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**ORIGINAL RESEARCH PAPER** 

# Stress or help, how does the grey heron Ardea cinerea L. modify the vegetation structure of the forest floor?

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## **Abstract**

The grey heron (Ardea cinerea) is a good example of an engineering species that forms nesting colonies (called heronries) composed of up to a few hundred nests during the breeding season. It exerts strong pressure on surrounding vegetation, mainly because of the heavy input of organic matter and high eutrophication. The birds also alter light conditions through direct tree damage. We aimed to examine the influence of a grey heron breeding colony on the soil properties and functional composition of the herb layer in two different forest communities: a suboceanic pine forest and a riparian mixed forest. We also wanted to establish whether these changes would make the forest ecosystem more vulnerable to colonization by nonforest species with higher light and trophic demands. Small-seeded, light demanding eutrophic species showed a tendency to be more abundant under the nests in both forest types. The calculated odds ratio (OR) showed that the probability of the presence of nonforest species under the nests was 29.5 times higher than that in the control plots (56 plants species were analyzed). Additionally, the nonforest species appeared to have high light and trophic demand (OR of 12.3 for light demand; OR of 7.0 for trophic demand), which explains the species turnover observed in the bird-affected microhabitats.

# Keywords

engineering species; vegetation transformation; ruderal species; pine forest; riparian forest; soil properties

# Introduction

The term "ecosystem engineers" was first used in ecology by Jones et al. [1,2]. As defined by the authors, an ecosystem engineer is an organism that indirectly changes the availability of resources for other organisms through physical modifications of the habitat [1]. Most, if not all, ecosystems owe their structure to the engineering activity of living organisms, although this activity might be easy to overlook because of its indirect nature. While most organisms influence the abiotic conditions of their environment in some way, the scale of the impact depends on many factors, including the qualities of both the engineering species and the modified ecosystem [1-3].

The grey heron (*Ardea cinerea* L.) can be considered one such engineering species. During the breeding season, it forms nesting colonies (called heronries) with a maximum of several hundred nests, with high density of individuals [4]. The presence of a heronry exerts strong pressure on the surrounding vegetation, mainly because of the heavy input of organic matter (feces, pellets, feathers, dropped or regurgitated food,

fallen nests with a large amount of nestling feces, bodies of dead individuals, etc.) into the soil, causing high salinity and eutrophication [5]. It also creates an ecosystem with patchy distribution of soil nutrients (higher concentrations directly underneath the nests than in their proximity), which in turn can influence the competitive interactions between plants and modify the floristic composition of the site [6]. Mun [5] reported increased levels of nitrogen, phosphorus, sulfur, magnesium, and calcium in the soil under a heronry located in a pine forest compared to the control site. Changes in soil pH are also often reported in heronries: some scientists have observed an increase [5] while others have detected a decline [7] in acidity. Changes in soil properties by deposition of guano and direct damage generate stressful conditions for trees (definition of stress according to Grime [8]) and often increases their mortality [5,7,9–11]. Topsoil properties and light conditions become highly variable in the microscale, which provides specific regeneration niches for many plant species and communities [11]. In the herb layer, increased colonization by ruderal and heliophilous plants accompanied by withdrawal of forest species is often reported [5,12].

In this study, we aimed to examine the influence of a grey heron breeding colony on the soil properties and functional composition of vegetation in two different forest communities: an oligotrophic pine forest and a riparian mixed forest. Based on the earlier studies [5,12], we hypothesized that the pattern of vegetation changes generated by engineering species directly (availability of soil nutrients) and indirectly (light availability) depends strongly on the type of ecosystem influenced. We also wanted to establish whether these changes would make different forest ecosystems more vulnerable to colonization by nonforest species with higher light and trophic demand. We hypothesized that species that are not usually present in undisturbed forest habitats have a higher chance of colonizing the heronry site if they are capable of long seed dispersal; therefore, the adaptation for seed dispersal was also considered.

# Material and methods

### Study site

The influence of a grey heron breeding colony on the soil properties and functional composition of vegetation was studied in two different forest communities: a suboceanic pine forest Leucobryo-Pinetum W. Mat. (1963) W. Mat. Et. J. Mat. 1973, hereafter called pine forest, and a degenerated form of riparian forest Ficario-Ulmetum minoris Knap 1942 em. J. Mat. 1976 (classification according to Matuszkiewicz [13]). Both are located in eastern Poland in close vicinity of river valleys (the Wieprz River for the pine forest and the Bug River for the riparian forest), which serve as foraging sites for the birds. The pine forest is located in the southern part of Lubartów Heights (Wysoczyzna Lubartowska) (51°33.371′ N, 22°21.448′ E) and the riparian mixed forest is situated in Dubienka Depression (Obniżenie Dubienki) (51°21.806′N, 23°36.815′E); the mesoregions follow the physico-geographical regionalization by Kondracki [14], revised by Solon et. al. [15]. The colonies identified within the forests had approximately 70 and 90 nests (the approximate area of the colonies was 12,000 m<sup>2</sup> and 6,000 m<sup>2</sup>, respectively). It is difficult to estimate the date of establishment of both colonies. We were informed that the heronry in the pine forest was noted in 1993 (23 nests were observed; Wójciak, unpublished data), while 21 and 93 nests were found in 1998 and 2002, respectively [4]. The earliest unpublished data from the second habitat (riparian forest) dates from 1969 (20 nests), and over 100 nests were observed there in 2002 [4].

# Field study

In both plant communities, we examined two types of microhabitats: a heronry (nesting site) and a control site. In each of the microhabitats, we established three rectangular research plots with an area of  $30 \text{ m}^2$  ( $3 \times 10 \text{ m}$  each; two types of plant community × two types of microhabitats × three replicates in each microhabitat type). The observations were conducted in 2015 and 2016. Soil samples for estimation of the content of nitrate,

ammonium ions, phosphorus, organic carbon and  $CaCO_3$ , soil pH, and granulometric group were collected in March 2016. Using a Kopecky cylinder, we collected 10 soil samples of 100-mL volume from each study plot, which were mixed and treated as one sample in further analysis. The dates of sample collection depended on the volatility of analyzed forms of the nitrogen in the soil, which necessitates sampling immediately after soil thawing before the beginning of the vegetation period [16]. After collection, the soil samples for nitrogen content analysis were tightly closed in plastic bags and stored at the temperature of  $4^{\circ}C$  until further analyses.

The structure of vegetation in each study plot was examined twice in July 2015 and 2016. The number of species and their estimated cover in all the forest layers was recorded (11-grade scale with 0.5 for sporadic species, 1 – for species with cover lower than 10%, 2 – for cover 10-20%, ..., 10-90-100%). Qualitative and quantitative characteristics of vegetation enabled us to define two group of species for log-linear analysis: species present in the breeding sites and species present in the control plots (Tab. S1).

# Laboratory analysis

The acidity of the soil samples was measured in distilled water using the potentiometric method. The content of  $CaCO_3$  in the examined soil samples was analyzed using Scheibler's volumetric method. In order to obtain better characteristics of the examined soils, their texture (percentage of sand, silt, and clay) was estimated using the Casagrande method with Prószyński's modification [17]. Nitrogen forms  $N-NH_4$  and  $N-NO_3$  were extracted with 1 M KCl and analyzed with the method of continuous flow analysis (CFA) with spectrophotometric detection [18,19].

# Data analysis

Plant functional traits are easily measured morphological or physiological plant features that can help to predict the responses of a group of plants to environmental changes [20,21]. The following plant traits and species characteristics were taken into consideration during statistical analysis (Tab. S1): seed size (small seeds were diaspores with dry weight lower than 3 mg, seed size data were taken from LEDA [22] and SID databases [23]), capability of long seed dispersal (seeds regarded as capable of long dispersal were wind-dispersed, epi- and endozoochorous seeds), seed dispersal mode according to [23–25], trophy and light requirements (simplified into two categories), and ecological groups according to [26]. The seed size was examined as an indicator of light requirement for germination [27,28], i.e., another life history trait characteristic for species with ruderal life strategies.

Assumptions for parametric tests were checked for a the dataset with tools offered by STATISTICA 12 software (normal probability plot followed by the Shapiro–Wilk test for normality of distribution, Levene's test for equity of variances with mean values vs. standard deviation plot). It appeared that the distribution was skewed only in the case of two variables, therefore appropriate transformations to improve symmetry were used. Statistical significance of differences between mean values was tested with a two-way ANOVA along with the post hoc Tukey test using STATISTICA 12 software with the  $\omega^2$  factor calculated additionally [29,30]. Two factors in two variants each were included into the analysis: habitat (nesting site vs. control plot) and community (pine forest vs. riparian forest). To investigate the plant life history traits that may influence its chance of establishing in the nesting site vs. the control site, log-line analysis was performed with calculation of an odd ratio (input data Tab. S1 [30]).

Detrended correspondence analysis (DCA) based on the species list with corresponding species cover was conducted to determine the main patterns of species turnover in the two different forest communities under the stress generated by colonial bird nesting (MVSP version 3.21 [31]). To analyze the main patterns in the vegetation structure turnover, Spearman rank correlation coefficients were calculated for vegetation variables and coordinated in a DCA diagram [30].

#### Results

# Soil conditions

Some soil properties are evidently bird-independent, i.e., the percent share of the three analyzed soil fractions and consequently granulometric groups, the content of organic C, and, surprisingly, the H–NH<sub>4</sub> content (Tab. 1, Fig. 1). The granulometric group was established as loose sand in the pine forest and sandy clay loam in the riparian mixed forest. The variable community explains almost 100% of the observed variation of the percentage of all soil fractions and 78% of the observed variability of the  $C_{\rm org}$  content ( $\omega^2$  value; Tab. 1).

The most striking impact of the presence of nesting birds was the significant increase in the  $N-NO_3$  content (63.8% of variability explained by the variable habitat) as well as the  $CaCO_3$  content, but only in the riparian forest (Tab. 1, Fig. 1). In terms of acidity, the presence of the heronry seemed to affect both types of forest communities differently. The acidity of soil in the nesting sites decreased in the pine forest slightly, albeit insignificantly, whereas a significant increase was observed in the riparian forest. The significant interaction of both studied variables (habitat type and plant community type) in the case of acidity indicates that the effect and the trend in the changes depend strongly on the community type (Fig. 1, Tab. 1). There were no differences in the P content (Fig. 1).

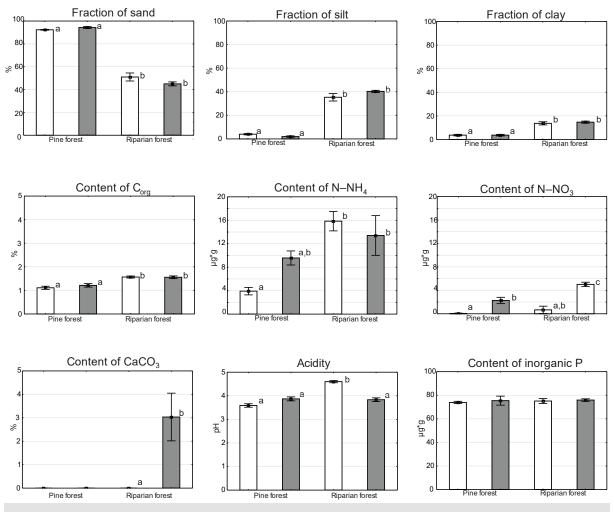
# Vegetation data

The presence of the nesting grey heron had an influence upon the vertical forest structure: it caused a decrease in the tree cover in both communities (Fig. 2, Tab. 2), yet it was only statistically significant in the riparian forest ( $\omega^2$  = 44% for the habitat type). As for the cover of the shrub layer, the effect of the heronry differed between both examined communities; we observed significant fruticetization in the riparian forest, whilst the shrub cover decreased in the pine forest (the interaction between the habitat and community explained 67.8% of the observed variation; Fig. 2, Tab. 2). The herb layer cover and the mean number of species in this layer were not altered (Fig. 2, Tab. 2). A consequence of the higher light availability under the heronries (nesting sites) was the higher number of small-seeded species, which are usually photoblastic (see [15,16]) in the pine forest, as well as light demanding taxa (both communities, Fig. 2, Tab. 2). Although the increase in the number of eutrophic species was observed in both communities, the differences between the control plots and nesting sites were

Tab. 1 Results of two-way ANOVA (habitat: nesting site vs. control site; community: pine forest vs. riparian forest).

Soil variable Sand fraction (%)		Indepen $F(1, 3)$	Interaction Habitat ×  Community $F(1, 8); \omega^2(\%)$			
	Habitat				Community	
	0.986 <sup>NS</sup>	-	13.712**	97.1	3.945 <sup>NS</sup>	-
Silt fraction (%)	0.779 <sup>NS</sup>	-	420.010***	96.5	4.240 NS	-
Clay fraction (%)	0.290 <sup>NS</sup>	-	128.033***	92.3	0.290 <sup>NS</sup>	-
C <sub>org</sub> (%)	0.573 <sup>NS</sup>	-	42.105***	78.0	0.845 <sup>NS</sup>	-
$N-NH_4^+$ (µg g <sup>-1</sup> )	0.643 <sup>NS</sup>	-	15.469**	49.6	4.083 <sup>NS</sup>	-
$N-NO_3^- (\mu g g^{-1})$	52.578***	63.8	13.712***	15.7	5.553*	5.6
CaCO <sub>3</sub> (%)	8.895*	56.8	-	-	-	-
Acidity (pH value)	11.446***	8.8	45.742***	37.6	58.895***	43.6
P (μg g <sup>-1</sup> )	0.262 NS	-	0.137 <sup>NS</sup>	-	0.025 NS	-

*p* value: \*\*\* <0.001; \*\* <0.01; \*<0.05; NS – nonsignificant differences;  $\omega^2$  values were calculated for significant test results. For CaCO<sub>3</sub>, differences were tested only in the riparian forest (nesting site vs. control site)



**Fig. 1** Mean values ( $\pm$  standard error) of edaphic parameters of the control plot (N = 3; white bars) and the nesting site (N = 3; grey bars). Two-way ANOVA was performed (Tab. 1) with the Tukey post hoc test; mean values with different letters are statistically different.

not statistically significant (Fig. 2). There were no significant differences in long-distance dispersed species either (Fig. 2, Tab. 2).

The habitat conditions changed by the birds triggered qualitative alteration in the plant species structure (Tab. 2). The number of ruderals increased in the nesting sites, which was especially evident in the riparian forest (Fig. 2, Fig. 3), and the number of meadow species increased in the pine forest, but the difference was not statistically significant (Fig. 2). A significant decrease in the number of pine forest species was observed in the pine forest community as well as tendency towards a decline in the number of broadleaved forest species (Fig. 2). The log-linear analysis of the presence in the nesting site as an explained variable suggests a significant relationship between the presence of the species under the nests and the ecological group they represent (nonforest versus forest species, model fitness for 56 species;  $\chi^2 = 7.667$ , df = 12, p = 0.811). The calculated odd ratio (OR) shows that the probability of the presence of nonforest species under the nests is 29.5 times higher than in the control plots. Additionally, nonforest species are usually high light and high trophy demanding (56 species, model fitness  $\chi^2 = 15.928$ , df = 26, p = 0.938; OR for light demand is 12.3, for high trophy is 7.0), which explains the species turnover observed in the bird-affected microhabitats.

### Discussion

The impact of engineering birds, especially big colonial predators, on occupied ecosystems has been widely recognized in the literature [5,7,9,32–38]. The grey heron possesses

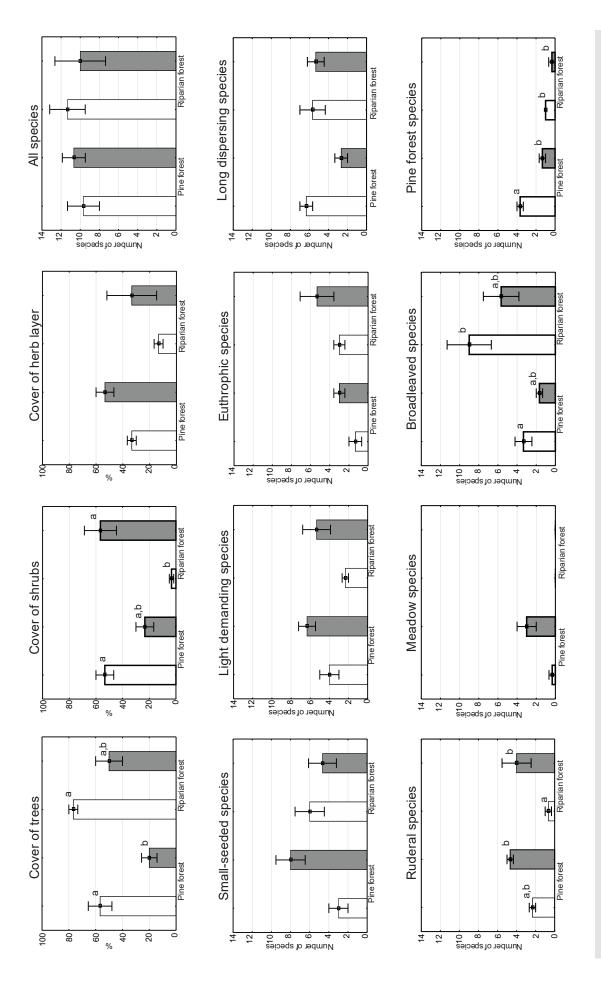


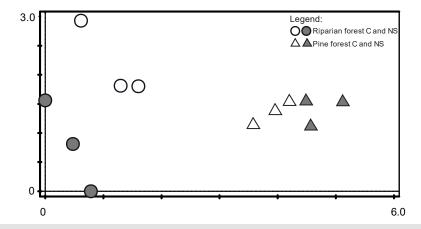
Fig. 2 Mean values ( $\pm$  standard error) of vegetation characteristics of the control plot (N = 3; white bars) and the nesting site (N = 3; grey bars). Two-way ANOVA was performed (Tab. 2) with the Tukey post hoc test; mean values with different letters are statistically different.

Tab. 2 Results of two-way ANOVA (habitat: nesting site vs. control site; community: pine forest vs. riparian forest).

		Independ <i>F</i> (1, 8	Interaction Habitat × Community $F(1, 8); \omega^2(\%)$									
Vegetation variable	Habitat				Community							
Cover (%)												
Trees	18.050**	44.0	11.250*	26.4	0.450 <sup>NS</sup>	-						
Shrubs	2.306 NS	-	1.176 NS	-	29.412***	67.8						
Herb layer	3.892 NS	-	3.892 <sup>NS</sup>	-	0.000	-						
		Num	ber of species									
Total number	0.008 NS	-	0.068 NS	-	0.037 <sup>NS</sup>	-						
Small seeded	1.728 <sup>NS</sup>	-	0.014 <sup>NS</sup>	-	5.157 NS	-						
Eutrophic	3.789 <sup>NS</sup>	-	3.789 <sup>NS</sup>	-	0.105 <sup>NS</sup>	-						
Light demanding	7.111*	33.9	1.778 NS	-	0.111 <sup>NS</sup>	-						
Long dispersing <sup>a</sup>	4.214 <sup>NS</sup>	-	0.783 <sup>NS</sup>	-	2.106 NS	-						
	I	Ecological gro	up (number of spec	cies)								
Broadleaf forest species	2.586 NS	-	9.667*	40.2	0.287 <sup>NS</sup>	-						
Pine forest species <sup>b</sup>	21.242**	31.3	32.063***	48.0	2.398 <sup>NS</sup>	-						
Ruderal species	12.042**	47.1	2.042 <sup>NS</sup>	-	0.375 <sup>NS</sup>	-						
Meadow species <sup>c</sup>	U = 0.00 NS	-	-	-	-	-						

p value: \*\*\* <0.001; \*\* <0.01; \* <0.05; NS – nonsignificant differences;  $\omega^2$  values were calculated for significant test results.

<sup>&</sup>lt;sup>c</sup> Significance tested with nonparametric *U* Mann–Whitney test (nesting site vs. control site).



**Fig. 3** Results of detrended correspondence analysis (DCA). White symbols – control plots (C); grey symbols – nesting sites (NS). Eigenvalues: Axis 1 – 0.821; Axis 2 – 0.455. Cumulative explained variation: Axis 1 – 20.74; Axis 2 – 32.25. Gradient length: Axis 1 – 5.11; Axis 2 – 2.93. Statistically significant Spearman rank correlation coefficients with Axis 1: cover of the herb layer ( $S_r = 0.582$ , p = 0.047); number of forest species  $S_r = -0.624$ , p = 0.030); with Axis 2: cover of the herb layer ( $S_r = -0.635$ , p = 0.027); number of nonforest species ( $S_r = -0.625$ ,  $S_r = 0.029$ ).

many features that help to predict if its engineering influence on the environment might be significant (as defined by Moore [3]): its body size is relatively big (length 85–100 cm, weight 1–2.3 kg, and wingspread approximately 155–195 cm) [39]; the birds appear abundantly during the breeding season [4] and their grouping can be regarded to have a weak cooperative tendency [7,40–42]. The distance from a heronry to the food source can sometimes be approximately 40 km [43]; therefore, during the breeding period, the

<sup>&</sup>lt;sup>a</sup> Transformation  $Y' = Y^2$ , recommended for left-skewed data.

<sup>&</sup>lt;sup>b</sup> Transformation  $Y' = \sqrt{(Y + 0.5)}$ , recommended for right-skewed abundance data.

grey heron population is provided with energy and matter from outside the modified ecosystem. However, the scale of the influence on the modified ecosystem depends not only on the characteristic of the engineering species, but also on the properties of the ecosystem itself, and may differ depending on such qualities as the initial fertility of the habitat [3,36,37]. This study compared the ecosystem transformations induced by the breeding colony of the grey heron in two differing phytocoenoses: a mesotrophic riparian forest, whose canopy comprises various broadleaved tree species (Fraxinus excelsior L., Ulmus minor Mill., and Quercus robur L., amongst many others), and an oligotrophic coniferous suboceanic pine forest [44]. The study showed that some patterns of soil modification were similar in both communities, such as the increase in nitrates resulting from the heavy input of leftover food and feces from the breeding colony [5]. Other effects seemed to be dependent on the environmental context, for example, soil active pH increased slightly under the breeding colony in the pine forest but decreased significantly in the riparian forest. Given the logarithmic nature of the pH scale, this difference can likely be explained by the varying initial level of pH in both communities. In the less acidic soils of the riparian forest, the heavy input of acidic feces might have caused a sharp decrease in soil pH in the vicinity of the nests, while the same amount of additional protons in the already highly acidic soils of the pine forest would not have induced the same change in the pH value. The varying influence of the grey heron colony on the soil pH depending on the initial features of the habitat might explain the differing results of this parameter obtained by other researchers [5,7]. The present study does not report an increase in the phosphorus or organic matter content under the heronry compared to that of the control sites, in contrast to Mun's results, where a twofold increase in soil organic matter and a nearly 32-fold increase in total phosphorus were observed [5].

The presence of the heronry decreased the tree cover in both examined communities, although the decrease was statistically significant only in the case of the pine forest. This is a good example of a strong impact of a favored and protected species on other coexisting species. Fedriani et al. [10] described such a strong conservation conflict "birds vs. oaks" in Doñana National Park (Spain), where temporally persistent habitat modification caused by the grey heron significantly decreased the vigor of *Quercus suber* individuals.

In our study, the shrub layer responded to the heron-generated stress differently in both examined communities: we observed a decrease in its cover in the heronry of the pine forest and a sharp increase in the riparian forest. This could possibly be explained by the different initial canopy densities in the two phytocoenoses. In the riparian forest, the initial dense cover of the tree layer may have inhibited the germination of shrub seeds and/or the growth of their seedlings and saplings, leading to accumulation thereof as a seedling/sapling bank. The change in the light regimes caused by the heronry was then quickly utilized by the shrub species, causing rapid fruticetization [44]. Compared to the riparian forest, in the pine forest, when the tree layer ensured additional light, the shrub layer was more abundant in the control sites. In conditions of sparser tree cover, the shrub layer is more likely to suffer (similarly to the tree layer), than benefit from the presence of the grey heron breeding colony, as the significant amount of feces fall on their leaves and the local accumulation of nutrients in soil might reach toxic levels more quickly in the absence of strong competitors (broadleaved trees).

In the case of the herb layer, which is regarded as to be the most sensitive indicator of community disturbance and stress, neither the total cover nor the number of species changed significantly in the heronry vs. the control sites. However, there was a statistically important shift in the composition of plant functional groups in both communities. The overall differences in the herb layer structure between the breeding and control site turned out to be bigger in the riparian forest, where the initial accumulation of nutrients was higher than in the pine forest, as indicated by the DCA diagram (Fig. 3). Again, some of the effects observed were common for both types of the forests, while others seemed to be community specific. In both types of communities, the increase in soil nitrates enhanced the percent share of eutrophic and ruderal species. Recent studies on seed germination suggest that the nitrate content may not only facilitate the growth of these species but also serve as a germination cue for many species with a ruderal life strategy [45]. Further studies on the soil seed bank are required to confirm whether the increase in such species abundance in the herb layer is caused by

their increased germination from the soil or by facilitation of their colonization from outside the ecosystem. In the pine forest, eutrophication of the soil additionally caused withdrawal of the native pine forest species, which are typically oligotrophic [5,44]. This effect was not observed in the riparian forest owing to the low initial number of such species. The abundance of broadleaved forest species seemed to be affected mainly by the type of community rather than the presence of the heronry, which caused only a slight decrease in the number of these species in the breeding sites compared to the control (Fig. 2).

Another aspect of grey heron activity that can influence the vegetation structure is worth mentioning as well. Waterbirds, including the grey heron, are important long-distance dispersal vectors for many plant species [46]. They provide connectivity of metacommunities in a patchy landscape and enhance the possibility of colonizing new areas, also for alien and invasive species [47–49]. Even carnivorous birds may significantly contribute to transportation of diaspores via ingesting prey that are carrying seeds by endo- or epizoochory. Such secondary dispersal pathways are currently being recognized in the literature [47,48]. Besides fish, grey heron may forage upon small mammals and therefore act as a secondary disperser for terrestrial, ruderal plant species [50]. *Urtica dioica* and *Betula pendula* seeds have been found in the pellets of great cormorants, *Phalacrocorax carbo* L. [47], while the lesser-black backed gull, *Larus fuscus* L., is said to be dispersal vector for *Juncus bufonius* L. [48]. The viability of diasporas dispersed by the grey heron might be limited in comparison to seeds transported by other waterbirds because of the extremely efficient digestive system of the former [50].

We also asked whether the presence of the heronry enhanced the possibility of the colonization by far-dispersing species, which we expected would accumulate a higher amount of seeds in soil waiting for gaps in the forest floor to enable them to germinate. A potential source of these seeds is the agricultural landscape surrounding the studied forest patches. This study did not confirm this hypothesis, as the percent share of long-distance dispersing species within the herb layer was similar both in the heronry and in the control site and even lower than in the control in the pine forest heronry. The cause of this decrease is unknown; perhaps the presence of the heronry and the resulting degradation of the tree and shrub layer caused a decline in the populations of frugivorous bird species and therefore reduce the number of zoochorous plants within the herb layer. This possible explanation, however, cannot be confirmed by the present data. It also cannot be ruled out that this effect was caused by a factor other than the habitat and community type, which was not analyzed in this study.

# Conclusions

The study showed the influence of a breeding colony of the grey heron on the edaphic conditions and plant cover structure of two different forest communities: a pine forest and a riparian forest. Some of the observed patterns of ecosystem modification were common, while others (like soil pH) appeared to be community specific. In both examined forests, the presence of the heronry caused a significant increase in nitrates in soil and a concomitant shift in the composition of plant functional groups in the herb layer (an increase in the number of eutrophic and ruderal species, and in the case of the pine forest, a decrease in native pine forest oligotrophic species). The examined communities differed in their response to the heronry-caused disturbance in terms of the vertical structure of the phytocoenosis and its penetrability by light. In the pine forest, the presence of the breeding site caused a decrease in the plant cover of both tree and shrub layers, which in turn resulted in the improvement of the light regime in the forest floor. In the case of the riparian forest, the decrease in the plant cover caused by the breeding site was compensated by an increase in shrub abundance; therefore, the light factor did not change the composition of plant functional groups in the herb layer.

Overall, from all the tested plant functional groups, the presence of ruderal species seems to be the most universal indicator of heronry-generated disturbance. The insignificant increase in the plant functional groups related to favorable light-regimes (photoblastic, light-demanding, and meadow species) was noted only in the case of the pine forest, where the canopy is relatively permissive to light compared to the canopy

of deciduous forests. In contrast to what we expected, the presence of the grey heron breeding site did not enhance colonization of the site by far-dispersing species. We also did not observe an increase in total phosphorus or soil organic matter in the soil under the nesting sites compared to the control sites, which is sometimes reported by other authors [5].

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### Supplementary material

The following supplementary material for this article is available at http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/asbp.3625/0:

**Tab. S1** Species structure of the herb layer in the studied sites.

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