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Size Matters: Diversity and Abundance of Small Mammal Community Varies with the Size of Great Cormorant Colony

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Abstract: Cormorant colonies are often viewed negatively by fishermen and foresters due to their extremely high impact on aquatic and terrestrial ecosystems. In forests, the habitats of nesting territories are destroyed, with concomitant impacts on the animal communities. In 2011–2022, investigating three colonies of Great Cormorants (*Phalacrocorax carbo*), we aimed to test whether their effect on small mammals depends on colony size. In the largest colony in Lithuania, a low species richness, lower diversity and relative abundance, as well as poorer body conditions of the most abundant species was found in the nesting zone. However, once the cormorants left the nesting site, all the parameters recovered. Two small colonies had a positive impact, with higher species richness in the territory of the colony (seven and ten species), diversity (H = 1.56 and 1.49), and relative abundance (27.00 ± 2.32 and 25.29 ± 2.91 ind. per 100 trap days) compared with the control habitat (three and eight species; H = 1.65 and 0.99; 12.58 ± 1.54 and 8.29 ± 1.05 ind./100 trap-days). We conclude that up to a certain colony size, cormorant pressure is a driver of habitat succession and has similar effects on the small mammal community as other successions in disturbed habitats.

Keywords: *Phalacrocorax carbo*; small mammals; relative abundance; body condition; diversity; habitat succession

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1. Introduction

Colonies of Great Cormorants (*Phalacrocorax carbo*) are one of the strongest natural environmental drivers, changing habitats in their colonies [1–3]. Cormorants are specialised piscivorous birds, which transport huge amounts of nutrients to a relatively small colony area [3–6]. The daily food requirement of adults is 300–600 g of fish per day when feeding chicks, producing considerable effects on fish populations [6–8]. One bird sheds 20–50 g of faeces per day, and about 80% of the faeces are deposited in the area of the breeding colony [2].

Fecal wastes of the colonial piscivorous birds overload the ecosystem with nitrogen and phosphorus [9,10], ammonia [11], and other chemical elements, including heavy metals [12,13]. Soil under cormorant colonies is more acidic [14]. Chemical loads negatively affect tree health [14], reduce canopy cover [15], and reduce the diversity of tree seedlings [16]. Cormorants' impact on the environment results in a huge ecosystem transformation in a very short time [2]. The effects of transported substances on vegetation changes remain even 60 years after the colony has left [1,17].

In the largest colony of Great Cormorants in Lithuania, situated near the Juodkrantė settlement in the western part of Lithuania, changes in the vegetation occurred in the years following the colony's establishment. Ten years later, all the pine trees in the colony had died, and plant species characteristic of the coniferous forest ecosystem had disappeared [18]. The active part of the colony (that is, area of the colony containing occupied nests) was characterized by the lowest abundance of myxomycete species [19] and the lowest number of lichen species [20]. The other cormorant colonies showed altered soil microbial communities and soil and litter fauna structures [21]. Significant impacts on arthropods have been observed [22–24].

Nest density and subsequent fecal deposition are the most important factors influencing changes in plant biodiversity and abundance [2] and the resulting changes in animal communities. Many studies have analyzed the impact of cormorant colonies, but rarely took into account the size of the colony. Cormorant numbers in Europe were constantly increasing from 1980 to the mid-2000s, however, currently "population in Europe is clearly levelling off and in some regions even declining. This is due to the combined effects of environmental factors", as said in Open letter to the Members of European Parliament about the initiative report (2021/2189(INI)), and in particular its paragraph 56 on cormorant management (2022). Cormorant colonies are characterized by very different numbers of breeding pairs [25]. Sizes range from very small colonies—e.g., in Austria, three colonies counted only 65 breeding pairs [26]—to very large colonies. The colony in Kąty Rybackie (Poland) has up to 11,000 breeding pairs [27]. An analysis of national reports from 23 European countries found that the average colony size in 2012 was 250 breeding pairs. There were 37 colonies larger than 1000 breeding pairs (less than 5% of the total surveyed) [28]. In Lithuania, cormorant colonies have been growing rapidly, passing the 500-nest mark in 1995, 1000 nests in 1999, and 2000 nests in 2003. In 2016, there were seven cormorant colonies in Lithuania with approximately 5600 occupied nests. The largest cormorant colony had 60–80% of the country's breeding population [29]. In 2022, the number of the occupied nests was over 9000, out of this number about 4000 were in the biggest colony in Juodkrantė [30].

In the forests, changes in vegetation structure, tree canopy, or forest understory composition have an impact on small mammal communities [31–34]. In our previous studies, we have found that cormorant colonies influence changes in small mammal communities, including species richness and diversity [35], the demographic parameters of dominant species and the body condition of individuals [36], and even morphological traits [37].

However, these studies did not take into account temporal variations and differences in the size of the Great Cormorant colonies studied. The aim of this study was to test whether changes in small mammal communities depend on the size of the cormorant colony and whether these changes are stable in time.

2. Materials and Methods

2.1. Study Sites

The study was carried out in three Great Cormorant colonies: the Juodkrantė cormorant colony, situated in western Lithuania, in 2011–2022; the Lukštas in eastern Lithuania, in 2014–2022; and the Naudžiūnai in southern Lithuania, in 2016–2022 (Figure 1).

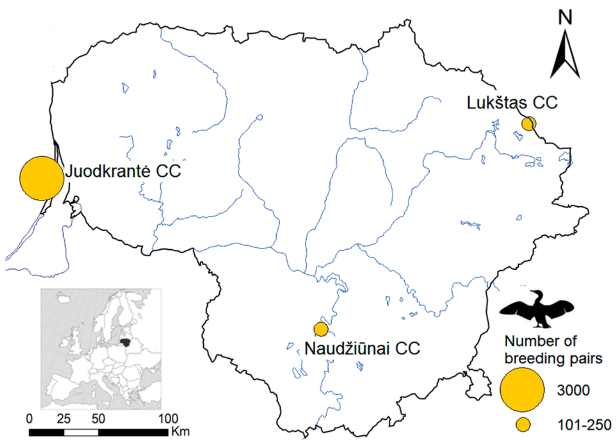

Figure 1. Investigation sites, referred as CC—cormorant colony, with main rivers and lakes shown in blue. Based on free map from https://d-maps.com/carte.php?num_car=2367&lang=en (accessed 4 January 2023); bird silhouette from https://www.behance.net/gallery/28579883/Cormorant-an-open-source-display-font-family (accessed 4 January 2023).

In Juodkrantė, Great Cormorants settled in 1989, in Naudžiūnai—in 1999. The exact date of the cormorant's appearance in Lukštas is not known because colony is remote. As the colony can already be identified on the orthophoto map of 1995–1999, we assumed that cormorants settled in Lukštas around 1992–1994, and in 2007 there were 130 active nests.

In the small colonies, Lukštas (90–130 breeding pairs, nest density 80–120 bp/ha) and Naudžiūnai (80–100 breeding pairs, nest density 100–125 bp/ha), two zones were identified: a zone of active colony influence, situated under the nests, and a control zone without cormorant influence in surrounding forest.

In the largest colony, Juodkrantė, containing up to 4000 breeding pairs of cormorants, three zones were referred based on the duration and degree of environmental impact of the colony:

1. Control zone, where cormorants do not affect the habitat.
2. Zone of active colony influence—the part of the colony where the impact is latest and still developing. Most of the viable nests are in this part of the colony, nest density 220–290 bp/ha. In this zone, some trees are still alive but their viability is reduced and others are dead or dying. The shrub and grass layer is reduced.
3. Zone of the former influence—an abandoned part of the colony with only a few nests remaining, containing dead trees, many of which are rotten, fallen and decaying, and covered with young trees and shrubs, with a thick herbaceous layer.

Size of the colonies differed, in Lukštas it was 1.1 ha, in Naudžiūnai 0.8 ha, and Juodkrantė it was 14 ha of the territory under nests and 11 ha abandoned. Two smaller colonies were stable during period of research, but in Juodkrantė the active zone expanded south and southwest, while abandoning proceeded from north.

The size of control areas far exceeded the size of the colonies because they were selected in adjacent forests. The distance between the active zone and the control zone was 150 m in the Lukštas, 200 m in Naudžiūnai, and 400 m in Juodkrantė. The control plots were chosen to be at a similar distance from the water, i.e., the Nemunas River in Naudžiūnai and Lake Lukštas in the Lukštas colony. We did our best to ensure similarity of forest stands in the colony and control areas.

The composition of forest in Juodkrantė colony is pine, spruce, birch, and oak; Lukštas—black alder, white alder, birch, willow, and pine; Naudžiūnai—pine and spruce. The composition of herbaceous plants in the control and colonies differed significantly. In the active zone of the small colonies, common nettle, great celandine, and brambles were abundant, while in the active zone of the colony in Juodkrantė, elder, red elderberry, common nettle, great celandine, and small balsam were abundant. In the control zone of Lukštas there was almost no herbaceous cover, and in Naudžiūnai the dominant species were lingonberry, European blueberry, wood sorrel, and various mosses. The control area of Juodkrantė is covered with grasses, sedges, and various mosses.

At Lukštas, vegetation in the control zone (Figure 2a) was not different from the zone of active influence (Figure 2b). At Naudžiūnai, vegetation in the control zone was not rich (Figure 2c), that in active zone thriving better with additional input of nutrients (Figure 2d). Most striking vegetation differences were characteristic to Juodkrantė, with limited undergrowth and grass layer in control zone (Figure 2e), devastated active zone (Figure 2f), and lush vegetation in the cormorant-abandoned zone (Figure 2g).

Figure 2. Investigated habitats: (**a**)—control zone of Lukštas in 2019; (**b**)—active zone of Lukštas, 2019; (**c**)—control zone of Naudžiūnai in 2019; (**d**)—active zone of Naudžiūnai in 2022; (**e**)—control zone of Juodkrantė in 2018; (**f**)—active zone of Juodkrantė in 2011; (**g**)—abandoned nesting zone of Juodkrantė in 2013.

2.2. Small Mammal Trapping

Small mammal trapping was performed using standard method of snap trap lines, each consisting of 25 traps spaced 5 m apart, details presented in [35–37].

Every year trapping was performed from September to November. At that time, breeding season is over and most of the birds are no longer present in the colonies, except for a few individuals staying for a night. In both small colonies four trap lines were set in the active zone and four in the control zone, and in the large one, four trap lines were set in active and abandoned zones each, and two in the control zone. In the two smaller colonies, the position of the trap lines remained the same throughout the study period, while in Juodkrantė, depending on the abandoned part of the active area and the spread of the colony, the position of some trap lines shifted for a distance of 50 to 100 m.

This resulted in 600 trap days per year (eight lines of 25 traps on three days each) between 2014 and 2022 in the Lukštas colony, except for 2016, when unexpected early snowfall resulted in only 200 trap days, as further trapping was not possible. In the

Naudžiūnai colony, the annual trapping effort for 2016–2022 was equal to 600 trap days. In Juodkrantė, 10 trap lines of 25 traps each, exposed for three days, resulted in 750 trap days per year in 2011 and 2015–2022. In 2012–2014, the annual trapping effort was equal to 2175–2400 trap days due to additional trapping sessions.

During the 12 years of research, total trapping effort in Juodkrantė was 13,550 trap days, in Lukštas (9 years of research) it was 5000 trap days, and in Naudžiūnai (7 years of research)it was 4200 trap days.

Trapped small mammals were identified by their external features, grey voles of the genus *Microtus* by their teeth at dissection or after cleaning skulls [38]. Before dissection, individuals were weighed with accuracy of 0.1 g, body length was measured using sliding callipers with accuracy of 0.1 mm.

2.3. Data Analyses

Relative abundance of small mammals was expressed as the number of individuals per 100 trap days, based on the number of individuals trapped on the first day of each trapping session.

The body condition index was calculated according to the formula: BCI = $(Q/L^3) \times 10^5$, where Q is the body mass in g and L is the body length in mm [39]).

We used Shannon's diversity index H (log base 2), Simpson's dominance index c, and Pielou's evenness index e, ($e = H/H_{max}$; $H_{max} = \ln N$). These three indices were calculated using an online calculator [40]. Significance of differences of diversity index and dominance index were calculated in PAST version 4.01 (Paleontological Museum, University of Oslo, Oslo, Norway).

Confidence intervals (95%) for species proportions were estimated using the online software from Institute of Clinical and Translational Sciences [41]. Differences in species proportions were assessed using a G-test and online calculator [42]. Differences in relative abundance and body condition were tested using the Student t-test in STATISTICA for Windows, version 6.0 (StatSoft, Inc., Tulsa, OK, USA). The minimum level of significance was set at $p < 0.05$.

3. Results

During this study, 2471 individuals of 12 small mammal species were captured in the three colonies of Great Cormorants and their control territories. The species were the striped field mouse (*Apodemus agrarius*), the yellow-necked mouse (*A. flavicollis*), the bank vole (*Clethrionomys glareolus*), the short-tailed vole (*Microtus agrestis*), the common vole (*M. arvalis*), the root vole (*M. oeconomus*), the harvest mouse (*Micromys minutus*), the house mouse (*Mus musculus*), the brown rat (*Rattus norvegicus*), the water shrew (*Neomys fodiens*), the common shrew (*Sorex araneus*), and the pygmy shrew (*S. minutus*).

3.1. Species Proportions in Different Zones of the Colony

During 2011–2022, the dominant species of the biggest Juodkrantė cormorant colony was *A. flavicollis*, accounting for 66.8% (CI = 64.2–69.4%) of all trapped individuals irrespective of zone. In the area currently affected by cormorants (active zone), domination was highest, 86.1% (CI = 80.0–90.9%), while in the abandoned part of the colony, the proportion of *A. flavicollis* was 62.5% (CI = 59.2–65.7%) (G = 39.2, $p < 0.001$). *C. glareolus* was subdominant in all zones of Juodkrantė, the proportions varied significantly between zones: 12.2% (CI = 7.7–18.1%) in the zone of active influence, 27.0% (CI = 21.2–33.4%) in the control, and 30.4% (CI = 27.4–33.5%) in the abandoned zone (G = 26.2, $p < 0.001$). Proportions of the other species were negligible, 0.5–1.4% in the control, 0.6% in the zone of active influence, and 0.2–2.7% in the zone of former influence (Table 1).

Table 1. Small mammal community structure, diversity, and relative abundance in Juodkrantė cormorant colony, 2011–2022.

Species	Control Zone	Active Zone	Abandoned Zone
A. flavicollis	149	148	551
C. glareolus	58	21	268
M. agrestis	0	1	13
M. arvalis	0	0	2
M. oeconomus	1	1	8
M. minutus	3	0	11
S. araneus	2	1	24
S. minutus	2	0	5
Total	215	172	882
Species number	6	5	8
Shannon's H	1.124	0.687	1.38
Simpson's c	0.551	0.754	0.483
Pielou e	0.435	0.296	0.460
RA ± SE	10.33 ± 1.41	4.12 ± 0.77	20.27 ± 1.44

The dominant species in Lukštas during 2014–2022 was *C. glareolus*. In the control zone, the *C. glareolus* proportion was 51.8% (CI = 45.0–58.6%), in the active zone it was bigger at 66.9% (CI = 62.4–71.2%) of all trapped individuals (G = 13.5, $p < 0.001$). The subdominant species differed: in the control zone it was *A. flavicollis*, accounting for 35.5% (CI = 29.1–42.2%) and in the zone of active influence the subdominant was *A. agrarius* with 14.9% (CI = 11.8–18.5%).

In the control zone, the proportion of *S. araneus* was 5.5%, that of *A. agrarius* was 4.5%, and other species comprised 0.5–0.9% each. In the zone with active cormorant influence, *A. flavicollis* accounted for 10.5%, *S. araneus* for 4.8%, while other species for 0.2–0.9% each (Table 2).

Table 2. Small mammal community structure, diversity, and relative abundance in Lukštas cormorant colony, 2014–2022.

Species	Control Zone	Active Zone
A. agrarius	10	68
A. flavicollis	78	48
C. glareolus	114	305
M. agrestis	2	5
M. arvalis	0	1
M. minutus	1	1
M. musculus	0	1
N. fodiens	1	1
S. araneus	12	22
S. minutus	2	4
Total	220	456
Species number	8	10
Shannon's H	1.647	1.559
Simpson's c	0.399	0.483
Pielou e	0.549	0.492
RA ± se	12.58 ± 1.54	27.00 ± 2.32

During 2016–2022, in Naudžiūnai the dominant species was *A. flavicollis*. The proportion of this species in the control zone was 70.6% (CI = 62.2–78.1%), in the zone of active influence it was 52.1% (CI = 47.0–57.1%), the difference being significant (G = 13.8, $p < 0.001$). The subdominant *C. glareolus* accounted for 27.2% (CI = 19.9–35.5%) of all trapped individuals in the control zone, while in the zone of active influence it was 35.9% (CI = 31.1–40.9%) (G = 3.1, $p = 0.08$). Proportions of *A. agrarius* were 2.2% and 10.5%, respectively. The rest of the species in the zone of active influence accounted for 0.3–0.5% each (Table 3).

Table 3. Small mammal community structure, diversity, and relative abundance in Naudžiūnai cormorant colony, 2016–2022.

Species	Control Zone	Active Zone
A. agrarius	3	41
A. flavicollis	96	203
C. glareolus	37	140
M. musculus	0	2
R. norvegicus	0	1
S. araneus	0	2
S. minutus	0	1
Total	136	390
Species number	3	7
Shannon's H	0.987	1.485
Simpson's c	0.573	0.411
Pielou e	0.623	0.529
RA ± se	8.29 ± 1.05	25.29 ± 2.91

3.2. Small Mammal Diversity Differences

The small mammal community of Juodkrantė in the active impact zone had the lowest number and diversity of species, an even distribution of species, and the highest dominance index (Table 1). Shannon's H and Simpson's c were significantly different from the control zone (t = 3.35, $p < 0.001$ and t = 4.08, $p < 0.001$, respectively) and the former impact zone (t = 6.33, $p < 0.001$ and t = 6.47, $p < 0.001$, respectively).

In the period of 2011–2022, the diversity of the small mammal community in the active zone (Shannon's H zero in 2014–2021, no small mammals in the active zone in 2022) was lower than in the control zone (H = 0.37–1.49) and in the abandoned zone (H = 0.98–2.49) of Juodkrantė colony.

In the period of 2014–2022 in Lukštas, more species were found in the active zone (10 species) than in the control zone (8 species), although there was no significant difference in the Shannon diversity index (t = 0.75, $p = 0.45$). The Simpson's index showed a higher dominance in the active zone (t = 2.56, $p < 0.05$). According to the evenness index, species were more evenly distributed in the control zone (Table 2). The diversity of the small mammal community in the active zone of Lukštas colony in 2015, 2019, and 2022 was higher than in the control zone.

In the period of 2014–2022 the active zone in Naudžiūnai had a higher number of small mammal species, a significantly higher diversity (t = 5.20, $p < 0.001$), and a lower dominance (t = 4.17, $p < 0.001$) compared with the control zone. Species were more evenly distributed in the control area (Table 3). These differences were characteristic to every year of the investigation.

3.3. Relative Abundances of Small Mammals in Great Cormorant Colonies

We have found that the relative abundance of small mammals is greatly reduced by the environmental impact of a large cormorant colony (Table 1). In the active zone of Juodkrantė, the relative abundance was less than half that in the control zone (t = 4.22, $p < 0.001$). The abundance increases when cormorants leave the area and there are no more active nests. The relative abundance in the abandoned zone (average 20.27 ± 1.44 ind./100 trap days) was significantly higher compared with the zone of active cormorant influence (t = 9.98, $p < 0.001$) and even compared with the control habitat (t = 4.49, $p < 0.001$).

Between 2011 and 2022, the relative abundance of small mammals in the control zone ranged from zero in 2011 to 22.0 individuals per 100 trap days in 2020, that in the abandoned zone ranged from 8.0 in 2022 to 38.0 individuals per 100 trap days in 2015. In the active zone of Juodkrantė, no small mammals were trapped in 2021–2022, and in other years their relative abundance ranged from 0.7 to 10.9 individuals per 100 trap days.

In both small cormorant colonies, Lukštas (Table 2) and Naudžiūnai (Table 3), the relative abundance within the colony was estimated to be more than twice as high compared with the control zone. These differences were statistically significant (t = 5.19, $p < 0.001$ and t = 5.49, $p < 0.001$, respectively).

These differences remained during the whole study period. In Lukštas, relative abundance in the active zone exceeded that in the control zone 1.7–4.2 times (in 2022, 9.0 vs. 15.0 and in 2017, 5.0 vs. 21.0 ind. per 100 trap days). In Naudžiūnai, differences were 1.5–5.0 times (in 2016, 11.0 vs. 16.0 and in 2022, 5.0 vs. 25.0 ind. per 100 trap days).

3.4. Body Condition of Two Dominant Small Mammal Species

The highest *A. flavicollis* body condition index in Juodkrantė was characteristic to individuals from the control zone (BCI = 3.48 ± 0.05). The body conditions of mice trapped in the active zone (BCI = 3.44 ± 0.05) and the abandoned zone (BCI = 3.44 ± 0.02) were the same; the differences were not statistically significant (t = 0.53, $p = 0.60$ and t = 0.79, $p = 0.43$, respectively).

C. glareolus in Juodkrantė showed a significant decrease in body condition index in the active zone of the colony (Figure 3a): BCI was less than in the control zone (t = 2.92, $p < 0.01$) and in the former zone of influence (t = 3.24, $p < 0.01$).

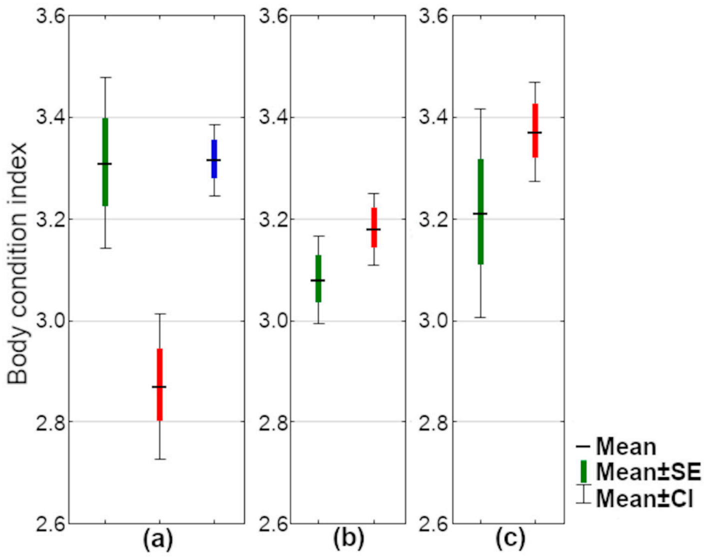

Figure 3. Body condition indexes of *C. glareolus* in Juodkrantė (**a**), Lukštas (**b**), and Naudžiūnai (**c**) colonies. Control zone shown in green, active zone in red, abandoned zone in blue.

In Lukštas, the body condition index of *C. glareolus* was higher in the active zone of the colony than in the control zone (Figure 3b), but the difference is not statistically significant (t = 1.55, $p = 0.12$). The same trend was also found in Naudžiūnai: the body condition of *C. glareolus* was higher in the active zone of the colony than in the control zone (Figure 3c), but not significantly (t = 1.49, $p = 0.14$).

As for the body condition index of *A. flavicollis* in both smaller Great Cormorant colonies, it was similar in the control and cormorant influenced zones. Values of BCI were 3.31 ± 0.05 vs. 3.27 ± 0.07 in Lukštas and 3.46 ± 0.05 vs. 3.54 ± 0.03 in Naudžiūnai, respectively, none of the differences were significant.

4. Discussion

Small mammals respond strongly to habitat features [43–47], with the dominant species varying from one habitat to the next and depending on latitude.

In the long term and irrespective of habitat, the dominant small mammal in Lithuania is *C. glareolus*, the proportion of this species being twice than that of *A. flavicollis* and three times than those of *A. agrarius*, *S. Araneus*, or *M. arvalis* [48]. In seasonally flooded grasslands, the dominant species were *M. oeconomus* and *A. agrarius* [49], in orchards—*M. arvalis*, *A.* flavicollis, and *A. agrarius* [50]. Natural grasslands are mostly dominated by *A. agrarius* [51–53] and forest plantations by *C. glareolus* [51,53,54].

The dominant species of small mammals in Lithuanian forests are *A. flavicollis* and *C. glareolus* [34,55,56]. These two species, with different proportions, also dominated all investigated cormorant colonies (Tables 1–3).

The number of small mammal species in successional conditions changes over a short period of time [57,58]. It has been shown that during forest succession, dominance indices in small mammal community increase and the number of species decreases [34,56]. In this study, a similar trend was found in the Juodkrantė colony of Great Cormorants where the impact lasted for decades. Small mammal diversity was reduced and *A. flavicollis* dominance increased (Table 1) in the area of active impact compared with the control following habitat deterioration. In a large colony, the abundance of small mammals has declined sharply as a result of damaging effects.

However, when cormorants leave the area, the dominance of one species is reduced, diversity rates recover, and the number of species increases. We found that the relative abundance of small mammals becomes even higher than in the control area after recovery (Table 1).

In contrast, the limited impact of small colonies was positive for small mammals, with higher species numbers and abundance of species recorded in areas of under cormorant impact. Even the body condition of the dominant species was slightly better in these zones.

How can these differences arise?

The abundance, species composition, and diversity of small mammals depend on vegetation composition, litter cover, sediment, and canopy cover [44,59,60], all of which are altered by cormorant activity [2]. High nutrient loads in the most impacted areas of a large colony can affect small mammals in a number of ways: through altered plant composition [15], lack of shelter, disturbance, and extremely high nitrogen and phosphorus concentrations. Large colonies of nesting cormorants can cause huge changes in ecosystems [2]. Negative impacts of colonies often affect plants [18], lichens [61], and myxomycetes [19]. Plants, shelter, and food sources are restored in the abandoned part of the large colony, e.g., in the abandoned part of the Juodkrantė, the diversity of myxomycetes has been partially restored [19], and both nitrophilous and mixed forest lichens have been recorded again [20], with different effects on the invertebrates [24]. Therefore, the initial impact of a new cormorant colony, as well as the restoration of an abandoned site, is a kind of succession that improves the habitat for small mammals. The response of the small mammal community is an increase in species richness, diversity, and relative abundance [31–34,43–47].

As shown by studies on other small mammal species [62,63], the negative influence of the large colony may be similar to that of pollution. However, as soon as the disturbing factor is removed, small mammals can quickly recover due to their short generation time, intense breeding, and migration [64]. The small mammal community is re-established through three main processes: succession of abandoned habitats, habitat selection by different species, and assembly rules, i.e., the rules by which the small mammal community is formed from different trophic groups [60]. As shown in Table 1, herbivores and insectivores are two groups mainly suppressed in the large colony, with their appearance in the abandoned area indicating recovery of the community.

A similar answer is given to the question: why is the effect of small colonies positive? Initially, cormorants form habitat mosaics, as forest die-off starts from the trees with nests, forming patches of different succession stages that are attractive to various invertebrate groups [24]. Therefore, plant-arthropod food webs are changing [65]. Small colonies initially do not accumulate extremely high levels of phosphorus and nitrogen. Small amounts of cormorant droppings do not kill plants, they only fertilize the soil and change the composition of the vegetation, allowing nitrophilic plants to grow. In small cormorant colonies, grass cover and shrubs are more abundant than in the surrounding areas (see Figure 2), providing shelter and food for small mammals. Moreover, at least some small mammal species can have their diet expanded by dead chicks, broken eggs, and eggshells constantly present on the ground underneath the nests in the breeding season [66].

5. Conclusions

Our study shows that small colonies of Great Cormorants with a low number of nests in the early stages of their formation have a positive effect on the small mammal community in terms of higher species richness, diversity, and relative abundance.

High breeding numbers, that is, a large colony size, have negative impacts on the small mammal community in the form of lower species richness, diversity, and relative abundance, as well as poorer body condition of the individuals. After the cormorants abandoned part of the colony with the nesting site, all former parameters in the area previously impacted recovered.

It can therefore be concluded that, up to a certain colony size, cormorant pressure is a driver of natural habitat succession and has a similar effect on small mammal communities as other successions in disturbed habitats.

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Institutional Review Board Statement: The study was conducted in accordance with Lithuanian (the Republic of Lithuania Law on the Welfare and Protection of Animals No. XI-2271, "Requirements for the Housing, Care and Use of Animals for Scientific and Educational Purposes", approved by Order No B1-866, 31 October 2012 of the Director of the State Food and Veterinary Service (Paragraph 4 of Article 16) and European legislation (Directive 2010/63/EU) on the protection of animals and approved by the Animal Welfare Committee of the Nature Research Centre, protocols No GGT-7 and GGT-8. Snap trapping was justifiable as we also studied reproduction parameters and collected tissues and internal organs for the analysis of pathogens, elemental content, and stable isotopes (not covered in this publication).

Data Availability Statement: This is an ongoing research and data are available from the corresponding author upon reasonable request.

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References

1. Kameda, K.; Koba, K.; Hobara, S.; Osono, T.; Terai, M. Pattern of natural ^{15}N abundance in lakeside forest ecosystem affected by cormorant-derived nitrogen. In *Limnology and Aquatic Birds. Developments in Hydrobiology*; Hanson, A.R., Kerekes, J.J., Eds.; Springer: Dordrecht, The Netherlands, 2006; pp. 69–86.
2. Klimaszyk, P.; Rzymsky, P. The complexity of ecological impacts induced by great cormorants. *Hydrobiologia* **2016**, *771*, 13–30. [CrossRef]
3. Harding, L.E.; Mesler, J.I. Cormorant abundance, diet, and foraging habits in Arizona. *J. Field Ornithol.* **2022**, *93*, 6. [CrossRef]
4. Ellis, J.C.; Farina, J.M.; Witman, J.D. Nutrient transfer from sea to land: The case of gulls and cormorants in the Gulf of Maine. *J. Anim. Ecol.* **2006**, *75*, 565–574. [CrossRef] [PubMed]
5. Otero, X.L.; Tejada, O.; Martin-Pastor, M.; Pena, S.; Ferreira, T.O.; Perez-Alberti, A. Phosphorus in seagull colonies and the effect on the habitats. The case of yellow-legged gulls (*Larus michahellis*) in the Atlantic Islands National Park (Galicia-NW Spain). *Sci. Total Environ.* **2015**, *532*, 383–397. [CrossRef] [PubMed]
6. Russell, I.C.; Cook, A.C.; Ives, M.J.; Davison, P.I. The diet of two sympatric Great Cormorant Phalacrocorax carbo subspecies wintering at freshwater fishery sites in England and Wales. *Ardea* **2022**, *109*, 443–456. [CrossRef]

7. Gremillet, D.; Schmid, D.; Culik, B. Energy requirements of breeding great cormorants *Phalacrocorax carbo sinensis*. *Mar. Ecol. Prog. Ser.* **1995**, *121*, 1–9. [CrossRef]
8. Ovegård, M.K.; Jepsen, N.; Bergenius Nord, M.; Petersson, E. Cormorant predation effects on fish populations: A global meta-analysis. *Fish Fish.* **2021**, *22*, 605–622. [CrossRef]
9. Garcia, L.V.; Ramo, C.; Aponte, C.; Moreno, A.; Dominguez, M.T.; Gomez-Aparicio, L.; Redondo, R.; Maranon, T. Protected wading bird species threaten relict centenarian cork oaks in a Mediterranean biosphere reserve: A conservation management conflict. *Biol. Conserv.* **2011**, *144*, 764–771. [CrossRef]
10. Oszust, M.; Klimaszyk, P. Soil conditions under cormorant colonies favor for mites excepting Oribatida. *Acarologia* **2022**, *62*, 974–988. [CrossRef]
11. Riddick, S.N.; Dragosits, U.; Blackall, T.D.; Daunt, F.; Wanless, S.; Sutton, M.A. The global distribution of ammonia emissions from seabird colonies. *Atmos. Environ.* **2012**, *55*, 319–327. [CrossRef]
12. Taraškevičius, R.; Motiejūnaitė, J.; Zinkutė, R. Pedogeochemical anomalies in surroundings of great cormorant colony (case study in Lithuania). *E3S Web Conf.* **2013**, *1*, 04006. [CrossRef]
13. La Peña-Lastra, D.; Pérez-Alberti, A.; Ferreira, T.O.; Huerta-Díaz, M.Á.; Otero, X.L. Global deposition of potentially toxic metals via faecal material in seabird colonies. *Sci. Rep.* **2022**, *12*, 22392. [CrossRef] [PubMed]
14. Lafferty, D.J.R.; Hanson-Dorr, K.C.; Prisock, A.M.; Dorr, B.S. Biotic and abiotic impacts of Double-crested cormorant breeding colonies on forested islands in the southeastern United States. *For. Ecol. Manag.* **2016**, *69*, 10–19. [CrossRef]
15. Veum, L.M.; Dorr, B.S.; Hanson-Dorr, K.C.; Moore, J.R.; Rush, S.A. Double-crested cormorant colony effects on soil chemistry, vegetation structure and avian diversity. *For. Ecol. Manag.* **2019**, *453*, 117588. [CrossRef]
16. Maesako, Y. Impacts of streaked shearwater (*Calonectris leucomelas*) on tree seedling regeneration in a warm-temperate evergreen forest on Kanmurijima Island, Japan. *Plant Ecol.* **1999**, *145*, 183–190. [CrossRef]
17. Ishizuka, K. Ecology of the ornithocoprophilous plant communities on breeding places of the black-tailed gull, *Larus crassirostris*, along the coast of Japan. *Ecol. Rev.* **1966**, *16*, 229–244.
18. Matulevičiūtė, D.; Motiejūnaitė, J.; Uogintas, D.; Taraškevičius, R.; Dagys, M.; Rašomavičius, V. Decline of a protected coastal pine forest under impact of a colony of great cormorants and the rate of vegetation change under ornithogenic influence. *Silva Fenn.* **2018**, *52*, 7699. [CrossRef]
19. Adamonytė, G.; Iršėnaitė, R.; Motiejūnaitė, J.; Taraškevičius, R.; Matulevičiūtė, D. Myxomycetes in a forest affected by great cormorant colony: A case study in Western Lithuania. *Fungal Divers.* **2012**, *13*, 131–146. [CrossRef]
20. Motiejūnaitė, J.; Iršėnaitė, R.; Adamonytė, G.; Dagys, M.; Taraškevičius, R.; Matulevičiūtė, D.; Koreivienė, J. Pine forest lichens under eutrophication generated by a great cormorant colony. *Lichenologist* **2014**, *46*, 213–228. [CrossRef]
21. Kolb, G.S.; Palmborg, C.; Taylor, A.R.; Baath, E.; Hamback, A.P. Effects of nesting cormorants (*Phalacrocorax carbo*) on soil chemistry, microbial communities and soil fauna. *Ecosystems* **2015**, *18*, 643–657. [CrossRef]
22. Craig, E.C.; Elbin, S.B.; Danoff-Burg, J.A.; Palmer, M.I. Impacts of Double-Crested Cormorants (*Phalacrocorax auritus*) and Other Colonial Waterbirds on Plant and Arthropod Communities on Islands in an Urban Estuary. *Waterbirds* **2012**, *35*, 4–12. [CrossRef]
23. Al Shehhi, H.; Muzaffar, S.B. Impact of nesting Socotra Cormorants on terrestrial invertebrate communities. *Insects* **2021**, *12*, 615. [CrossRef] [PubMed]
24. Machač, O.; Ivinskis, P.; Rimšaitė, J.; Horňák, O.; Tuf, I.H. In the Shadow of Cormorants: Succession of Avian Colony Affects Selected Groups of Ground Dwelling Predatory Arthropods. *Forests* **2022**, *13*, 330. [CrossRef]
25. Onmuş, O.; Soydan, E.; Tavares, J.P. Population dynamics and wintering strategies of great cormorant (*Phalacrocorax carbo*): What are the factors for selecting wintering sites? *Hydrobiologia* **2023**, *850*, 151–166. [CrossRef]
26. Parz-Gollner, R.; Zuna-Kratky, T.; Niederer, W.; Nemeth, E. Status of the breeding population of Great Cormorants in Austria in 2012. In *Breeding Numbers of Great Cormorants Phalacrocorax carbo in the Western Palearctic, 2012–2013*; Bregnballe, T., Lynch, J., Parz-Gollner, R., Marion, L., Volponi, S., Paquet, J.-Y., Carss, D.N., van Eerden, M.R., Eds.; Danish Centre for Environment and Energy: Aarhus, The Netherlands, 2014; No. 99; pp. 61–64.
27. Goc, M.; Iliszko, L.; Stempniewicz, L. The largest European colony of great cormorant on the Vistula spit (N Poland) an impact of the forest ecosystem. *Ecol. Quest.* **2005**, *6*, 93–103.
28. Bregnballe, T.; Lynch, J.; Parz-Gollner, R.; Volponi, S.; Marion, L.; Paquet, J.-Y.; van Eerden, M.R.; Carss, D.N. Status of the breeding population of Great Cormorants Phalacrocorax carbo in the Western Palearctic in 2012. In *Breeding Numbers of Great Cormorants Phalacrocorax Carbo in the Western Palearctic, 2012–2013*; Bregnballe, T., Lynch, J., Parz-Gollner, R., Marion, L., Volponi, S., Paquet, J.-Y., Carss, D.N., van Eerden, M.R., Eds.; Danish Centre for Environment and Energy: Aarhus, The Netherlands, 2014; No. 99; pp. 13–58.
29. Knyva, V.; Rumbutis, S. Didžiųjų Kormoranų Populiacijos Gausos Reguliavimo Programos Priemonių Įgyvendinimas 2015–2016 Metais. [Implementation of the Measures of the Programme for the Control of the Abundance of the Great Cormorant Population in 2015–2016.] Report. Available online: https://nerija.lrv.lt/uploads/nerija/documents/files/Kormoranu_2017_ataskaita__red.pdf (accessed on 10 October 2022).
30. Lietuvos Respublikos Aplinkos Ministerija. Šiemet Suskaičiuota Daugiau Kaip 9 Tūkst. Didžiųjų Kormoranų Porų. [More than 9000 Pairs of Great Cormorants Were Counted This Year]. Available online: https://am.lrv.lt/lt/naujienos/siemet-suskaiciuota-daugiau-kaip-9-tukst-didziuju-kormoranu-poru (accessed on 2 January 2023).

31. Fox, B.J. *Long-Term Studies of Small Mammal Communities from Disturbed Habitats in Eastern Australia*; Academic Press: Orlando, FL, USA, 1995; pp. 467–501.
32. Bryja, J.; Heroldova, M.; Zejda, J. Effects of deforestation on structure and diversity of small mammal communities in the Moravskoslezské Beskydy Mts (Czech Republic). *Acta Theriol.* **2002**, *47*, 295–306. [CrossRef]
33. Briani, D.C.; Palma, A.R.T.; Vieira, E.M.; Henriques, R.P.B. Post-fire succession of small mammals in the Cerrado of central Brazil. *Biodivers. Conserv.* **2004**, *13*, 1023–1037. [CrossRef]
34. Čepukienė, A.; Jasiulionis, M. Small mammal community changes during forest succession (Pakruojis district, north Lithuania). *Zool. Ecol.* **2012**, *22*, 144–149. [CrossRef]
35. Balčiauskienė, L.; Jasiulionis, M.; Balčiauskas, L. Loss of diversity in a small mammal community in a habitat influenced by a colony of great cormorants. *Acta Zool. Bulgar.* **2014**, *66*, 229–234.
36. Balčiauskas, L.; Balčiauskienė, L.; Jasiulionis, M. Mammals under a colony of great cormorants: Population structure and body condition of yellow-necked mice. *Turk. J. Zool.* **2015**, *39*, 941–948. [CrossRef]
37. Balčiauskienė, L.; Balčiauskas, L.; Jasiulionis, M. Skull variability of mice and voles inhabiting the territory of a great cormorant colony. *Biologia* **2015**, *70*, 1406–1414. [CrossRef]
38. Prūsaitė, J. *(Comp.). Fauna of Lithuania. Mammals*; Mokslas: Vilnius, Lithuania, 1988; p. 295.
39. Moors, P.J. Norway rats (*Rattus norvegicus*) on the Noises and Motukawao islands, Hauraki Gulf, New Zealand. *N. Z. J. Ecol.* **1985**, *8*, 37–54.
40. Biodiversity Calculator. Available online: https://www.alyoung.com/labs/biodiversity_calculator.html (accessed on 12 November 2022).
41. Sample Size Calculators. Available online: https://sample-size.net/confidence-interval-proportion/ (accessed on 12 November 2022).
42. G-Test Calculator. Available online: https://elem.com/~{}btilly/effective-ab-testing/g-test-calculator.html (accessed on 12 November 2022).
43. Presley, S.J.; Cisneros, L.M.; Klingbeil, B.T.; Willig, M.R. Landscape ecology of mammals. *J. Mammal.* **2019**, *100*, 1044–1068. [CrossRef]
44. Palmeirim, A.F.; Santos-Filho, M.; Peres, C.A. Marked decline in forest-dependent small mammals following habitat loss and fragmentation in an Amazonian deforestation frontier. *PLoS ONE* **2020**, *15*, e0230209. [CrossRef] [PubMed]
45. Benedek, A.M.; Sirbu, I.; Lazar, A. Responses of small mammals to habitat characteristics in Southern Carpathian forests. *Sci. Rep.* **2021**, *11*, 12031. [CrossRef]
46. Paniccia, C.; Carranza, M.L.; Frate, L.; Di Febbraro, M.; Rocchini, D.; Loy, A. Distribution and functional traits of small mammals across the Mediterranean area: Landscape composition and structure definitively matter. *Ecol. Indic.* **2022**, *135*, 108550. [CrossRef]
47. Torre, I.; Jaime-González, C.; Díaz, M. Habitat Suitability for Small Mammals in Mediterranean Landscapes: How and Why Shrubs Matter. *Sustainability* **2022**, *14*, 1562. [CrossRef]
48. Balčiauskas, L.; Balčiauskienė, L. Small Mammal Diversity Changes in a Baltic Country, 1975–2021: A Review. *Life* **2022**, *12*, 1887. [CrossRef]
49. Balčiauskas, L.; Balčiauskienė, L.; Janonytė, A. Reproduction of the root vole (*Microtus oeconomus*) at the edge of its distribution range. *Turk. J. Zool.* **2012**, *36*, 668–675. [CrossRef]
50. Stirkė, V.; Balčiauskas, L.; Balčiauskienė, L. Common Vole as a Focal Small Mammal Species in Orchards of the Northern Zone. *Diversity* **2021**, *13*, 134. [CrossRef]
51. Pakeltytė, G.; Andriuškevičius, A. Smulkiųjų žinduolių bendrijos rūšių įvairovė ir gausumas Nevėžio kraštovaizdžio draustinio monitoringo vietose [Species diversity and abundance in small mammal community at monitoring sites of Nevezis landscape reserve]. *Theriol. Litu.* **2004**, *4*, 43–53.
52. Alejūnas, P.; Stirkė, V. Small mammals in northern Lithuania: Species diversity and abundance. *Ekologija* **2010**, *56*, 110–115. [CrossRef]
53. Balčiauskas, L.; Alejūnas, P. Small mammal species diversity and abundance in Žagarė Regional Park. *Acta Zool.Litu.* **2011**, *21*, 163–172. [CrossRef]
54. Mažeikytė, R. Small mammals of the Kanio Raistas Botanical-Zoological Reserve. *Theriol. Litu.* **2002**, *2*, 58–69.
55. Balčiauskienė, L.; Balčiauskas, L.; Čepukienė, A. Demographic and morphometric parameters of the yellow-necked mouse (*Apodemus flavicollis*) in late autumn-early spring in Lithuania. *Acta Biol. Univ. Daugavp.* **2009**, *9*, 25–34.
56. Jasiulionis, M.; Čepukienė, A.; Balčiauskas, L. Small mammal community changes during succession of the planted forest. *Acta Zool. Litu.* **2011**, *22*, 293–300. [CrossRef]
57. Hlôška, L.; Saniga, M.; Chovancová, G.; Chovancová, B.; Homolová, Z. Temporal and spatial changes in small mammal communities in a disturbed mountain forest. *Folia Oecologica* **2022**, *49*, 9–22. [CrossRef]
58. Heske, E.J.; Rodgers, T.W. Species composition and abundance of small mammals on forest edge in southern Illinois in summer. *Therya* **2022**, *13*, 57–66. [CrossRef]
59. Carey, A.B.; Harrington, C.A. Small mammals in young forests: Implications for management for sustainability. *For. Ecol. Manag.* **2001**, *154*, 289–309. [CrossRef]
60. Fox, B.J. How habitat selection, succession, and assembly rules can influence landscape ecology in natural and disturbed areas. *Therya* **2022**, *13*, 5–15. [CrossRef]

61. Zolkos, K.; Kukwa, M.; Afranowicz-Cieślak, R. Changes in the epiphytic lichen biota in the Scots pine (*Pinus sylvestris*) stands affected by a colony of grey heron (*Ardea cinerea*): A case study from northern Poland. *Lichenologist* **2013**, *45*, 815–823. [CrossRef]
62. Velickovic, M. Measures of the developmental stability, body size and body condition in the black-striped mouse (*Apodemus agrarius*) as indicators of a disturbed environment in northern Serbia. *Belg. J. Zool.* **2007**, *137*, 147–156.
63. Tête, N.; Fritsch, C.; Afonso, E.; Coeurdassier, M.; Lambert, J.C.; Giraudoux, P.; Scheifler, R. Can body condition and somatic indices be used to evaluate metal-induced stress in wild small mammals? *PLoS ONE* **2013**, *8*, e66399. [CrossRef] [PubMed]
64. Bush, E.R.; Buesching, C.D.; Slade, E.M.; Macdonald, D.W. Woodland recovery after suppression of deer: Cascade effects for small mammals, wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*). *PLoS ONE* **2012**, *7*, e31404. [CrossRef] [PubMed]
65. Kolb, G.S.; Jerling, L.; Hambäck, P.A. The impact of cormorants on plant–arthropod food webs on their nesting islands. *Ecosystems* **2010**, *13*, 353–366. [CrossRef]
66. Balčiauskas, L.; Skipitytė, R.; Jasiulionis, M.; Balčiauskienė, L.; Remeikis, V. Immediate increase in isotopic enrichment in small mammals following the expansion of a great cormorant colony. *Biogeosciences* **2018**, *15*, 3883–3891. [CrossRef]