1
UD wet rich O	16 ± 0	5.3	0.7	2	0	22	74	1	0	55	1	1.23	50	3	3.7
UD wet poor O	9 ± 0	3.8	5.1	3	0.1	38	53	0	0	84	3.1	0.08	10	7	2.2

[1] *See* Table 2.

Appendix 3. Likelihood ratio tests of the logistic regression models exploring the mechanism of forest management impact on the breeding site preferences of brown frogs. In the first two panels, the Type I approach has been used to test the *additional* effects of clear cut vicinity and the origin of the waterbody (anthropogenic *vs*. natural), respectively, to each environmental factor, which had a univariate effect on the incidence of breeding frogs. In the last panel, the *independent* effects of those two forest management variables have been tested via Type III approach.

Habitat factors in bivariate models	LL	χ^2	p	Group means	
				Non-breeding ($n = 350$)	Breeding ($n = 21$)
Depth	–77.9	5.6	0.018	17.87 cm	30.52 cm
100 m vicinity: clear cuts	–74.7	6.5	0.011		
Shoreline length per area	–74.4	12.6	< 0.001	3.73 m $\times$ m^{-2}	1.41 m $\times$ m^{-2}
100 m vicinity: clear cuts	–71.7	5.2	0.022		
Flowing *vs*. standing water	–77.7	6.0	0.01	14% with flow	0% with flow
100 m vicinity: clear cuts	–75.7	3.9	0.048		
Shading	–72.7	15.6	< 0.001	52%	24%
100 m vicinity: clear cuts	–71.7	1.9	0.167		
Submerged vegetation	–78.7	3.9	0.047	2%	8%
100 m vicinity: clear cuts	–76.2	5.1	0.024		
Nutrient rich *vs*. poor soil	–74.7	12.1	< 0.001	74% on rich soil	100% on rich soil
100 m vicinity: clear cuts	–72.7	3.9	0.049		
Depth	–77.9	5.6	0.018		
Anthropogenic *vs*. natural	–75.4	5.1	0.024		
Shoreline length per area	–74.4	12.6	< 0.001		
Anthropogenic *vs*. natural	–70.0	8.8	0.003		
Flowing *vs*. standing water	–77.7	6.0	0.014		
Anthropogenic *vs*. natural	–73.3	8.8	0.003		
Shading	–72.7	15.6	< 0.001		
Anthropogenic *vs*. natural	–68.6	8.1	0.005		
Submerged vegetation	–78.7	3.9	0.047		
Anthropogenic *vs*. natural	–75.7	6.1	0.013		
Nutrient rich *vs*. poor soil	–74.7	12.1	< 0.001		
Anthropogenic *vs*. natural	–71.9	5.5	0.019		
100 m vicinity: clear cuts	–77.4	3.7	0.056	12%	27%
Anthropogenic *vs*. natural	–78.1	5.1	0.023	48% anth.	73% anth.