Influence of forest stand on the reproductive biology of the edible dormouse *Glis glis*

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Abstract

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In this study, carried out between 2018 and 2024, we investigated how stand species composition, stand age, and tree mast cycles affect selected life functions of the edible dormouse. A total of 81 nesting boxes were installed in eight study plots in south-western Poland in an area of low hills covered by deciduous and mixed forests. The locations varied in tree species composition and stand age. The number of inspections conducted annually ranged from 1 to 7. A total of 208 dormice (including 128 juveniles from 28 litters) were recorded. There was no association between the average number of litters per year and stand age, but there was a clear difference in this trait between oak and beech forests (in favour of the former). The number of litters increased in mast years, while the total number of dormice observed in mast and non-mast years did not differ significantly. Juveniles outnumbered adults in seeded years, but the difference was not significant. The study showed that nest boxes were more readily occupied in younger stands. More nest boxes were occupied in oak forests than in beech forests.

Keywords

age of trees, dormice, mast seeding, nesting boxes, reproduction

Introduction

For most animals, the availability of sufficient food is one of the most important factors influencing their reproduction (Karels et al., 2000; Koskela et al., 2004). Food resources are usually not evenly distributed but are subject to temporal and spatial fluctuations. They can be stable (constantly available) or unstable (pulsating—appearing periodically in excess and then showing a drastic decline in quantity) (Yang et al., 2008). A good example of unstable food resources is tree species that irregularly produce seeds (e.g., oaks *Quercus* sp. and common beech *Fagus sylvatica*). In these species, an abundance of seeds appears every few years (i.e., a mast year), while in other years there are no seeds at all (i.e., a non-mast year). Apart from these extreme cases, most years are so-called intermediate masting years, when some trees fruit abundantly and others do not fruit at all (Hilton and Packham, 2003). Among mammals, rodents (Rodentia) are the main consumers of these irregularly appearing fruits. The consequences of fluctuations in food availability are rapid, and periods of high seed yields are followed by periodic increases in the numbers of these animals (Murúa and Briones, 2005; Selås et al., 2002).

One species in which reproduction is highly dependent on sufficient high-energy food resources is the edible dormouse (*Glis glis* Linnaeus, 1766). It is an arboreal rodent with nocturnal activity, inhabiting mainly deciduous and mixed forests. In Poland, it inhabits mainly the southern part of the country, although isolated localities of this mammal (partly the result of its reintroduction) are also found in eastern and northern Poland (https://www.iop.krakow.pl/Ssaki/gatunek/84). Edible dormice hibernate for extremely long periods (>8 months), choosing underground burrows as hibernacula (Bieber and Ruf, 2004).

Although the diet of the edible dormouse is varied,

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including leaves, buds, and fruits of various tree species, as well as animal food (insects, snails, eggs, and breeding birds), its preferred food is the high-energy seeds of the beech tree. Beech periodically produces large seed crops, meaning that seeds can be completely absent in some years but overabundant in mast years. Mast years of beech occur, on average, every 7 years (Hilton and Packham, 2003), and nearly 50% of all years are intermediate mast years. Oak is another tree important for *G. glis*, and its abundant seed crops occur once every 4–6 years. However, acorns are a less preferred food than beech nuts (Jurczyszyn, 2018). The energy value of acorns of pedunculate oak (*Quercus robur*) and sessile oak (*Quercus petraea*) is much lower than that of seeds of European beech (*Fagus sylvatica*) (Grodziński and Sawicka-Kapusta, 1970).

Consequently, dormice are temporally and spatially exposed to enormous variability in food resources, responding to these fluctuations with differing reproductive intensities. Most individuals reproduce in years of abundant beech or oak seed crops, and entire populations do not reproduce in non-mast years (Bieber, 1998; Pilastro et al., 2003; Schlund et al., 2002). Only a fraction of dormice reproduce in intermediate years (Lebl et al., 2011). Dormice usually have only one litter per year; the young are typically born between July and August and leave the nest in September (Pucek, 1984; Vekhnik, 2020). Sometimes a female may have two litters in a year (if the first is lost) (Holcová Gazárková et al., 2016). The availability of high-energy food in September and October (the masting period of beech and oak) is essential for young individuals after weaning, as they must obtain sufficient fat reserves in a very short time to survive their first hibernation season. Individuals born in a given year start hibernation a month, or sometimes even 2 months, later than adult dormice (Vekhnik, 2020).

In addition, in years when beech trees do not bear fruit, many dormice (especially those in good "fat" condition) return to underground burrows after a short period of spring activity and enter a state of estivation (Cornils et al., 2017).

Among the many aspects of edible dormouse biology, the influence of stand composition and stand age on its abundance is little studied (Marteau and Sara, 2015). For this reason, our study aimed to examine the extent to which the species composition and age of forest stands inhabited by dormice, as well as mast cycles, influence the reproduction of this arboreal rodent in the habitat of the Niemczańsko-Strzelińskie Hills (Poland).

Materials and methods

The study area was the Niemczańsko-Strzelińskie Hills (Sudeten Foreland) in south-western Poland (Fig. 1). It is an area of low hills separated by wide depressions, with the highest peak, Gromnik (393 m a.s.l.) (Kondracki, 2002). The hills are covered mainly by deciduous and mixed forests, with species such as pedunculate oak (*Quercus robur*) and beech (*Fagus sylvatica*) clearly dominating.

The study was conducted over seven consecutive years, from 2018 to 2024. In habitats suitable for dormice (described below), dedicated boxes were installed across eight study plots: (1) Sadowice, (2) Zarzyca, (3) Nieszkowice, (4) Muszkowicki Las, (5) Krzywina, (6) Nowolesie, (7) Witostowice, and (8) Źródło Cyryla (Fig. 1 and Table 1). All nest boxes were mounted at similar heights above the ground (2.5–3 m).

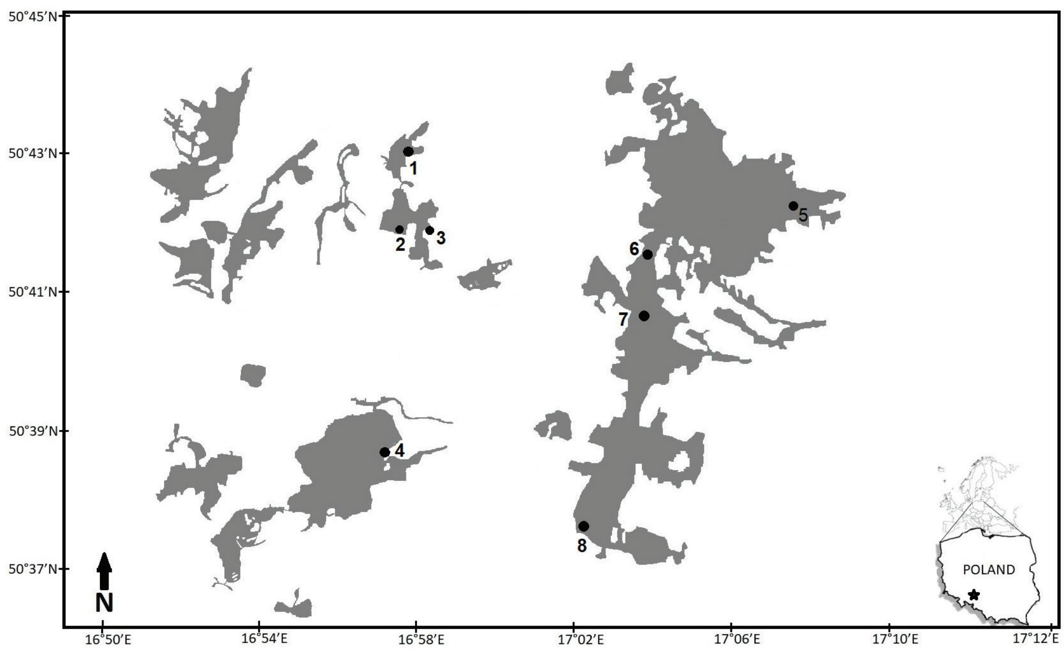

Fig 1. Map of the studied area – the Niemczańsko-Strzelińskie Hills: (1) Sadowice, (2) Zarzyca, (3) Nieszkowice, (4) Muszkowicki Las, (5) Krzywina, (6) Nowolesie, (7) Witostowice, (8) Źródło Cyryla.

Table 1. Number of nest boxes per site, inspections carried out and dormice found in nest boxes at each site (data in brackets indicate the number of young)

Plot	Number of nest boxes	Number of inspections	Number of dormice in nest boxes						
			2018	2019	2020	2021	2022	2023	2024
1	10	4	–	7 (2)	4 (14)	0 (5)	–	–	–
2	16	3	–	–	–	–	8 (10)	6 (0)	–
3	10	2	–	–	2 (2)	2 (0)	–	–	–
4	20	14	4 (13)	4 (2)	0 (1)	0 (0)	0 (1)	0 (0)	1 (6)
5	15	5	3 (12)	1 (5)	0 (6)	–	–	13 (0)	–
6	5	6	1 (10)	6 (0)	–	0 (0)	–	0 (0)	–
7	10	6	1 (2)	5 (12)	–	0 (0)	–	0 (0)	–
8	15	5	7 (16)	5 (9)	–	0 (0)	0 (0)	0 (0)	–
Total	–	45	16 (53)	28 (30)	6 (23)	2 (5)	8 (11)	19 (0)	1 (6)

Symbol "–" indicates no nest box inspection.

Except for 2024, when only 20 nest boxes were inspected, the number of boxes inspected each year ranged from 51 (in 2022) to 81 (in 2023) (5–20 per site). The number of inspections carried out annually ranged from 1 to 7 (45 in total, varying by year) (Table 1). In all locations, nest box inspections were consistently carried out between 1 June and 31 October (at least once per month). In subsequent years, inspections were performed on the same or similar dates.

All captured individuals were genetically identified through the analysis of selected polymorphic microsatellite loci. Total genomic DNA was isolated from hair with bulbs (see Moska et al., 2021, 2023 for details).

The study plots differed in species composition and stand age (Table 2). In locations 1, 2, 3, 5, and 8, pedunculate oak was the clearly dominant species, while in locations 4, 6, and 7, common beech dominated. Stand age was divided into two groups: younger stands, consisting of trees aged 53–78 years, and older stands, consisting of trees aged 88–188 years (most over 100 years old).

On the basis of data obtained from the State Forests (Henryków Forestry Division) and own observations, it is known that in the years 2018–2024, the beech and oak yields in the area of the Niemczańsko-Strzelińskie Hills varied. For analyses, all years in the study period were classified as either mast years (2018, 2020, 2021, 2022) or non-mast years (2019, 2023, 2024).

Statistical analyses and visualization of the results were performed in the R package (R Core Team, 2024). Due to small group sizes and clustering with two-level factors, statistical significance was assessed using two-sample permutation tests at the 0.05 significance level.

Results

During the entire 7-year period, 208 dormice were found in the study area (Table 1).

Analysis of the relationship between the number of all individuals (without division by age) and the species composition of the stands in which the nest boxes were located indicates that dormice preferred stands in which oak was the dominant species. A similar pattern was observed when analyses were conducted separately for adults and juveniles. In the case of adult individuals, the observed correlation was significant ($p = 0.05$) (Fig. 2).

Subsequent analyses examined the dependence of dormouse abundance on the age of the stand in which the nest boxes were hung. However, these analyses showed no significant differences, whether considering all individuals together or separating them into the two age groups.

Because beech and oak masting varied from year to

Table 2. Species composition and average age of stands (with coordinates) at each site

Locality	Coordinates	Stand composition	Stand age (in years)
1	50°43', 16°57'	O – 80%, S – 10%, A – 10%	88, 103
2	50°71', 16°95'	O – 100%	98, 113
3	50°71', 16°97'	O – 60%, L – 20%, AS – 10%, SP – 10%	103
4	50°38', 16°57'	B – 100%	168
5	50°43', 17°07'	O – 70%, L – 10%, BI – 10%, H – 10%	58
6	50°42', 17°04'	B – 60%, O – 20%, S – 10%, SP – 10%	60,78
7	50°69', 17°06'	B – 90%, O – 10%	113, 148, 188
8	50°37', 17°02'	O – 70%, B – 30%	118, 138, 153

O – oak *(Quercus robur)*, S – sycamore *(Acer pseudoplatanus)*, A – acacia *(Robinia pseudoacacia)*, L – larch *(Larix decidua)*, AS – ash *(Fraxinus excelsior)* , SP – spruce *(Picea abies)*, B – beech *(Fagus sylvatica)*, BI – birch *(Betula pendula)*, H – hornbeam *(Carpinus betulus)*.

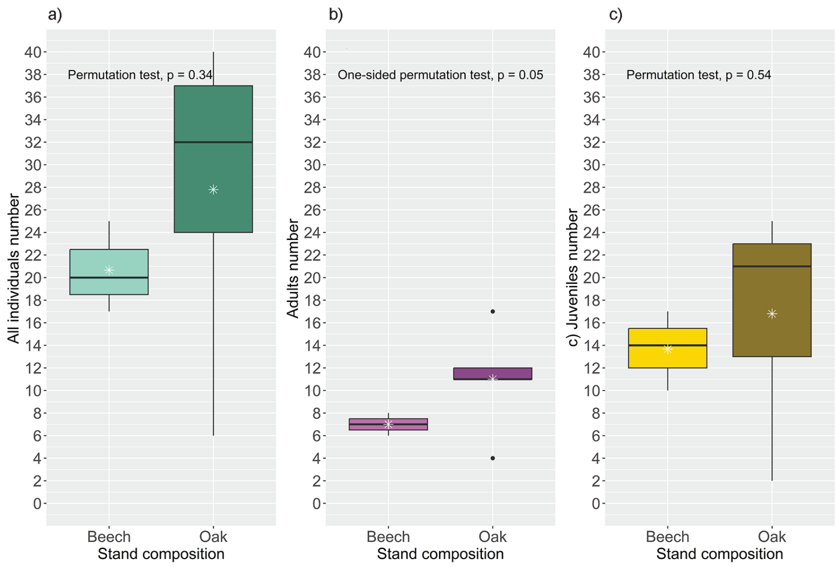

Fig. 2. The relationship between the number of: a) all individuals, b) adults, c) juveniles and stands composition (* – mean).

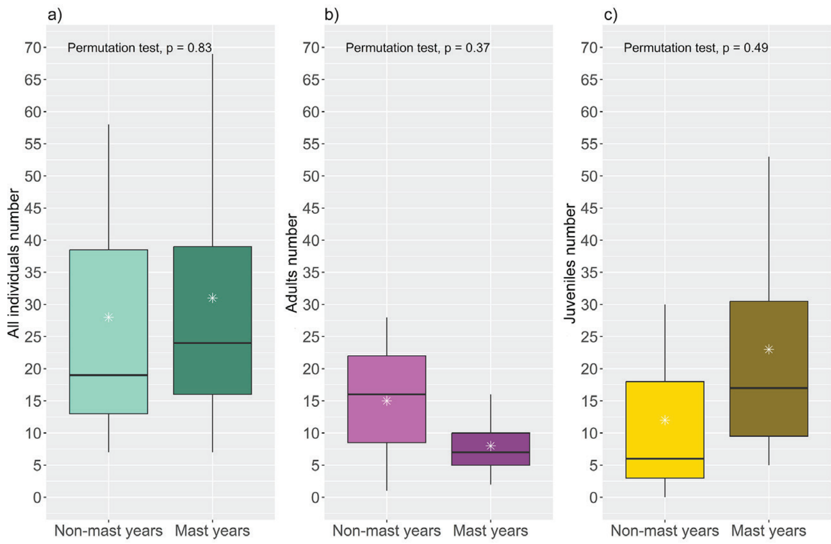

Fig. 3. The relationship between the number of: a) all individuals, b) adults, c) juveniles and non-mast and mast years (* – mean).

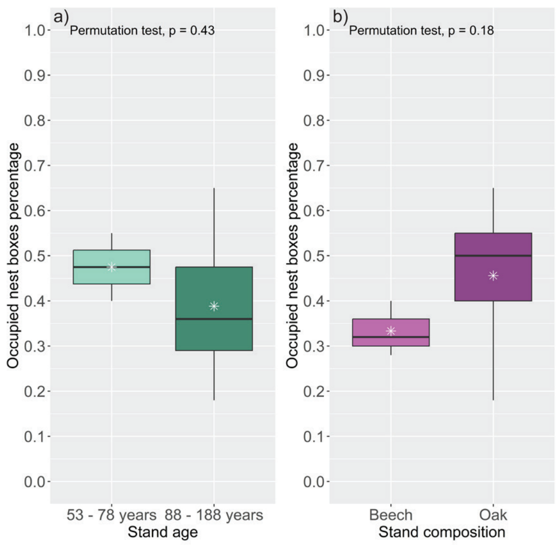

Fig. 4. Comparison of nest box occupancy in stands differing in age (a) and composition (b). (* – mean).

year during the study period, the relationship between seed abundance and the number of individuals found in the nest boxes was analysed. When comparing the abundance of all dormice in mast and non-mast years, no significant differences were found. After dividing the population into adults and juveniles, a statistically insignificant increase in the number of juveniles was observed in mast years (Fig. 3).

When comparing nest box occupation in younger and older stands, the study showed that nest boxes in younger stands—i.e., those in which tree age did not exceed 78 years—were occupied more readily. When analyzing the same parameter in relation to stand composition, more nest boxes were occupied in oak than in beech stands. However, both relationships were statistically nonsignificant (Fig. 4).

Additionally, the percentage of occupied nest boxes was higher in masting years (not statistically significant). In contrast, seed yield did not affect the average

Fig. 5. The relationship between the percentage of occupied nest boxes (a) and the dormice number per nest box (b) in non-mast and mast years (* – mean).

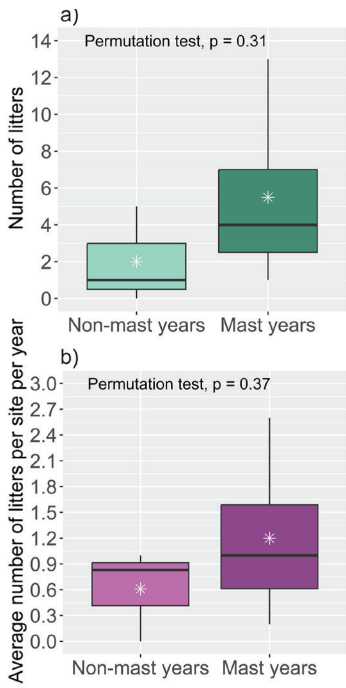

Fig. 7. The relationship between: the number of litters (a) and the average number of litters per site per year (b) and non-mast and mast years (* – mean).

number of individuals per nest box (Fig. 5).

During the 7-year study, 28 dormouse litters (128 young in total) were found in the study area. Litter size ranged from 2 to 7 individuals (average 4.5 ± 1.47 per litter). The mean number of litters was analysed in relation to stand age and composition. There was no association between the number of litters and stand age, but a statistically significant difference (p = 0.05) was found between oak and beech stands, with more litters recorded in oak stands (Fig. 6). In addition, both the total and the average number of litters per site per year increased in years when trees fruited abundantly, although these differences were not statistically significant (Fig. 7).

A maximum of two adults (i.e., individuals after their second hibernation) were found sharing a nest box at the same time during the 7-year nest checks. In contrast, nest-box sharing among yearling individuals (after the first hibernation) was more frequent. In this age group, up to seven individuals were found in a single nest box at the same time.

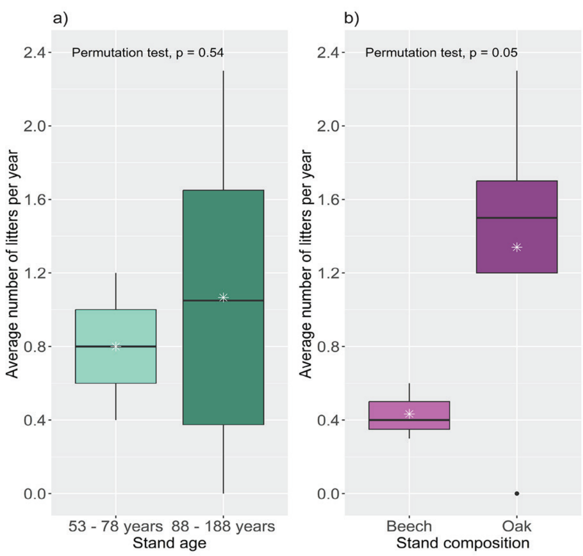

Fig. 6. The relationship between the average number of litters per year and the stand age (a) and the stand composition (b) (* – mean).

Discussion

The edible dormouse is a species associated primarily with deciduous forests with a high proportion of beech, whose fruit forms the basis of its diet, especially in the second half of summer and in autumn (Jurczyszyn, 2018). However, in the Niemczańsko-Strzelińskie Hills, a higher abundance of these rodents (almost 67% of individuals) was observed in forests where pedunculate oak was the dominant species and where, except for one plot, beech did not occur. The analysis of litter size in relation to stand composition showed the same trend, i.e., larger litters were found in oak-dominant stands than in stands clearly dominated by beech. The data obtained support the hypothesis that one of the responses of rodents to the cyclical abundance of their preferred seeds may be the choice of habitats where, in addition to their favourite food, alternative food sources are also available during periods of scarcity of the former (i.e., common beech fruit in the case of dormice) (Cornils et al., 2017; Ruf and Bieber, 2020).

The edible dormouse is a nocturnal arboreal rodent that nests most readily in tree hollows. Considering stand age, it is known that older stands provide more natural shelters. Thus, it would be expected that in older stands the level of nest box occupation by this species should be lower compared to younger stands. Although the analysis did not show a significant association between the number of dormice and stand age, a difference was observed in nest box occupation between younger and older stands. Nest boxes in younger stands were inhabited more readily, likely due to the lower availability of natural shelters.

We also found that the percentage of occupied nest boxes was higher in masting years. This may be explained by the fact that, as shown by Cornils et al. (2017), during non-masting years, many dormice (especially those with large fat reserves in spring) return to underground burrows and enter a state of temporary torpor, becoming inactive. As a result, in non-masting years, the percentage of nest boxes inhabited by dormice decreases by half compared to years with large seed crops.

Based on literature data, it is known that the litter size of *Glis glis* can range from 1 to 11 young (Kryštufek, 2010; Vekhnik, 2020; Vekhnik and Dyuzhaeva, 2022), which was confirmed by our research, where litter size ranged from 2 to 7. The lower litter size found in 2018–2024 may be because 3 years during the 7-year study period (2019, 2023, and 2024) were non-masting years, and only two of the remaining years (2020 and 2022) were years in which the tree species in question fruited very intensively. The results of a study by Lebl et al. (2011) showed that average litter size is larger in years with higher seed availability.

When we analyzed the number of litters in a given year, we found that the fewest litters occurred in 2021 and that in 2023, no young dormice were found at all. Our observations correspond closely with the findings of Schlund et al. (2002). These researchers showed that in the year following a large crop of beech nuts, dormice are characterised by low reproductive rates. According to these authors, this is an adaptation to predictable low food availability, as it is unlikely that trees will fruit abundantly for two consecutive years. During our study period, the highest abundance of fruiting was recorded in 2020 and 2022. As shown by Schlund et al. (2002), in the subsequent years (i.e., 2021 and 2023, respectively) the decrease in the number of litters was almost five-fold (in 2021) and as much as eleven-fold (in 2023) compared to the masting years (with a comparable number of checked boxes and number of controls, according to our observations). The absence of young in unseeded years was also reported by Bieber and Ruf (2004).

A maximum of two adults (females) were found in a nest box at the same time during the seven years of shelter inspections. Co-use of nest shelters by dormice has been demonstrated in several previous studies. The simultaneous presence of several females was observed, among others, by Pilastro et al. (1996) and Pilāts et al. (2009). Pilastro et al. (1996) found several closely related females (sometimes called helpers) sharing nest boxes and showed that these individuals were close relatives, particularly mother–daughter pairs.

In 2024, extreme temperature fluctuations during the beech masting period in the Niemczańsko-Strzelińskie Hills led to an almost complete failure of seed production, following a previous non-masting year. Daytime temperatures reached exceptionally high values of 27–29 °C in early April, followed by sudden night frosts of −4 °C and −6 °C on 22–24 April. These conditions disrupted beech masting and resulted in a lack of viable seeds. Consequently, the availability of high-energy food resources for dormice was severely reduced. During the study period (June–October 2024), only one female with six young was recorded across 20 nest boxes during seven inspections, indicating an exceptionally low breeding rate.

This case illustrates how abrupt climatic anomalies—particularly sharp spring temperature drops following early warm spells—can disrupt the masting cycles of key forest tree species and, in turn, strongly affect the population dynamics of dependent fauna. The observed collapse in dormouse reproduction emphasizes the potential for increasing climate instability to decouple long-established ecological interactions and to threaten species adapted to cyclic resource availability. Such conditions likely triggered extended periods of estivation among dormice after hibernation (Ruf and Bieber, 2020).

Climate change, including above all a noticeable increase in the average temperature of the Earth's atmosphere, which has been intensifying since the middle of the 20th century, is not negligible for living organisms (Abbass et al., 2022). In the temperate climate zone, which characterises most of Europe (including Poland), noticeable consequences of rising temperatures include the blurring of seasonal boundaries, a decrease in the number of days with snow cover, changes in the duration of the vegetation period, and, importantly, the loss of cyclicity and synchronisation in the fruiting of some plant species, including trees.

Recent studies on *Fagus sylvatica* (Bogdziewicz et al., 2020) show that climate warming disrupts the temperature sequence that historically triggered abundant fruiting. Beech trees produced the highest seed yields when a cool summer was followed by a warm one, but such sequences have become rare, as hot summers now occur almost every year. This frequent stimulation of flowering prevents trees from rebuilding their reserves. As a result, flowering synchronisation has deteriorated, pollination efficiency has fallen, and the percentage of seeds destroyed by the moth *Cydia fagiglandana* has increased from 1% to 40% over the past four decades, leading to a 50–80% decline in the number of seeds capable of germinating.

Similar patterns appear among moderately fruiting tree species, where more frequent favourable conditions reduce interannual variability but also weaken the ecological advantages of synchronised reproduction (Hacket-Pain and Bogdziewicz, 2021). Consequently, mast events have become less synchronised and more resource-limited, resulting in reduced viable seed production and increased pest pressure (Pureswaran et al., 2018). Altered seed availability also affects seed-dependent mammal and bird populations, changing trophic dynamics and feedback loops within the ecosystem. Increased frequency of partial or failed masting may reduce the amount of food available to sustain small-mammal populations, whereas frequent but smaller masting may promote rapid population growth in generalist species such as wild boar (*Sus scrofa*; Touzot et al., 2020).

Such cascading effects suggest that climate-induced desynchronisation of tree reproduction is not only a reproductive problem for plants but also a broader disruption of the community structure of temperate forests and their regenerative potential. Over the next few years, a continuous abundance of beech nuts may persist, accompanied by a decline in the number of viable seeds. This phenomenon may be very detrimental to dormice, as the cyclical and synchronised nature of masting—on which they rely—is disappearing, and years with significantly reduced beech nut production are becoming increasingly dominant. Progressive climate change, therefore, poses a considerable challenge for dormice, particularly given their several-month hibernation. Further comprehensive research is needed to determine how these rare rodents, which are protected in Poland, will cope with ongoing climate change.

This study investigated the relationship between stand age and composition and the abundance and biology of the edible dormouse. While the relationship between dormouse reproduction and the mast cycles of trees is well documented (Vekhnik et al., 2022), the effects of stand age and composition on dormouse populations remain poorly studied, so any attempt to fill this research gap requires special scientific attention. Although the study was limited to the territory of Poland, the results may be viewed as part of a broader pattern of processes occurring globally, illustrating the impact of climate change and human forest management on the interactions between forest stands and the organisms inhabiting these ecosystems.

Acknowledgements

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