

Amphibian decline in a Central European forest and the importance of woody debris for population persistence

Maciej Pabijan^{a,*}, Sara Bąk-Kopaniarz^a, Maciej Bonk^b, Stanisław Bury^{a,c}, Wioleta Oleś^{c,d}, Weronika Antoń^{c,d}, Izabela Dyczko^{a,c}, Bartłomiej Zając^{a,d}

^a Department of Comparative Anatomy, Institute of Zoology and Biomedical Research, Faculty of Biology, Jagiellonian University, ul. Gronostajowa 9, 30-387 Kraków, Poland

^b Institute of Nature Conservation, Polish Academy of Sciences, al. A. Mickiewicza 33, 31-120 Kraków, Poland

^c NATRIX Herpetological Association, Opolska 41/1 52-010 Wrocław, Poland

^d Institute of Environmental Sciences, Faculty of Biology, Jagiellonian University, ul. Gronostajowa 7, 30-387 Kraków, Poland

ARTICLE INFO

Keywords:

Species abundance
Body condition index
Forest management
Deadwood
Conservation
Removal sampling

ABSTRACT

Achieving an understanding of species' temporal and spatial abundance patterns is a prerequisite for proper conservation and management decisions. Little is known of the ecological indicators of census size or biomass of terrestrial amphibian communities and historical estimates of population size are rare. Here we took advantage of abundance and biomass data collected in 1967/1968 for a leaf-litter amphibian community in Niepołomice Forest (NF) in south-central Poland. Using the same technique (removal sampling), we censused the amphibian community of this forest 50 years later (2016/2017), spatially matching a subset of current plots with the historical sampling sites. Averaged over all plots, we revealed at least a fourfold decline in amphibian abundance from 2817 ± 776 individuals/ha in 1967 to 674 ± 508 individuals/ha currently, paralleled by a decline in biomass from roughly 15.5 ± 1.7 to 3.8 ± 3.1 kg/ha. The decline was more striking (over 15-fold) for current plots placed in the same forest division as the historical plots (mean counts of 157 ± 103 individuals/ha corresponding in biomass to 1.0 ± 0.5 kg/ha). We also recorded a change in species composition between surveys, and propose that conversion of aquatic habitat and forest succession have decreased amphibian diversity and abundance in NF. Further, we estimated densities of anuran amphibians in forest plots differing in management regime and local habitat characteristics for contemporary plots (all historical plots were placed in managed forest). We found that unmanaged, old growth forest plots with coarse woody debris on the forest floor held on average twice as many anurans compared to plots in managed stands. Average body condition of the most common species, *Rana temporaria*, measured as a scaled mass index, was enhanced in plots situated in old growth forest. Our findings suggest that the preservation of old growth forests containing coarse woody debris may boost anuran abundance, biomass and body condition, and has the potential to buffer against long-term demographic decline. Moreover, the retention of deadwood could be a means of increasing the conservation potential of managed forests for terrestrial amphibian communities.

1. Introduction

With 40 % of assessed species threatened with demise (IUCN, 2018), amphibians are iconic of the sixth great mass extinction affecting our planet (Wake and Vredenburg, 2008). Among the many factors contributing to amphibian declines, habitat alteration is one of the most serious (Ficetola et al., 2015; Nowakowski et al., 2017). The biphasic life cycles of many species and general reliance on aquatic or moist habitats put them at odds with the needs of an expanding human population.

Deforestation and the drainage of wetlands has decimated amphibian populations in many areas of the world (Cushman, 2006). Synergistic interactions with other factors such as environmental pollutants, invasive species, pathogens and atmospheric change are probably commonplace (Blaustein et al., 2011; Pabijan et al., 2020). Declines have been noted in relatively secure or even pristine habitat (McMenamin et al., 2008), emphasizing that conservation policies need to factor in threats other than habitat destruction to be effective. Moreover, natural fluctuations in amphibian abundance make it challenging to

* Corresponding author.

E-mail address: maciej.pabijan@uj.edu.pl (M. Pabijan).

<https://doi.org/10.1016/j.ecolind.2023.110036>

Received 28 July 2022; Received in revised form 22 January 2023; Accepted 13 February 2023

Available online 21 February 2023

1470-160X/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

determine whether an observed decline was human-induced or the result of a natural dip in population size (Pechmann et al., 1991). Halting or mitigating amphibian loss thus requires careful consideration of the evidence for a decline and the anthropogenic and natural factors that determine population dynamics at the appropriate spatial scale (Grant et al., 2016). Key to determining whether a population is under decline are reliable abundance estimates that can be compared to population sizes in previous years as a frame of reference.

Forests harbour most of the Earth's terrestrial biodiversity (FAO and UNEP, 2020) and provide habitat for 80 % of the world's amphibian species (Vié et al., 2009). Forest management is clearly relevant for amphibian conservation. In general, clearcutting has a detrimental effect on amphibian numbers and diversity, however, its long term consequences are variable and depend upon the amount and complexity of microhabitat retained after timber extraction (DeMaynadier and Hunter 1995; Dupuis et al., 1995; Homyack and Haas, 2009). Intact old growth forest with a microhabitat-rich forest floor is particularly valuable for amphibians (Thompson and Donnelly, 2018). Decaying wood provisions forest-litter amphibians with cool and moist microhabitats for foraging, breeding and overwintering and is typically associated with high amphibian abundance (DeMaynadier and Hunter, 1995; Otto et al., 2013). However, in regions with a long history of forest management, as in many European countries, old growth forests with abundant deadwood are scarce (Forest Europe, 2020). Moreover, intense or misguided forest management continuously threatens even the best preserved European forest ecosystems such as Białowieża Primeval Forest (Selva et al., 2020).

Forest management strategies also affect amphibian population vital rates such as survival and age structure, as well as body condition (Todd and Rothermel, 2006; Homyack and Haas, 2009; Homyack et al., 2011; Veysey Powell and Babbitt, 2015). These parameters provide direct measures of the effect of habitat alteration on amphibians and also offer insight into amphibian population dynamics in forests subjected to different degrees of anthropogenic impact. For instance, canopy removal was shown to decrease body mass and survival but not abundance of southern toads (Todd and Rothermel, 2006). Rittenhouse et al. (2008) found elevated juvenile mortality due to desiccation in three anuran species inhabiting clearcuts, while Veysey Powell and Babbitt (2015) showed that clearcutting is associated with strong sublethal effects on size and body condition in forest litter amphibians. Homyack et al. (2011) revealed greater energy expenditure in salamanders from forests with a history of disturbance. These examples suggest that integrating changes in abundance and species richness with population vital rates may help to achieve effective population management (Armstrong, 2005).

Here, our first aim is to compare historical and contemporary terrestrial amphibian abundance and biomass from a Central European deciduous forest. Based on previous results that showed moderate to severe declines of most amphibian species at the regional scale of south-central Poland (Bonk and Pabijan, 2010), we expect to find negative demographic trends at the local level. Replicating a previous study, we obtained abundance estimates by employing removal sampling in contemporary plots representing different forest habitats and compared them to data collected 50 years earlier (Głowaciński and Witkowski, 1970). We augmented the historical and contemporary abundance data by modelling imperfect detection using a Bayesian implementation of removal sampling (Mäntyniemi et al., 2005; White et al., 1982).

Our second aim is to gauge whether differing forest management regimes and habitat characteristics influence anuran abundance, biomass and body condition based on data from contemporary plots. We hypothesize that increased microhabitat complexity of old growth forest supports a larger number and higher biomass of litter-dwelling anurans compared to plots in managed forest. Moreover, we predict that frogs from managed woodland have lower body condition on account of poorer habitat quality. We assessed whether a set of four local habitat variables could explain the spatial variation in abundance and biomass

of anuran amphibians. We included coarse downed woody debris as a habitat variable because it is a potential determinant of amphibian abundance and also clearly differentiates between forest management strategies in NF (i.e., conservation vs exploitation). Using morphometric data for the most common species (*Rana temporaria*) collected from contemporary plots, we also tested for differences in body condition in frogs from unmanaged old growth vs managed forest.

2. Materials and methods

2.1. Study area

The study site (Fig. 1A) encompassed the northernmost fragment of Niepołomice Forest (NF, 50°05'N, 22°22'E) located about 30 km east of Kraków in southcentral Poland. This forest fragment (~1500 ha), managed by the State Forests National Forest Holding of Poland, is deciduous with a predominance of oaks (*Quercus* sp.), small-leaved lime (*Tilia cordata*), common hornbeam (*Carpinus betulus*) and common alder (*Alnus glutinosa*) and is mostly used for timber extraction. The study area encompasses Lipówka reserve (25.7 ha) which has been legally protected since 1957, contains old growth oak forest >180 years of age and is not subject to management. The forest floor in this reserve contains numerous decaying logs, woody and herbaceous debris and a diverse biota (Głowaciński and Kaźmierczakowa, 1978; Holeksa et al., 2020). This microhabitat contrasts with the structure of the forest floor in younger, managed forest in which woody debris is routinely removed.

2.2. Historical data

Quantitative data on amphibian abundance and biomass was collected in August of 1967 and 1968 by Głowaciński and Witkowski (1970) in NF. These authors surveyed 5 plots (3 plots in 1967 and 2 plots in 1968) of 30 m × 30 m dimensions and captured and removed all amphibians present over a period of five to seven days (10–14 consecutive removal sessions during early morning and late evening). Precise locations, i.e. GPS coordinates, of historical plots are unavailable. For the three plots surveyed in 1967, we obtained the original field notes (courtesy of Z. Głowaciński) which included detailed species counts per each removal session. Only summary statistics are available for plots from 1968.

2.3. Sampling design

In 2016 and 2017 we replicated and expanded the field design of Głowaciński and Witkowski (1970) by constructing 16 plots (Fig. 1A, Table 1) of 30 m × 30 m dimensions. We placed six plots (group N, Fig. 1A) in the same forest subdivisions (rectangular 700 m × 350 m sections of forest in this part of NF) as the previous study. We consider these plots as direct revisits of the historical sampling sites. We situated the remaining 10 contemporary plots over a broader area of NF, including protected old growth forest in Lipówka reserve as well as managed forest towards the east (groups L and E, respectively, Fig. 1A–C). One plot from group L (L12) was placed in managed forest at the border of the reserve. These additional plots were used to (1) obtain robust current abundance and biomass estimates through increasing sample size and habitat representativeness of contemporary plots, and (2) assess the influence of forest management regimes on amphibian abundance, biomass and body condition. Drift fences (agrofabric canvas buried 5–10 cm into the ground, fastened to wooden stakes for support) were erected along the full perimeters of 11 plots. Five plots lacked perimeter fencing but were delimited by placing colored string along their borders. Unfenced plots allowed for potential movement of individuals into and out of the plots. The presence/absence of perimeter drift fencing was part of the removal sampling protocol and was not a modality used in data analysis. Distances between plots within groups were at least 100 m.

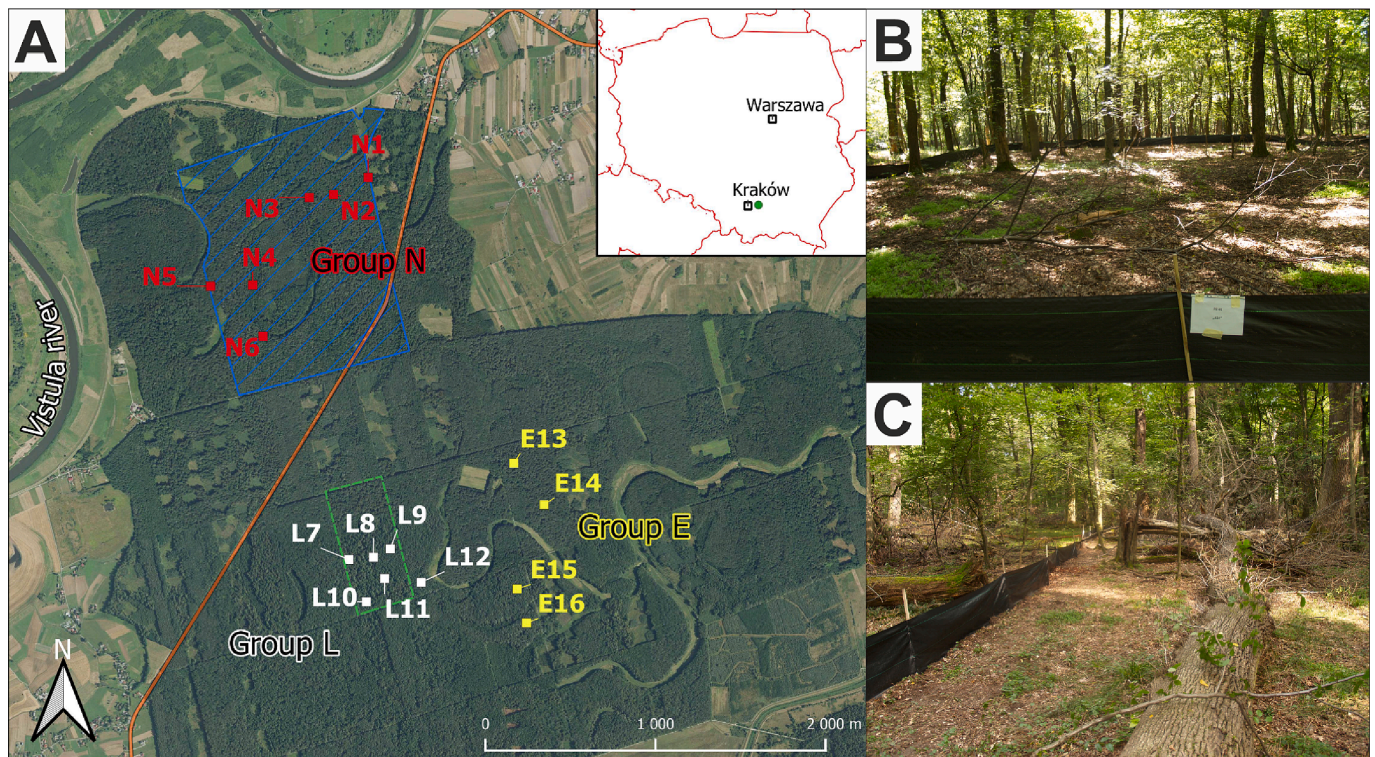


Fig. 1. Map of sampling plots (A) in the northeastern corner of Niepolomice Forest in south-central Poland (inset). The plots are split into three groups indicated by color coding: group N in managed forest north of a main road (solid line), group E in managed forest southeast of the main road, and group L in Lipówka reserve (green rectangle) in old growth, unmanaged forest. Blue stippling shows area in which five historical plots were located (Głowaciński and Witkowski 1970). Photographs of fragments of sampling plots in managed forest (B, plot N1) and old growth forest (C, plot L8). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Description of plots used for amphibian removal sampling, including year sampled and type of plot (O - open or C - closed), dominant tree species with age of tree stand (tree/age), the volume of coarse woody debris (deadwood), total number of removed amphibians (count) and their biomass (biomass), median abundance values with 97.5% quantiles of the Bayesian posterior distributions, abundance and biomass calculated per hectare. Groups N and E designate plots in managed forest, group L refers to plots in old growth, unmanaged forest. Group H denotes historical data from Głowaciński and Witkowski (1970); biomass for P1 and P2 (asterisks) was reported as a single value and therefore divided by two. Bottom rows show summary statistics (means and SDs) for different forest types.

Region	Plot	Year/type	Tree/age	Deadwood (m ³)	Count	Median (97.5 %)	Biomass (g)	Count/ha	Biomass/ha (g)
group L	L7	2016/O	oak/185	15.41	76	111.3 (84.2–611.1)	791.9	1237	8799
	L8	2017/C	oak/185	10.72	82	97.9 (84.2–464.0)	734	1088	8155
	L9	2016/C	oak/185	12.93	24	35.7 (25.1–248.8)	348.2	397	3869
	L10	2016/C	oak/185	6.93	34	43.0 (34.9–214.5)	396.3	478	4403
	L11	2017/C	oak/185	17.56	120	150.6 (124.1–685.6)	643.2	1673	7147
	L12	2016/C	oak/85	1.11	64	87.7 (68.2–566.9)	684.7	974	7608
group N	N1	2016/C	oak/125	0.16	3	3.4 (3.0–14.1)	51.5	38	572
	N2	2016/O	oak/125	0.37	11	19.0 (11.3–206.7)	122.5	211	1361
	N3	2016/C	oak/125; 75	1.35	6	6.3 (6.0–11.5)	121.5	70	1350
	N4	2017/C	alder/65	3.65	13	15.5 (13.1–67.8)	148.1	173	1645
	N5	2017/O	oak/115	0.1	11	29.1 (12.2–603.8)	83.65	323	929
	N6	2017/O	oak/120	0.29	7	11.7 (7.2–152.7)	19.6	130	218
group E	E13	2017/C	oak/120	0.2	74	78.0 (74.3–151.6)	661.3	867	7348
	E14	2017/C	oak/120	0.61	66	75.5 (66.9–282.2)	329.6	839	366
	E15	2016/C	oak/100	0.26	87	112.5 (88.9–206.8)	362.3	1250	4025
	E16	2016/O	oak/100	0.08	61	94.3 (67.9–640.8)	294.6	1047	3273
group H	H1	1967/O	–	–	242	269.2 (253.5–347.7)	3148.2*	2991	16569*
	H2	1967/O	–	–	209	314.4 (256.3–592.6)	3148.2*	3493	16569*
	H3	1967/O	–	–	174	177.2 (174.2–208.7)	1222.8	1969	13,587
old growth forest 2016/2017				12.71 (4.13)	–	87.7 (43.1)	599.7 (183.7)	974.5 (479.5)	6663.5 (2041.1)
managed forest 2016/2017				0.74 (1.05)	–	44.5 (41.0)	219.5 (195.5)	494.8 (455.6)	2108.7 (2215.9)
all forest 2016/2017				–	–	60.7 (45.8)	362.1 (265.2)	674.7 (508.6)	3816.7 (3085.7)
managed forest 1967				–	–	253.6 (69.9)	2506.4 (1111.6)	2817.7 (776.6)	15,575 (1721.6)

2.4. Fieldwork

The seasonal timing and weather conditions of the fieldwork in 2016/2017 were similar to those of the reference study (Głowaciński

and Witkowski, 1970). Fieldwork took place between 18–24 of August 2016 and 19–25 of August 2017 during or after periods of relatively heavy rainfall (Supp. Fig. 1) and elevated surface activity of amphibians. The timing of the fieldwork coincided with a sedentary (foraging) phase

of the seasonal cycle of amphibians in NF because breeding migrations of adults and dispersal of juveniles from natal sites are limited at this time of year, while migration towards overwintering sites has not yet commenced.

Each plot was systematically traversed by two people in 10–12 removal sessions conducted in the early morning (6:00 am–9:00 am, for 40 min.) and late evening (21:00 pm–01:00 am, for 60 min.) with headlamps for illumination after dark, resulting in sampling effort of 16–20 person/hours per plot over the removal period. Field workers were rotated among study plots. Amphibians were identified to species, counted and measured immediately after each removal session. Measurements included snout vent length (SVL) and body mass (BM) taken using digital calipers to the nearest 0.1 mm and Pesola scales to the nearest 0.1 g. All captured amphibians were placed in temporary enclosures and released at their sites of capture after completion of the study.

2.5. Local habitat variables

In March and April of 2016 and 2017, we collected data on local habitat variables that are biologically relevant to amphibians and may influence their abundance and biomass: deadwood volume, number of potential breeding sites in the vicinity of plots, distance to potential overwintering site, and distance to nearest paved road. We georeferenced and surveyed (visual survey and dip-netting) all potential amphibian breeding sites, defined as permanent or semi-permanent lentic water bodies holding water at least until May. Because the most common amphibian noted in our study, *Rana temporaria*, typically overwinters underwater (Juszczyk, 1987), we also noted all potential aquatic wintering sites for this species, defined as permanent lentic water bodies, deep ditches and streams. The volume of coarse woody debris (WD_v) was estimated in all contemporary forest plots by measuring stumps, lying tree logs and branches of diameter > 10 cm, using the following formulas (Wolski 2002) for calculations:

$$WD_v = \sum_i \left(3.14 \left((W_i/2 + T_i/2)^2 L_i \right) \right) / 40000 \text{ for tree logs and branches}$$

$$WD_v = \sum_i \left(3.14 (D_i)^2 L_i \right) / 40000 \text{ for tree stumps}$$

where W is the diameter at the wider end of the log or branch (cm), T is the diameter at the thinner end of the log (cm), L is the total length/height of the log/stump (m), D is the diameter of the stump (cm) and 40,000 is a constant used to convert obtained values to m³.

2.6. Data analysis

The raw data used for obtaining abundance estimates consisted of counts of amphibians per removal session for 16 plots surveyed in 2016/2017 and for three plots surveyed in 1967. We applied a Bayesian model of population size estimation (Mäntyniemi et al., 2005) that relaxes the assumption of constant capture probability among individuals and can deal with non-declining catches in successive removal trials. The Bayesian model assumes that the size of the population does not change over the sampling period and that individual probability of capture is randomly distributed in the population. Mean probability of capture q and population sizes n for each removal trial are drawn from user-specified prior probability density functions. To avoid systematic bias in capture probabilities resulting from alternating nighttime and daytime searches, we combined morning and evening searches, obtaining 5–7 removals per plot, each composed of two counts of removed individuals. We followed Mäntyniemi et al. (2005) in assuming a Beta distribution, $\mu \sim \text{Beta}(1.1, 1.1)$ for the initial distribution of q and a vague uniform prior, $\log(\eta) \sim \text{Unif}(0, 10)$, on the variation in q in subsequent removals. A flat prior was also placed on population size, $\log$

(N) $\sim \text{Unif}(0, 8)$, translating to population sizes from 0 to ~ 3000 individuals per removal. The upper limit of ~ 3000 individuals was selected as approximately 10x the highest median posterior population size. We modified the code from Mäntyniemi et al. (2005) and used OpenBUGS 3.2.3 (Lunn et al., 2009) with Markov chain Monte Carlo simulation (MCMC) to obtain posterior distributions of the parameters. After compiling the model (refer to Supp. Material 1 for code and data) we ran two chains. The number of iterations depended on how quickly the chains converged (between 100,000–200,000) which was assessed by examining sample traces for n and q using the sample monitoring tool in OpenBUGS. Estimates for n and q were obtained by removing the first 50 % of the iterations as burnin, thinning by 50–100, and then combining the remaining samples (2000 from each chain). Mann-Whitney tests were used to compare differences in abundance and biomass between historical and contemporary data.

Linear mixed models calculated in the R library lme4 (Bates et al., 2015) were used to assess the influence of environmental (predictor) variables (Table 1; Table S1) on median amphibian abundance values and total amphibian biomass (response variables) obtained for contemporary plots. As predictors, we used continuous variables including the volume of coarse woody debris, number of breeding sites in 500 m perimeter to plot, distance to nearest wintering site and distance to road. We defined a random variable, area, referring to the geographical location of a plot with three levels: groups L, N and E (Fig. 1). This variable accounts for the unexplained similarity in amphibian abundance/biomass between closely situated plots. We first tested for normality of residual values in the predictor variables and for correlations among variables (Table S2). Next, we standardized predictor variables by subtracting their means from all values and dividing by twice the standard deviation. We applied Akaike's information criterion corrected for small sample size (AICc) for model selection using the dredge function in the R package MuMin (Bartoń, 2009) but compared only eight models (plus the intercept only null model) by limiting the number of predictor variables in a single model to two and by removing models containing variables with correlation coefficients > 0.6.

Body condition indices were calculated from measurements of snout vent length (SVL) and body mass (BM) on a dataset consisting of individuals of the most numerous species, *Rana temporaria* ($n = 607$, Table S3). We did not attempt this analysis for the second most numerous species, *Bufo bufo* ($n = 101$), as only 21 individuals of this species were collected from managed forest. We deemed the sample sizes for *B. bufo* and all remaining species in the community as too low for a meaningful analysis.

For *Rana temporaria*, we calculated the scaled mass index of body condition (SMI) that accounts for the allometric relationship between mass and linear body structures and standardizes each measure enabling direct comparisons among different populations (Peig and Green, 2009). We followed Peig and Green (2009) by first regressing mass on length, extracting the slope of the linear regression of the natural logarithms of mass and length which we divided by Pearson's r of the same variables, and used this ratio as the power function in the SMI calculation. Finally, we computed the SMI for each individual using mean SVL as a constant in the calculation. We removed one outlier with an extremely high SMI and used t -tests to compare body condition between *R. temporaria* from managed and old growth forests. The SMI has advantages over other body condition indices and has been recommended for anuran amphibians (MacCracken and Stebbings, 2012; Brodeur et al., 2020). However, to gauge the robustness of our results, we also calculated the widely applied residual body condition index (Jakob et al., 1996). For calculations, we regressed the logarithm of body mass against the logarithm of snout–vent length. We extracted residuals from this analysis and used them as a body condition index; t -tests were used for comparisons among groups.

3. Results

3.1. Temporal trends in amphibian abundance and biomass

In 2016/2017 we captured and removed 739 amphibians from 16 experimental plots (Table 1, Fig. 2A,B, Table S4). Three species predominated: *Rana temporaria* (607 individuals, 82.1 %), *Bufo bufo* (101 ind., 13.7 %) and *R. arvalis* (25 ind., 3.4 %). The numbers of individuals removed per plot varied from 3 to 120 (Table 1, Fig. 2B). In 1967/1968, Głowaciński and Witkowski (1970) removed 1144 individuals from five plots, in which *B. bufo* (64.9 %), *R. arvalis* (18.4 %) and *R. temporaria* (10.7 %) predominated, with smaller shares of *Pelophylax* sp. (3.3 %), *Bombina bombina* (1.95 %) and *Lissotriton vulgaris* (0.6 %). Direct counts of individuals (and not proportions as in the original publication) were available from field notes for three of these plots (Fig. 2B, Table S4) showing similar shares of species and between 174 and 242 amphibians removed per plot (Table 1).

The MCMC simulations applied in the Bayesian estimates of abundance converged for the study plots, revealing declining probability of capture and population sizes over successive removal passes. Bayesian estimates of abundance, accounting for heterogeneity in probability of capture, were up to ~30 % higher than the raw counts of individuals per plot (Fig. 2C, Table 1). Plots characterized by relatively low depletion (i. e., numbers of captured animals in consecutive removal passes) produced wider 97.5 % quantiles of the posterior distribution of n , i. e., higher uncertainty in the posterior estimates of abundance. Nonetheless, the posterior distributions of n for all experimental plots were highly skewed towards low values compared to the prior distribution, with most median values and interquartile ranges well below 200 individuals (Fig. 2C). We did not find differences in median values of amphibian abundance between open and closed plots (53.1 ± 46.3 vs 64.1 ± 47.5 , respectively; Mann-Whitney test, $P = 0.82$), nor between sampling years 2016 and 2017 (57.1 ± 44.6 vs 65.5 ± 50.4 , respectively; Mann-Whitney test, $P = 0.92$) and we therefore did not differentiate between these plot types when presenting summary statistics below.

Based on median values of Bayesian abundance estimates, historical plots contained larger numbers of amphibians compared to contemporary plots (means $\pm$ SDs of 253.6 ± 69.9 vs 60.7 ± 45.8 , respectively; Mann-Whitney test, $P < 0.01$; Table 1, Fig. 2C). This difference was even more pronounced when the comparison was limited to current plots positioned in the same forest division as the historical plots (group N, current mean abundance 14.2 ± 9.3). Contemporary mean $\pm$ SD amphibian biomass per plot (Table 1, Table S5), calculated as the sum of weights for all individuals removed from a plot in 2016–2017, amounted to 362.7 ± 265.6 g (range 19.6–791.9 g) and was considerably lower than historical biomass estimates (2506.4 ± 1111.6 g, Mann-Whitney test, $P < 0.01$).

3.2. Current spatial trends in amphibian abundance and biomass

We found substantial heterogeneity in amphibian abundance estimates for contemporary plots (Fig. 2). Mean abundance estimates for plots in old growth forest (group L, 87.7 ± 43.1) tended to be higher than those in managed forest (44.5 ± 41.0 ; Mann-Whitney test, $P = 0.05$). However, when partitioned by geographic location, we found that abundance estimates of northern sampling sites (group N, 14.2 ± 9.3) were significantly smaller than those of group E (90.6 ± 17.1) and L (Mann-Whitney tests: $P < 0.01$ for both tests, see also Fig. 3). Moreover, we found that mean amphibian biomass in old growth forest was significantly higher than for managed forest plots (599.7 ± 183.7 g vs 219.5 ± 195.5 g; Mann-Whitney test, $P < 0.05$), although this relationship was driven mostly by low biomass values in group N (91.1 ± 48.7) as the trend was apparent but not significant between groups L and E (599.7 ± 183.7 g vs 411.9 ± 168.5 g; Mann-Whitney test, $P = 0.11$).

AICc-based model selection showed that three of the four best models explaining amphibian abundance included the volume of coarse

woody debris (Table 2, Table S6, Fig. 3) and all models scored higher than the null with intercept only (Table S6). The linear mixed model indicated that most of the variance in amphibian abundance among plots was determined by the random factor geographic area (Table S7), however, higher deadwood volume also increased the number of captured amphibians (Table S7, Fig. 3). The best models explaining amphibian biomass (Table 2, Table S8) included different combinations of all four predictor variables, but their effects explained only a small part of the variance in amphibian biomass among plots (Table S9). We note a positive but weak effect of volume of coarse woody debris, and weak negative effects of distance to road and overwintering site (Table S9).

3.3. Amphibian body condition in managed vs. old growth forest

The distributions of body size (SVL) and body mass (BM) were clearly bimodal and showed significantly higher mean values for frogs from old growth forest plots (Fig. S2). SVL and BM were highly correlated ($r^2 = 0.94$, $df = 604$, $P < 0.001$). The scaled mass index of body condition (SMI) was about 10 % higher in *Rana temporaria* from old growth forest (5.03 ± 1.537) compared to individuals from managed forest (4.54 ± 0.881 , t -test $df = 503.03$, $P < 0.001$, Fig. 4). Results for the residual index (RI) were fully consistent with those obtained for SMI (Fig. S3). Mean RI was higher and positive in frogs from old growth forest compared to individuals from managed forest (0.046 ± 0.2603 vs -0.049 ± 0.1751 , t -test $df = 549$, $P < 0.001$).

Inspection of Fig. 4 and Fig. S3 revealed that enhanced body condition was particularly apparent in smaller frogs. Using a cut-off value of $\ln(3.75)$ [corresponding to 4 cm] which roughly partitioned the bimodal distribution of $\ln(\text{SVL})$ into small and large frogs (Fig. 4 and Fig. S2), a *post-hoc* test showed that mean SMI in small frogs from old growth forest was ~14 % higher than mean SMI in small frogs from managed forest (5.2 ± 1.71 vs 4.5 ± 0.88 ; t -test $df = 320.36$, $P < 0.0001$). This was not the case for mean SMI values in large frogs from old growth vs managed forest (4.7 ± 0.91 vs 4.6 ± 0.81 ; t -test $df = 81.75$, $P = 0.6$).

4. Discussion

4.1. Main conclusions and pitfalls

This study has three important results with implications for amphibian conservation and management in temperate forest ecosystems. First, we showed that amphibian abundance in a forested environment in Central Europe has substantially declined over the last half century: the leaf-litter amphibian community of NF contained at least four times as many individuals in 1967/1968 as it did in 2016/2017 (Table 1; Głowaciński and Witkowski, 1970). This is a conservative estimate that takes into account spatial variation in current amphibian abundance; a direct longitudinal comparison (group H vs group N) revealed a more dramatic local decline (see below). Second, current amphibian abundance and biomass varied among our study plots and was generally higher in or near old growth (i. e., unmanaged) forest stands. The volume of coarse woody debris on the forest floor partially explained this variation by increasing both parameters (Fig. 3). Third, we found that common frogs (*Rana temporaria*) captured in old growth forest had, on average, enhanced body condition compared to individuals from managed forest.

However, caution is required when interpreting these results. Our demographic conclusions are not based on a continuous time series but data from four field seasons (1967–1968 and 2016–2017). Because of episodic recruitment, amphibian populations will tend to decline over most years and then rebound in favorable years (Alford and Richards, 1999), meaning that demographic inference drawn from a small number of surveys may not be reliable. Temporal and spatial differences in exposure to sampling, as well as variable detection probabilities among

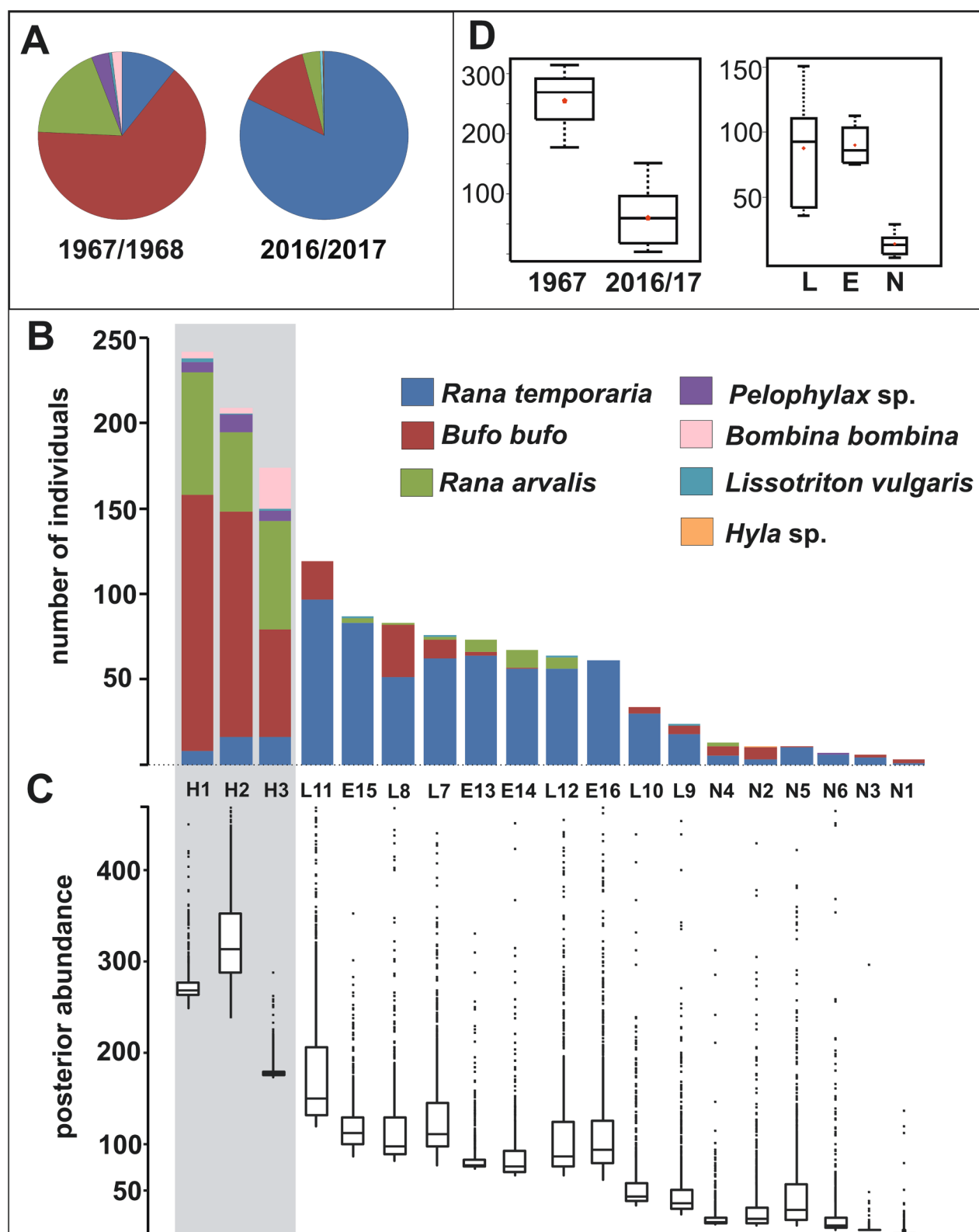


Fig. 2. (A) Proportions of amphibian taxa removed in 1967/1968 (1144 individuals from 5 sampling plots) and in 2016/2017 (742 individuals from 16 sampling plots). Species are color coded as in B. (B) Amphibian counts and species compositions per plot. (C) Distributions of Bayesian posterior abundance estimates for each sampling plot. Outliers above 500 individuals were omitted. Historical plots are shaded, see Table 1 for plot abbreviations. (D) Longitudinal (1967 vs 2016–2017) and cross-sectional (only 2016–2017) comparisons of mean numbers of amphibians removed per plot; group L - old growth forest in Lipówka reserve, E - managed forest, eastern group, N - managed forest, northern group. Boxes show interquartile range (25th to 75th percentile) with lines and red dots representing medians and means, respectively; whiskers include higher and lower values, single points show outliers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

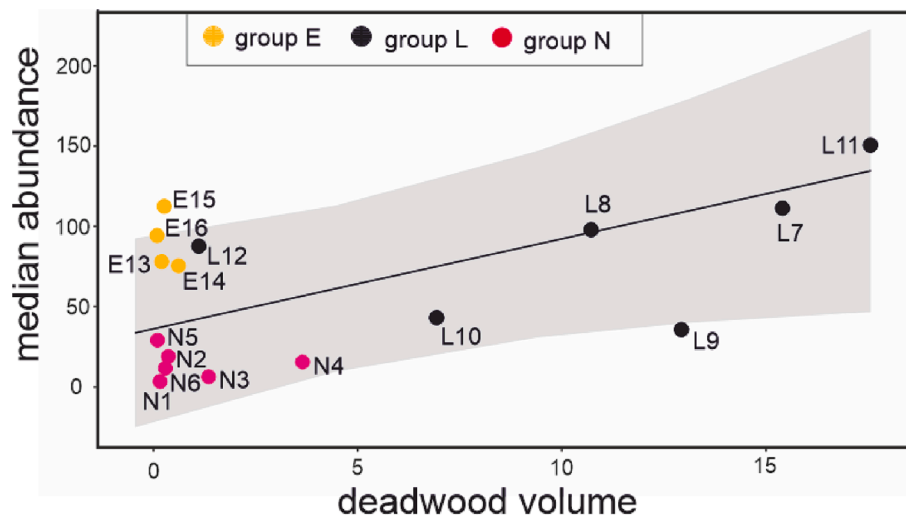


Fig. 3. Relationship between median amphibian abundance per plot and deadwood volume (m^3) with color-coded geographic sampling areas. Regression line and 95% confidence intervals (gray shading) are derived from the global mixed effects model.

Table 2

Best models ($\Delta \text{AICc} < 6$) explaining median abundance (n) and biomass (b) of amphibians per sampling plot. A random variable (area) describing the spatial position of each plot (L, N, E, see Table 1) was used in each model. See Tables S6 and S8 for full list of models. d – volume of coarse woody debris in each plot; nb – number of breeding sites in 500 m perimeter of plots; w – distance to nearest overwintering site; r – distance to paved road; AICc – Akaike information criterion corrected for small sample size; weight – model weight, df – degrees of freedom.

model	ΔAICc	weight	df
$n \sim d + r$	0	0.55	5
$n \sim d + w$	1.32	0.29	5
$n \sim nb + r$	3.82	0.08	5
$n \sim d$	5.47	0.03	4
$b \sim d + r$	0	0.43	5
$b \sim r + w$	0.92	0.27	5
$b \sim r + nb$	1.7	0.18	5
$b \sim d + w$	2.7	0.11	5

species, age groups, plots and years may further distort abundance estimates (Schmidt and Pellet, 2010). Although these factors may have affected our results, we argue the data reflected a true decline for two reasons. First, we do not expect all species in a community to exhibit the same demographic trend at a given time point (e.g. Martínez-Solano et al., 2003). Nonetheless, our data revealed downtrends in absolute numbers of individuals for all surveyed species, despite a substantially greater sampling effort in 2016/2017. Second, we adhered to the sampling technique used previously (Głowaciński and Witkowski, 1970) under similar seasonal timing and weather conditions and optimized datasets from both survey periods by applying a Bayesian method accommodating heterogeneous capture probabilities.

A further weakness of our study is that the historical data relied on five sampling plots of which only three could be used directly for the temporal comparison and hence may not have been representative of amphibian abundance in NF at that time. If the historical plots were placed in optimal amphibian habitat, the estimates may be biased towards high amphibian densities. Half a century ago, the environmental conditions of this forest fragment contained a larger proportion of small, open, marshy wetlands (Dubiel, 1995; Barabasz, 1997; Wężyk and Matyja, 2007; see section 4.2) implying a greater extent of high-quality amphibian habitat, which argues against overestimation of historical amphibian abundance. Nonetheless, we acknowledge that this part of

NF, lying in the floodplain of a large river, most likely maintained a higher amphibian density than the surrounding agricultural landscape.

Our inference of higher anuran abundance in old growth vs managed forests should likewise be treated cautiously because all plots in the former category (group L) were located within a single nature reserve and therefore may not be representative of other old growth stands. Unfortunately, unmanaged deciduous forest approaching 200 years of age, as in the studied Lipówka reserve, is rare in Central Europe (Forest Europe, 2020). Comparable stands occur in the Białowieża Primeval Forest in eastern Poland in which Pikulik et al. (2001) detected a similar pattern of highest anuran abundance in old growth forest with ample deadwood.

4.2. Amphibian decline in Niepołomice forest

Although there is general agreement that amphibians have declined in Central Europe (Heatwole and Wilkinson, 2019), few studies have provided quantitative evidence, mostly due to a lack of historical census data. In a recent meta-analysis of amphibian demographic trends in Europe, only five out of 843 time series came from Central European amphibian populations (Falaschi et al., 2019). Our study thus offers a unique glimpse into local demographic trends of a forest litter amphibian community from a region that has received little attention. Sadly, we revealed a precipitous decline in amphibian abundance and biomass in this area of southern Poland. The magnitude of the decline was fourfold if counts and biomass are averaged over all historical and contemporary sampling sites (Table 1). However, it is notable that in plots from group N, which can be considered as actual revisits to the historical sites, the counts (2817 ± 776 to 157 ± 103 individuals/ha) and biomass (from 15.5 ± 1.7 to 1.0 ± 0.5 kg/ha) of amphibians plummeted around fifteenfold between 1967 and 2016/2017 (Table 1). This area encompasses a spatially and temporally continuous stand of forest managed for sustainable yield involving forestry practices such as thinning, clearing of downed woody debris, small-scale harvest and afforestation. However, the forest subdivisions encompassing our sampling plots have not been clear-cut over the intervening 50 year period, suggesting that the underlying cause(s) of the amphibian decline are of general concern. Nonetheless, we note that the current low volume of deadwood found in plots N may have exacerbated the decline in this part of NF. Unfortunately, deadwood volumes for the historical plots are unavailable.

Many factors have had a detrimental impact on amphibian populations in Poland in recent decades (Pabijan and Ogielska, 2019), but

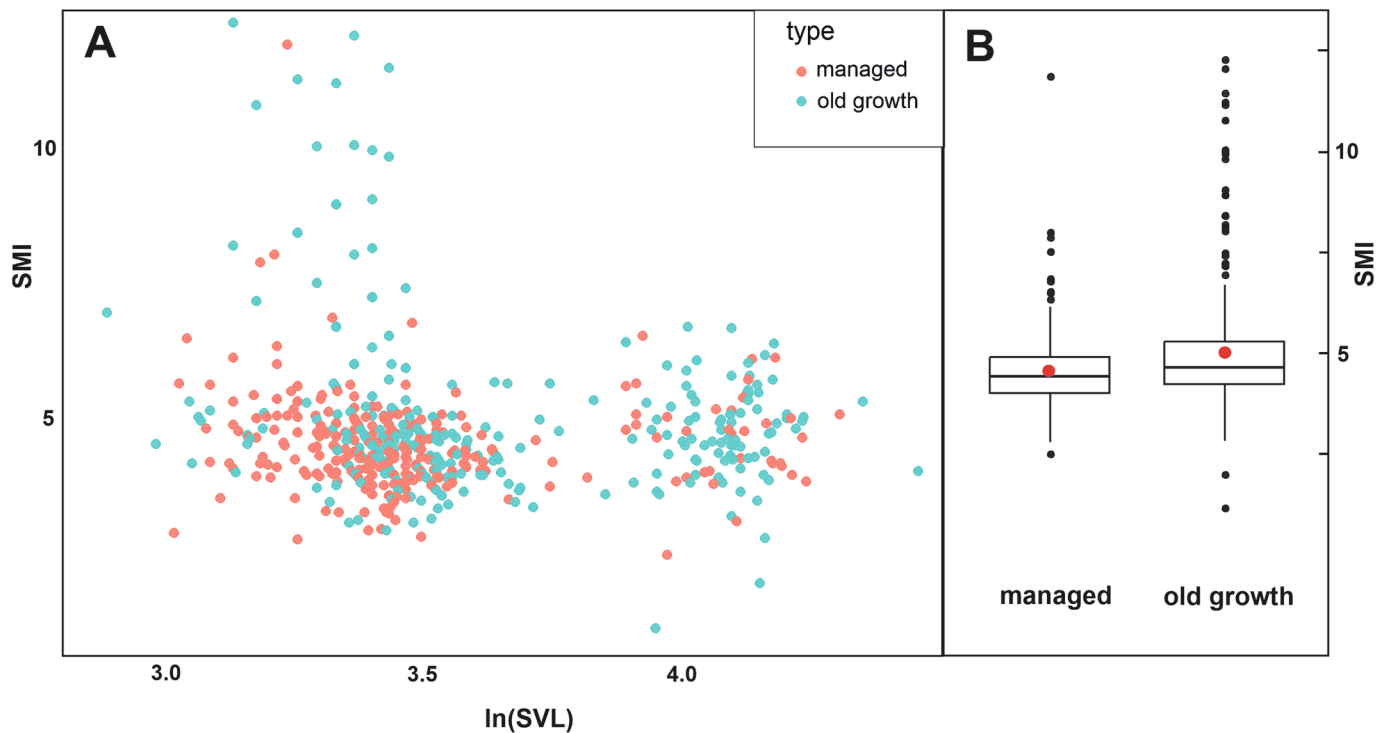


Fig. 4. Relationship between the scaled mass index of body condition (SMI) and the natural log of snout-vent length, calculated for *Rana temporaria* and divided into individuals from managed and old growth forest (see legend). This figure shows the existence of two size classes with smaller frogs from old growth forests exhibiting higher SMI. (B) Boxplots showing the distributions of SMI values for *R. temporaria* from managed and old growth forest plots. Boxes show interquartile range (25th to 75th percentile) with lines and red dots representing medians and means, respectively, whiskers include higher and lower values, single points show outliers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

three stand out in the case of NF. First, the twentieth century brought about large-scale river regulation and embankment detrimental to floodplain habitat, and drainage of natural wetlands to make way for cropland, urban and industrial areas (Ciepielowski and Gutry-Korycka, 1993). This resulted in the destruction of aquatic habitat and an overall drop in groundwater levels. Semi-natural, forested areas were not exempt from water loss: between the 1950's and early 2000's, the area of inundated meadows and marshes (mostly remnants of oxbows of the Vistula river and its tributaries) in NF declined by over 50 % from 158 ha to 77 ha (Węzyk and Matyja, 2007). In the northern part of NF, in close proximity to our study plots, the drop in available surface- and groundwater led to a decrease in plant species typical of wet meadows and marshes (Dubiel, 1995; Barabasz, 1997), and most likely to a decrease in available aquatic and high-quality terrestrial habitat for amphibians. Second, from the 1950's to the late 1980's, NF was exposed to enormous amounts of industrial pollution from a nearby metallurgic complex (Weiner et al., 1997). Third, a public road cutting through this forest fragment (Fig. 1) was paved in the 1970's, and probably inflicted considerable amphibian mortality through collisions with motor vehicles. We speculate that this combination of habitat-degrading anthropogenic factors could have decimated the local amphibian community, although other agents, such as the spread of infectious diseases (Palomar et al., 2021) may have also played a role. Unfortunately, the habitat degradation that has likely led to the decline of amphibians and deterioration of their habitat in NF is affecting wetland biodiversity at a global scale (Albert et al., 2021; Naidu et al., 2021).

We also noted a change in amphibian species composition in NF. In 1967/1968 *Bufo bufo* and *Rana arvalis* clearly dominated, while in 2016/2017 *R. temporaria* was by far the most numerous species (Fig. 2A, B). We attribute this shift to habitat change within NF: non-forested wet meadows and marshes have given way to shaded and closed canopy stands of deciduous forest over the last half century (Węzyk and Matyja, 2007). Moreover, the number of relatively large and permanent water

bodies has dwindled, with most contemporary amphibian breeding sites being small, semi-permanent and shaded. This type of habitat seems to be better tolerated by the generalist *R. temporaria* (Van Buskirk, 2003; 2005; Vági et al., 2013) compared to either *B. bufo* or *R. arvalis* that typically breed in larger water bodies or prefer more sunlit areas. It is likely that the transition from a mosaic of forest and marshland/wet meadow habitat to a more consolidated and dense deciduous forest resulted in the gradual decline of amphibian species preferring open environments. Further support for this hypothesis stems from the effective loss of two semi-aquatic species (*Bombina bombina* and *Pelophylax lessonae*) from the study sites, though both are still present in nearby ponds beyond the forest. We conclude, similar to Skelly et al. (1999), that habitat changes associated with forest succession have had a negative impact on amphibian diversity and abundance in NF.

4.3. Spatial variation in amphibian abundance, biomass and body condition

Our results demonstrated that the local abundance of amphibians in NF, in apparently suitable and continuous forest habitat, was determined by fine-scale environmental cues and likely reflected silvicultural heterogeneity in which small forest parcels are allocated to conservation while large areas are dedicated to wood production in managed plantations. On average, we found twice as many amphibians in old growth compared to managed forest. Out of four studied environmental variables, only the volume of coarse woody debris had an unambiguously positive effect on number and biomass of amphibians. The structure of the forest floor was the single most striking difference between the sites. In managed forest (especially plots from group N) the forest floor was almost completely barren (Fig. 1B), with the only refuges being crevices in the roots or trunks of standing trees. In contrast, old growth forest had a well-developed understory and ample downed woody debris (Fig. 1C). Forest floor complexity increases humidity, protects against thermal

extremes, and provides refuges and an abundant invertebrate prey base (de Maynadier and Hunter, 1995; Otto et al., 2013; Thompson and Donnelly, 2018), all of which are of direct or indirect benefit to the amphibian forest litter community and likely explain the association between microhabitat complexity and amphibian abundance observed in this study and others (e.g. Dupuis et al., 1995; Costa et al., 2016). However, our results should be considered preliminary as other unmodelled factors associated with geographic grouping (Fig. 3) determined a considerable part of the variance in amphibian abundance and biomass among plots.

Apart from increased numbers, our results suggest that individuals of the most numerous frog species, *Rana temporaria*, had on average ~ 10 % higher body condition (based on the scaled mass index, SMI) in old growth stands compared to individuals from managed forest. This conclusion holds if the comparison is made using the residual body condition index (Fig. S3). Further, we found that this pattern was driven mainly by higher SMI in small frogs (<4 cm) from old growth stands (Fig. 3 and Fig. S3), a size class typical of juveniles in their 1st-2nd years of life (Miaud et al., 1999). Higher juvenile body mass could be attributed to larger tadpole size at metamorphosis or faster post-metamorphic growth compared to the same cohort in managed forest. Nearly all breeding sites near the old growth stands of Lipówka reserve were small, temporary shaded pools with, we suspect, rather low primary productivity. We did not find any association between number of breeding sites or distance to breeding site and biomass, a relationship that could be expected if tadpole size contributed to body condition of juveniles. Instead, we hypothesize that juvenile frogs living in the leaf litter of unmanaged, old growth forest find more prey and, due to a cooler and more humid microclimate, spend more time and less energy at foraging, leading to a higher calorie intake and enhanced body condition compared to juvenile frogs from managed forest.

SMI reflects energy stores and physiological traits in larval and juvenile *R. temporaria* and decreases in a stressful environment (Ruthsatz et al., 2020). MacCracken and Stebbings (2012) reported a 17–32 % decrease in mean SMI in starved juvenile bullfrogs and other amphibians. The body condition of frogs in August in south-central Poland reflects their state after two to four months of feeding activity during which energy stores are built up for the upcoming winter and subsequent spring breeding (Juszczyk, 1987; Elmberg, 1991a; Elmberg and Lundberg, 1991). Reduced SMI in frogs from managed forest during late summer implies lower chances of successful overwintering (Chen et al., 2011), poorer performance (e.g. migration distance; Ponsero and Joly, 1998) and possible negative reproductive impacts via lower mating success or fewer eggs (Gibbons and McCarthy, 1986; Elmberg, 1991b). The consequences of lower body condition in froglets may be particularly acute due to a strong association between energy stores and overwintering survival (Scott et al., 2007; Garner et al., 2011). We conclude that intensive forest management likely leads to poorer habitat quality that may lower both the abundance and fitness of leaf-litter anurans, which in consequence may weaken population resilience to environmental disturbances and anthropogenic stressors.

4.4. Conservation and management implications

We found evidence for a significant and sizable amphibian decline in a temperate, Central European forest over the last 50 years. In contrast to most studies focusing on single species (e.g. Nyström et al., 2007), we documented a decline in an entire amphibian community, including both common and rare species. The species composition, habitat and perceived threats to the amphibian assemblage in our study area are common to large parts of the Western Palearctic, and we therefore suspect that declines in amphibian abundance and their underlying drivers in this region could be more widespread than currently recognized. Due to their roles as high-efficiency biomass converters and a potentially ample food source for larger predators, the decline of leaf-litter amphibian guilds may have systemic consequences for forest

ecosystems and associated ecosystem services (Hocking and Babbitt, 2014). However, our data also suggest that old growth forest containing coarse woody debris can partially mitigate long-term declines of forest-dwelling amphibians by maintaining high quality terrestrial habitat that supports relatively numerous individuals and enhances body condition of some species. Thus, our results emphasize the high conservation value of old growth forest due to its role in maintaining the abundance, biomass and body condition of forest litter amphibians.

Nearly all European temperate forests are secondary and managed to some degree (Forest Europe, 2020). Our results bear significance for secondary forest management geared towards improving habitat quality for forest litter amphibians. We found that elevated amounts of coarse woody debris on the forest floor may increase amphibian abundance by a factor of two and lead to improved body condition in the dominant anuran, *Rana temporaria*. In our study plots, deadwood volume in managed forest averaged 8.3 m³/ha (range 0.9–40 m³/ha) which is slightly higher than mean values of deadwood throughout NF (~7 m³/ha; Holeksa et al., 2020), but closer to the current average of 9.8 m³/ha in Poland (Biuro Urządzania Lasu i Geodezji Leśnej, 2022). Deadwood in plots situated in old growth forest averaged about 141 m³/ha (range 77–195 m³/ha). We propose that leaving deadwood in quantities approaching values for old growth deciduous forest examined in our study would likely increase anuran abundance and may be attainable even in commercial woodlands, in particular in managed forest in the process of recovering old growth attributes (Vandekerckhove et al., 2009; Meyer and Schmidt, 2011; Paillet et al., 2015). Further, although our conclusions are based mainly on anurans, they likely extend to urodele amphibians because of their lower mobility and dependence on high quality terrestrial habitat (Homyack et al., 2011; Otto et al., 2013), as well as saproxylic and forest specialist taxa (Paillet et al., 2010). Our recommendations may help to strike a balance between wood extraction and biodiversity conservation in woodland ecosystems of temperate regions, reduce the negative impact of forestry on amphibians and restore habitat of old growth forest biota.

CRediT authorship contribution statement

Maciej Pabijan: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Funding acquisition. **Sara Bąk-Kopaniarz:** Investigation, Data curation. **Maciej Bonk:** Conceptualization, Investigation, Writing – review & editing, Funding acquisition. **Stanisław Bury:** Investigation, Writing – review & editing. **Wioleta Oleś:** Investigation. **Weronika Antoń:** Investigation. **Izabela Dyczko:** Investigation. **Bartłomiej Zajac:** Investigation, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

The code and raw data is part of the [Supplementary Material](#)

Acknowledgments

This study was supported by a Societas Europaea Herpetologica (SEH) Grant in Herpetology (2016) to MP and MB. We thank Andrzej Antoń, Agata Bury, Joanna Kajzer-Bonk, Marta Gryzlo, Elżbieta Rożej-Pabijan, Adam Solecki and Antoni Żygadło for help during fieldwork, and three anonymous reviewers for improving a previous version of the manuscript. We would also like to thank Zbigniew Głowaciński for providing field notes from 1967, Łukasz Piechnik for field measurements of woody debris and Samu Mäntyniemi for modelling advice in

OpenBUGS. Permission for amphibian capture was given by the Regional Directorate for Environmental Protection in Kraków (decisions OP-I.6401.143.2016.MMr and OP-I.6401.37.2017.MMr.) We thank Nadleśnictwo Niepołomice of the State Forests for allowing access to the area. The open-access publication of this article was funded by the programme “Excellence Initiative – Research University” at the Faculty of Biology of the Jagiellonian University in Kraków, Poland.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.110036>.

References

- Albert, J.S., Destouni, G., Duke-Sylvester, S.M., Magurran, A.E., Oberdorff, T., Reis, R.E., Winemiller, K.O., Ripple, W.J., 2021. Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio* 50, 85–94.
- Alford, R.A., Richards, S.J., 1999. Global amphibian declines: a problem in applied ecology. *Annu. Rev. Ecol. Syst.* 30, 133–165.
- Armstrong, D.P., 2005. Integrating the metapopulation and habitat paradigms for understanding broad-scale declines of species. *Conserv. Biol.* 19, 1402–1410.
- Barabasz, B., 1997. Zmiany roślinności łąk w północnej części Puszczy Niepołomickiej w ciągu 20 lat. *Studia Naturae* 43, 1–99.
- Bartoń, K., 2009. MuMIn: multi-model inference. <http://r-forge.r-project.org/projects/mumin/>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48.
- Biuro Urządzania Lasu i Geodezji Leśnej 2022. Wielkoobszarowa inwentaryzacja stanu lasów. Wyniki za okres 2017–2021. Sękocin Stary.
- Blaustein, A.R., Han, B.A., Relyea, R.A., Johnson, P.T., Buck, J.C., Gervasi, S.S., Kats, L.B., 2011. The complexity of amphibian population declines: understanding the role of cofactors in driving amphibian losses. *Ann. N.Y. Acad. Sci.* 1223, 108–119.
- Bonk, M., Pabijan, M., 2010. Changes in a regional batrachofauna in south-central Poland over a 25 year period. *North-West. J. Zool.* 6, 225–244.
- Brodeur, J.C., Damonte, M.J., Candiotti, J.V., Poliserpi, M.B., D'Andrea, M.F., Bahl, M.F., 2020. Frog body condition: basic assumptions, comparison of methods and characterization of natural variability with field data from *Leptodactylus latrans*. *Ecol. Indic.* 112, 106098.
- Chen, W., Zhang, L.X., Lu, X., 2011. Higher pre-hibernation energy storage in anurans from cold environments: a case study on a temperate frog *Rana chensinensis* along a broad latitudinal and altitudinal gradients. *Ann. Zool. Fennici* 48, 214–220.
- Ciepielowski, A., Gutry-Korycka, M., 1993. Wpływ melioracji wodnych. In: Dynowska, I. (Ed.), *Przemiany Stosunków Wodnych W Polsce W Wyniku Procesów Naturalnych I Antropogenicznych*. Uniwersytet Jagielloński, Kraków, pp. 313–328.
- Costa, A., Crovetto, F., Salvidio, S., 2016. European plethodontid salamanders on the forest floor: local abundance is related to fine-scale environmental factors. *Herpetol. Conserv. Biol.* 11, 344–349.
- Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biol. Conserv.* 128, 231–240.
- DeMaynadier, P.G., Hunter Jr, M.L., 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environ. Rev.* 3, 230–236.
- Dubiel E., 1995. Puszcza Niepołomska. Środowisko abiotyczne, flora roślin naczyniowych i roślinność Puszczy Niepołomickiej, in Mirek Z., Wójcicki, J.J., (Eds.), *Szata roślinna parków narodowych i rezerwatów Polski południowej*. Przewodnik Sesji Terenowych 50 Zjazdu PTB. Polish Botanical Studies, Guidebook Series, pp. 33–72.
- Dupuis, L.A., Smith, J.N., Bunnell, F., 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. *Conserv. Biol.* 9, 645–653.
- Elmberg, J., 1991a. Ovarian cyclicity and fecundity in boreal common frogs *Rana temporaria* L. along a climatic gradient. *Funct. Ecol.* 5, 340–350.
- Elmberg, J., 1991b. Factors affecting male yearly mating success in the common frog, *Rana temporaria*. *Behav. Ecol. Sociobiol.* 28, 125–131.
- Elmberg, J., Lundberg, P., 1991. Intraspecific variation in calling, time allocation and energy reserves in breeding male common frogs *Rana temporaria*. *Ann. Zool. Fennici* 28, 23–29.
- Falaschi, M., Manenti, R., Thuiller, W., Ficetola, G.F., 2019. Continental-scale determinants of population trends in European amphibians and reptiles. *Glob. Chang. Biol.* 25, 3504–3515.
- FAO and UNEP., 2020. The State of the World's Forests 2020. Forests, biodiversity and people. Rome. DOI: <https://doi.org/10.4060/ca8642en>.
- Ficetola, G.F., Rondinini, C., Bonardi, A., Baisero, D., Padoa-Schioppa, E., 2015. Habitat availability for amphibians and extinction threat: a global analysis. *Divers. Distrib.* 21, 302–311.
- FOREST EUROPE, 2020. State of Europe's Forests 2020. Bratislava, www.forest-europe.org.
- Garner, T.W., Rowcliffe, J.M., Fisher, M.C., 2011. Climate change, chytridiomycosis or condition: an experimental test of amphibian survival. *Glob. Chang. Biol.* 17, 667–675.
- Gibbons, M.M., McCarthy, T.K., 1986. The reproductive output of frogs *Rana temporaria* (L.) with particular reference to body size and age. *J. Zool.* 209, 579–593.
- Głowaciński, Z., Kaźmierczakowa., 1978. Ogólna charakterystyka przyrodnicza rezerwatu leśnego Lipówka w Puszczy Niepołomickiej. *Studia Naturae* (A), 17, 9–36.
- Głowaciński, Z., Witkowski, Z., 1970. Numbers and biomass of amphibians estimated by the capture and removal method. *Wiadom. Ekol.* 16, 328–340.
- Grant, E.H.C., Miller, D.A., Schmidt, B.R., Adams, M.J., Amburgey, S.M., Lambert, T., Cruickshank, S.S., Fisher, R.N., Green, D.M., Hossack, B.R., Johnson, P.T.J., Joseph, M.B., Rittenhouse, T.A.G., Ryan, M.E., Waddle, J.H., Walls, S.C., Bailey, L.L., Fellers, G.M., Gorman, T.A., Ray, A.M., Pilliod, D.S., Price, S.J., Saenz, D., Sadinski, W., Muths, E., 2016. Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. *Sci. Rep.* 6, 1–9.
- Heatwole, H., Wilkinson, J.W., 2019. *Amphibian Biology, Volume 11: Status of Conservation and Decline of Amphibians: Eastern Hemisphere, Part 5: Northern Europe*. Pelagic Publishing, Exeter.
- Hocking, D.J., Babbitt, K.J., 2014. Amphibian contributions to ecosystem services. *Herpetol. Conserv. Biol.* 9, 1–17.
- Holeksa, J., Kapusta, P., Budziakowska-Kubik, E., Izwska, K., Kurek, P., Piechnik, Ł., Szarek-Lukaszewska, G., Wojterska, M., Zielenka, T., Żywiec, M., 2020. Stan martwego drewna na terenie Puszczy Niepołomickiej jako wynik długotrwałego użytkowania lasu i krótkotrwałej ochrony w ramach sieci Natura 2000. *Fragm. Florist. Geobot. Pol.*, XXVII, 119–139.
- Homyack, J.A., Haas, C.A., 2009. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. *Biol. Conserv.* 142, 110–121.
- Homyack, J.A., Haas, C.A., Hopkins, W.A., 2011. Energetics of surface-active terrestrial salamanders in experimentally harvested forest. *J. Wildl. Manag.* 75, 1267–1278.
- IUCN, 2018. The IUCN Red List of Threatened Species. Version 2018-2. <http://www.iucnredlist.org>.
- Jakob, E.M., Marshall, S.D., Uetz, G.W., 1996. Estimating fitness: a comparison of body condition indices. *Oikos* 77, 61–67.
- Juszycki, W., 1987. *Plazy i gady krajowe*. Państwowe Wydawnictwo Naukowe, Warszawa.
- Lunn, D., Spiegelhalter, D., Thomas, A., Best, N., 2009. The BUGS project: Evolution, critique and future directions. *Statistics Med.* 28, 3049–3067.
- MacCracken, J.G., Stebbings, J.L., 2012. Test of a body condition index with amphibians. *J. Herpetol.* 46, 346–350.
- Mäntyniemi, S., Romakkaniemi, A., Arjas, E., 2005. Bayesian removal estimation of a population size under unequal catchability. *Can. J. Fish. Aquat. Sci.* 62, 291–300.
- Martínez-Solano, I., Bosch, J., García-París, M., 2003. Demographic trends and community stability in a montane amphibian assemblage. *Conserv. Biol.* 17, 238–244.
- McMenamin, S.K., Hadly, E.A., Wright, C.K., 2008. Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proc. Nat. Acad. Sci.* 105, 16988–16993.
- Meyer, P., Schmidt, M., 2011. Accumulation of dead wood in abandoned beech (*Fagus sylvatica* L.) forests in northwestern Germany. *For. Ecol. Manag.* 261, 342–352.
- Miaud, C., Guyétant, R., Elmberg, J., 1999. Variations in life-history traits in the common frog *Rana temporaria* (Amphibia: Anura): a literature review and new data from the French Alps. *J. Zool.* 249, 61–73.
- Naidu, R., Biswas, B., Willett, I.R., Cribb, J., Singh, B.K., Nathanail, C.P., Coulon, F., Semple, K.T., Jones, K.C., Barclay, A., Aitken, R.J., 2021. Chemical pollution: a growing peril and potential catastrophic risk to humanity. *Environ. Internat.* 156, 106616.
- Nowakowski, A.J., Thompson, M.E., Donnelly, M.A., Todd, B.D., 2017. Amphibian sensitivity to habitat modification is associated with population trends and species traits. *Glob. Ecol. Biogeogr.* 26, 700–712.
- Nyström, P., Hansson, J., Månsson, J., Sundstedt, M., Reslow, C., Broström, A., 2007. A documented amphibian decline over 40 years: possible causes and implications for species recovery. *Biol. Conserv.* 138, 399–411.
- Otto, C.R., Kroll, A.J., McKenny, H.C., 2013. Amphibian response to downed wood retention in managed forests: a prospectus for future biomass harvest in North America. *Forest Ecol. Manag.* 304, 275–285.
- Pabijan, M., Ogińska, M., 2019. Conservation and declines of amphibians in Poland, in: Heatwole, H., Wilkinson, J.W., (Eds.), *Amphibian Biology, vol. 11: Status of Conservation and Decline of Amphibians: Eastern Hemisphere, Part 5: Northern Europe*, p. 26–45. Pelagic Publishing, Exeter.
- Pabijan, M., Palomar, G., Antunes, B., Antol, W., Zieliński, P., Babik, W., 2020. Evolutionary principles guiding amphibian conservation. *Evol. Appl.* 13, 857–878.
- Paillet, Y., Bergès, L., Hjaltn, J., Odor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., de Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastián, M.-T., Schmidt, W., Standová, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol.* 24, 101–112.
- Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., 2015. Quantifying the recovery of old-growth attributes in forest reserves: a first reference for France. *Forest Ecol. Manag.* 346, 51–64.
- Palomar, G., Jakóbk, J., Bosch, J., Kolenda, K., Kaczmarek, M., Joško, P., Rocas-Díaz, J. V., Stachyra, P., Thumsová, B., Zieliński, P., Pabijan, M., 2021. Emerging infectious diseases of amphibians in Poland: distribution and environmental drivers. *Dis. Aquat. Org.* 147, 1–12.
- Pechmann, J.H., Scott, D.E., Semlitsch, R.D., Caldwell, J.P., Vitt, L.J., Gibbons, J.W., 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253, 892–895.
- Peig, J., Green, A.J., 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118, 1883–1891.

- Pikulik, M.M., Sidorovich, V.E., Jędrzejewska, B., Jędrzejewski, W., 2001. Summer abundance and habitat distribution of frogs (*Rana temporaria*, *R. arvalis*, *R. kl. esculenta*) and toads (*Bufo bufo*) in the Białowieża Primeval Forest, E Poland. *Folia Zool.* 50, 65–73.
- Ponsoero, A., Joly, P., 1998. Clutch size, egg survival and migration distance in the agile frog (*Rana dalmatina*) in a floodplain. *Arch. Hydrobiol.* 142, 343–352.
- Rittenhouse, T.A., Harper, E.B., Rehard, L.R., Semlitsch, R.D., 2008. The role of microhabitats in the desiccation and survival of anurans in recently harvested oak–hickory forest. *Copeia* 2008, 807–814.
- Ruthsatz, K., Dausmann, K.H., Paesler, K., Babos, P., Sabatino, N.M., Peck, M.A., Glos, J., 2020. Shifts in sensitivity of amphibian metamorphosis to endocrine disruption: the common frog (*Rana temporaria*) as a case study. *Conserv. Physiol.* 8 (1), coaa100.
- Schmidt, B.R., Pellet, J., 2010. Quantifying abundance: counts, detection probabilities, and estimates. In: Dodd, C.K. (Ed.), *AmphibiAn Ecology And Conservation: A Handbook of Techniques*. Oxford University Press, Oxford, pp. 465–479.
- Scott, D.E., Casey, E.D., Donovan, M.F., Lynch, T.K., 2007. Amphibian lipid levels at metamorphosis correlate to post-metamorphic terrestrial survival. *Oecologia* 153, 521–532.
- Selva, N., Chylarecki, P., Jonsson, B.G., Ibsch, P.L., 2020. Misguided forest action in EU Biodiversity Strategy. *Science* 368, 1438–1439.
- Skelly, D.K., Werner, E.E., Cortwright, S.A., 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. *Ecology* 80, 2326–2337.
- Thompson, M.E., Donnelly, M.A., 2018. Effects of secondary forest succession on amphibians and reptiles: a review and meta-analysis. *Copeia* 106, 10–19.
- Todd, B.D., Rothermel, B.B., 2006. Assessing quality of clearcut habitats for amphibians: effects on abundances versus vital rates in the southern toad (*Bufo terrestris*). *Biol. Conserv.* 133, 178–185.
- Vági, B., Kovács, T., Băncilă, R., Hartel, T., Anthony, B.P., 2013. A landscape-level study on the breeding site characteristics of ten amphibian species in Central Europe. *Amphibia-Reptilia* 34, 63–73.
- Van Buskirk, J., 2003. Habitat partitioning in European and North American pond-breeding frogs and toads. *Divers. Distrib.* 9, 399–410.
- Van Buskirk, J., 2005. Local and landscape influence on amphibian occurrence and abundance. *Ecology* 86 (7), 1936–1947.
- Vandekerckhove, K., De Keersmaecker, L., Menke, N., Meyer, P., Verschelde, P., 2009. When nature takes over from man: Dead wood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. *For. Ecol. Manag.* 258, 425–435.
- Veysey Powell, J.S., Babbitt, K.J., 2015. Despite buffers, experimental forest clearcuts impact amphibian body size and biomass. *PLoS One* 10 (11), e0143505.
- Vié, J.-C., Hilton-Taylor, C., Stuart, S.N., 2009. *Wildlife in a Changing World – An Analysis of the 2008 IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland.
- Wake, D.B., Vredenburg, V.T., 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proc. Nat. Acad. Sci.* 105, 11466–11473.
- Weiner, J., Fredro-Boniecki, S., Reed, D., Maclean, A., Strong, M., 1997. Niepołomice Forest—a GIS analysis of ecosystem response to industrial pollution. *Environ. Poll.* 98, 381–388.
- Węzyk, P., Matyja, W., 2007. Określenie dynamiki zmian w Puszczy Niepołomickiej na podstawie ortofotomapy wygenerowanej z archiwalnych zdjęć lotniczych z 1949 roku. *Archiwum Fotogrametrii, Kartografii i Teledetekcji* 17b, 801–809.
- White, G.C., Anderson, D.R., Burnham K.P., Otis D.L., 1982. *Capture-recapture and removal methods for sampling closed populations*. Los Alamos National Laboratory, New Mexico.
- Wolski, J., 2002. Measurements of downed deadwood in the forest – theoretical assumptions and course of field works. *Prace Inst. Bad. Leś A.* 2, 27–45.