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Using public-sourced photos to track changes in moose antler size during a 20-year hunting ban

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Abstract

Hunting directly impacts the population dynamics of ungulates and can have a significant effect on the quality of phenotypic traits such as horns or antlers. In Poland, following a demographic collapse in the 1990s and the introduction of a hunting ban in 2001, the population of moose (*Alces alces*) has increased from 1,800 to over 20,000 individuals, recolonising its former range. As the moose is a charismatic species and a popular subject for nature photography, we analysed changes in antler size and shape in this cervid between 2005 and 2021 based on photos of male moose and antler casts provided by photographers or available in social media. Our findings indicate that during the hunting ban, the probability of observing the cervina antler type significantly decreased over time, from 47% in 2012 to 28% in 2021. Meanwhile, the probability of observing the intermediate and palmate antler types significantly increased from 44 to 53% and from 9 to 19%, respectively. The mean number of tines significantly increased from 3.2 in 2005 to 4.7 in 2021, and the antler size index significantly increased from 3.4 to 3.9. The most likely mechanism behind the observed changes could be the ageing of a population released from hunting pressure. We also observed regional variation in antler size, which is likely related to differences in environmental conditions. Our study serves as an example of how passive citizen science can contribute to our understanding of ecological trends and the quantification of population patterns. It also has important implications for management of species affected by trophy hunting.

Keywords Alces alces · Hunting release · Large herbivore · Citizen science · Trophy hunting

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Introduction

The secondary sexual traits, such as antlers or horns, have evolved through sexual selection (Clutton-Brock et al. 1980; Coltman et al. 2002; Bro-Jørgensen 2007). Males utilize horns and antlers to demonstrate their quality when selecting mates or displaying fighting ability towards other males, serving as weapons during combat (Clutton-Brock et al. 1980; Hoem et al. 2007; Bergeron et al. 2008; Vanpé et al. 2007). The size of secondary sexual traits can influence the mating success of males (Coltman et al. 2002). While their size is heritable, it is also strongly influenced by other factors, including age, body mass, and environmental conditions. Additionally, management practices, such as selective culling, may impact the size of horns or antlers (Pozo et al. 2016; Balčiauskas et al. 2017). Body and antler size are important criteria for hunters' preferences (Allendorf and Hard 2009; Solberg et al. 2000), which can have long-term consequences for animal populations and result in genetic

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and phenotypic deterioration of harvested populations (Coltman et al. 2003; Pigeon et al. 2016).

The moose (Alces alces) is the largest member of the Cervidae family and the second largest herbivore in the northern hemisphere. Moose antlers exhibit significant variation in shape and size, ranging from deer-like cervina types to large palmates with numerous tines, with various intermediate forms also common (Nygrén et al. 2007). Antler characteristics are influenced by several factors, including genetic and environmental factors (Schmidt et al. 2001; Kruuk et al. 2002). Generally, moose antler size increases with age until around 10 years and then declines (Gasaway et al. 1987; Stewart et al. 2000; Nygrén et al. 2007). Similar age-dependent differences have been observed within antler shape types, with cervina types dominating in the youngest age groups, while the proportion of intermediate and palmated types is highest at prime age (Engan 2001; Nygrén et al. 2007).

The moose population in Poland is situated at the southwestern edge of the species' distribution range in Europe (Niedziałkowska et al. 2016). After being drastically reduced during World War II, the population recovered in the following decades until the 1990s, when it experienced another collapse due to overestimation of population size and hunting harvest exceeding population growth (Bobek et al. 2005). At that time, the moose population numbered below 2,000 individuals and was confined to a few areas encompassing wetlands in Biebrza, Polesie, and Kampinos National Parks, located in central and eastern Poland. Hunting of moose, which has been a game species since 1945, was suspended in 2001 to facilitate population recovery (Regulation of the Minister of the Environment, 2001). Over the course of the 20-year hunting moratorium, the moose population has increased to over 20,000 individuals and has progressively expanded throughout the country (Dziki-Michalska et al. 2019; Borowik et al. 2021). The highest population densities are recorded in eastern and northeastern Poland (Borowik et al. 2021). Despite several attempts by government officials, moose hunting has not been resumed primarily due to environmental pressure from wildlife biologists and non-governmental organizations (Borowik et al. 2018). These groups have emphasized the significance of this charismatic species for nature and tourism and have expressed concerns regarding the sustainability of hunting practices that had pushed the moose population to the brink of extirpation (Putkowska-Zmoter and Niedziałkowski, 2021). Given the rarity of palmated antler types prior to the hunting ban, it was widely accepted that the most typical form of moose antlers in Poland is the cervina type, primarily due to genetic factors and environmental conditions (Dzięciołowski and Pielowski 1993).

Citizen science has emerged as a cost-efficient method to support scientific research and gather data for wildlife monitoring that extends beyond the spatial and temporal capacities of researchers (Shirk et al. 2012; Sun et al. 2021). With the widespread accessibility of the internet and the development of social media, citizen science has increasingly been employed to document and study wildlife (Bonney et al. 2009; Follett and Strezov 2015; Liberatore et al. 2018). While traditional citizen science typically relies on organized campaigns to collect specific data, there are also numerous ad hoc wildlife observations available on social media. These data represent a valuable resource for "passive citizen science" - the utilization of social media data that are not associated with any particular citizen science program but represent an untapped source of valuable ecological data (Edwards et al. 2021). The advent of digital photography and the growing interest in nature photography, coupled with the resources provided by social media, grant access to a large number of animal photos that can be analyzed for various characteristics (Vieira et al. 2017; Drury et al. 2019; Nowak et al. 2020).

The moose is a popular subject of nature photography, with an increasing number of photos being shared on social media platforms. Thus, in this study, we utilized photos of male moose and cast antlers sourced from social media and provided by nature photographers to investigate the influence of a 20-year hunting ban on the size of moose antlers in Poland. We hypothesized that the release from hunting pressure would lead to population ageing, resulting in an increase in antler size and a higher proportion of intermediate and palmate antler forms. Additionally, we examined regional variations in antler size to elucidate the environmental factors influencing antler growth, which could serve as a foundation for more comprehensive studies in the future.

Methods

Study area

The study covered all of Poland, however majority of data originated from core areas of moose distribution in northeastern, eastern and central Poland. Forests cover 30.9% of Poland, ranging from 21.5 to 25.8 in central Poland to 35.7– 49.3% in north-western and south-eastern parts of the country. Forests are dominated by Scotch pine (*Pinus sylvestris*) (75.5% of tree stands) (Statistics Poland, 2020). There are thirteen wetlands of international importance included in Ramsar Convention on Wetlands, covering 0.5% of Poland. Majority of these wetlands are located in north-eastern Poland. Fig. 1 The distribution of moose

regions in Poland



 Table 1 Characteristic of regions of moose distribution in Poland

Region	Forest cover (%)	Habitat characteristic	Human density <i>n</i> /km ²
Warmia and Masuria (= Masuria)	31.7	Broadleaved forests in the northern part, coniferous and mixed forests in the south, concentration of glacial lakes (2,700 in total) covering over 11% of the area.	59
Biebrza and Narew (=Biebrza)	20.9– 22.8	Marshlands along the river valleys surrounded by coniferous forests and farmland.	30–50
Podlasie	31.0	The largest in Poland forests complexes of Białowieża (decidu- ous and mixed forest) and Knyszyn (coniferous forests)	58
Polesie	23.4	Mosaic landscapes of farmland, coniferous and mixed forests, wet- lands and the Bug river valley	83
Kampinos	23.4	Coniferous forests interspersed with meadows and farmland along the Vistula river valley	153
Newly recolonised area	21.5– 38.3	Southern and western parts of Poland dominated by coniferous forest and farmland	77–133

Climate of Poland has both maritime and continental traits. It is characterized by a high degree of weather variability with hot summers and cold winters. Mean ambient temperature is 8.7 °C (https://climateknowledgeportal.worldbank.org/country/poland/climate-data-historical) and mean annual precipitation -624.5 mm (Ziernicka-Wojtaszek and Kopcińska 2020).

We divided the area of Poland covered by the study into six regions which represented the main areas of moose distribution (Fig. 1; Table 1). The regions covered areas differing in habitats structure and were historically recognised as geographically distinct.

Photo collection and analysis

We collected photos of moose males with antlers or cast antlers from photographers and published in social media. We took photos from several Facebook groups which provided large amount of photos of moose males or cats antlers from Poland (#JESTEMZŁOSIEM, https://www.facebook.com/ groups/2233163306956079 or RosochyŁosiaCałaPolska https://www.facebook.com/groups/2673283752714439). Only pictures of moose with fully grown antlers without velvet were used. Yearlings with single tine antlers were Fig. 2 Antler measurements (drawing by Tomasz Samojlik) (A) and examples of moose photos from social media showing different types of antlers: cerivna (photo by Krzysztof Górecki) (B); intermediate (photo by Piotr Tałałaj) (C); and palmated (photo by Patryk Sacharewicz) (D)



excluded from the analysis due to lack of variability in antler type and sizes in this age class.

For each photo, we defined a year of the antler growth, author of the photo and region where the photo was made. For many photos, we directly contacted the photographers to obtain or clarify data on year and location. The photos from the same years and locations with similar antler parameters were carefully inspected to eliminate duplicate individuals. The number of photos included in the analysis increased from year to year, probably related to the growth and spread of the moose population and the development of social media and moose-related Facebook groups. In total, the final analyses included 1371 photos taken between 2005 and 2021 (Fig. SI 1 and SI 2).

Antler parameters

Based on the photos we described the following parameters of antlers: 1) antler type: (a) cervine (with few rough and long tines, but no flattenings), (b) intermediate (antlers with flattenings or narrow palms and long tines), and (c) palmated (distinct palm with short tines) (Engan 2001) (Fig. 2B-D, SI 4); 2) number of tines as maximal number of tines on one of the antlers; 3) antler size index – ratio between maximum spread of antlers (in pixels measured in IrfanView software) and the width of head (in pixels) below the antler base (only for frontal photos of moose) (Fig. 2A). We did not analyse total number of tines on both antlers, because pairs of antlers were not available for majority of antler casts and the number of tines on both antlers was strongly correlated (N=876; r=0.98; P<0.0001).

Table 2 Specification of models used in statistical analyses. Year in
Model 2 and 3 was fitted as a quadratic polynomial. GLM - general-
ized linear model; OLR – ordinal logistic regression

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	Model type	Dependent variable	Independent variables
Model 1	OLR	Antler type	Year
Model 2	Binomial GLM	Number of antler tines	Year, Region
Model 3	Gaussian GLM	Antler size index	Year, Region

Antler spread and number of antler tines are regarded as a good indicators of antler size (Gauthier and Larsen 1985; Solberg and Sæther 1994).

Statistical analyses

We tested for temporal change in antler type using ordinal logistic regression ("clm" package; Christensen 2019) (Model 1; Table 2). The response variable was antler type, coded as follows: 1 - cervine, 2 - intermediate, 3 - palmated (Engan 2001). As the palmated type was only observed since 2012, we restricted the analysis of antler types to 2012–2021. The assumption of proportional odds was not violated (P = 0.06). To test the temporal change and regional differences in number of antler tines we ran negative binomial generalized linear model (GLM; "MASS" package; Venables and Ripley 2002) (Model 2; Table 2), while GLM with Gaussian error structure (Model 3; Table 2) was used to study the differences in antler size index. In both models the year of antler growth and region were set as independent variables. As we expected non-linear relationship between year and studied antler parameters, we fitted year as a quadratic polynomial. For model with a Gaussian error structure, we checked model assumptions by visual inspection of diagnostic plots (residuals vs. fitted values and Q-Q residuals) (Fig. SI 3). As the model residuals were not heteroscedastic and normally distributed, we assumed that the model assumptions were met. All statistical analyses were performed in R (R Core Team 2024).

Results

The proportion of antler types changed over the study period (z=3.57, P<0.001; Fig. 3). The probability of observing cervina type decreased with time from 47% (95% CI [38, 56]) in 2012 to 28% (95% CI [25, 31]) in 2021, while the probability of observing intermediate and palmate type during this period increased from 44% (95% CI [38, 50]) to 53% (95% CI [50, 56]), and from 9% (95% CI [7, 14]) to 19% (95% CI [17, 22]), respectively (Fig. 3).

Median number of tines was 4.0 (range: 2–11) and median antler size index was 3.97 (range: 1.6–7.5). The number of tines significantly increased in time from 3.2 in 2005 to 4.7 in 2021 (z = -2.11, P = 0.03; Fig. 4A; Table 3). However, the highest increase was observed between 2005 and 2015 and then stabilization in the number of tines was observed (Fig. 4A). Similar temporal trend was observed for the antler size index (z = -3.02, P = 0.003; Table 4). This index increased from 3.4 in 2005 to 3.9 in 2021 (Fig. 4B).

We recorded some regional differences in the number of tines and antler size index (Fig. 5). The largest antlers (the highest number of tines and antler size index) were observed in Masuria and Polesie, while the smallest in the Biebrza and newly recolonised area (Tables 3 and 4; Fig. 5).

Discussion

Hunting is a common tool in ungulate management worldwide. It may significantly influence not only population dynamics but also many other aspects of animal ecology including behavior (Ericsson and Wallin 1996), space and habitat use (Reyna-Hurtado and Tanner 2005; Mols et al. 2022), sex ratio and age structure (Langvatn and Loison 1999) as well as size of sexually selected organs such as horns and antlers (Coltman et al. 2003). In some countries, including Poland, trophy hunting is dominating motivation for hunting cervid males (moose, red deer, roe deer) with selection rules depending mainly on antler characteristics and age. It was showed that both, selective and intensive hunting may influence size of male weapons (Pozo et al. 2016; Balčiauskas et al. 2017).

The ban on moose hunting in Poland created a unique field experiment to investigate how the lack of culling will affect not only the number and distribution of moose, but also size and shape of their antlers. Our study showed that the size of moose antlers significantly increased during 20 years of hunting ban.

The most plausible mechanism responsible for an increase in moose antler size in Poland during hunting ban was most probably ageing of the population. Hunting usually results in higher population mortality and reduced life expectancy, with old individuals becoming rare (LaSharr et





Fig. 4 Change in the number of tines (A) and antler size index (B) in moose in Poland in 2005–2021. Results of GLMs (Model 2 and 3)

al. 2019; Pozo et al. 2016). Thus, an inverse relationship is expected between hunting intensity and age structure – populations intensively harvested exhibit a downward shift in age structure (Langvatn and Loison 1999; Jenks et al. 2002; Kvalnes et al. 2016; Schindler et al. 2017). Decreasing horn and antler size often reflect younger male age structure in hunted populations (Schmidt et al. 2007; Monteith et al. 2013; Rivrud et al. 2013). Unfortunately, we were not able to recognize age of males on public sourced photos, but lack of culling and increasing population number certainly led to the population ageing. In effect, males got older and grew larger antlers, as antler size strongly depends on age of males and the largest antlers are observed for males of 9–11 years (Stewart et al. 2000; Nygrén et al. 2007).

Beside the size, proportion of different forms of antlers in population is also strongly related to age structure of Table 3Temporal changes and regional differences in the maximumnumber of tines in moose antlers in 2005–2021. Results of the negativebinomial generalized linear model (Model 2). Region: MW – Masuriaand Warmia, BN – Biebrza and Narew, POD – Podlasie, POL – Polesie, KAM – Kampinos, NC – Newly colonised area. Significant effectsare shown in bold

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Variable	Estimate \pm SE	z-value	Р
Year	7.66 ± 3.61	2.12	0.03
Year^2	-0.002 ± 0.001	-2.11	0.03
Region			
POD vs. BN	0.14 ± 0.05	2.89	0.004
POL vs. BN	0.11 ± 0.04	2.93	0.003
MW vs. BN	0.23 ± 0.05	4.60	< 0.001
KAM vs. BN	0.05 ± 0.05	1.08	0.28
NC vs. BN	-0.009 ± 0.10	-0.09	0.93
POL vs. POD	-0.02 ± 0.04	-0.55	0.58
MW vs. POD	0.09 ± 0.05	1.81	0.07
KAM vs. POD	-0.09 ± 0.05	-1.82	0.07
NC vs. POD	-0.15 ± 0.10	-1.42	0.16
MW vs. POL	0.11 ± 0.04	2.69	0.007
KAM vs. POL	-0.06 ± 0.04	-1.64	0.10
NC vs. POL	-0.12 ± 0.10	-1.25	0.21
KAM vs. MW	-0.18 ± 0.05	-3.66	< 0.001
NC vs. MW	-0.24 ± 0.10	-2.31	0.02
NC vs. KAM	-0.06 ± 0.10	-0.58	0.56

Table 4 Temporal changes and regional differences in the moose antler size index in 2005–2021. Results of the generalized linear model (Model 3). Region: MW – Masuria and Warmia, BN – Biebrza and Narew, POD – Podlasie, POL – Polesie, KAM – Kampinos, NC – Newly colonised area

Variable	Estimate ± SE	z-value	P
Year	20.0 ± 6.61	3.02	0.003
Year^2	-0.005 ± 0.002	-3.02	0.003
Region			
POD vs. BN	0.07 ± 0.09	0.77	0.44
POL vs. BN	0.17 ± 0.08	2.10	0.04
MW vs. BN	0.34 ± 0.12	2.77	0.006
KAM vs. BN	0.12 ± 0.07	1.61	0.11
NC vs. BN	-0.21 ± 0.22	-0.97	0.33
POL vs. POD	0.11 ± 0.09	1.12	0.26
MW vs. POD	0.27 ± 0.13	2.07	0.04
KAM vs. POD	0.05 ± 0.09	0.58	0.56
NC vs. POD	-0.28 ± 0.22	-1.25	0.21
MW vs. POL	0.16 ± 0.12	1.32	0.19
KAM vs. POL	-0.06 ± 0.08	-0.69	0.49
NC vs. POL	-0.39 ± 0.22	-1.76	0.08
KAM vs. MW	-0.22 ± 0.19	-1.84	0.07
NC vs. MW	-0.55 ± 0.23	-2.34	0.02
NC vs. KAM	-0.33 ± 0.22	-1.52	0.13

males in the population (Nygrén et al. 2007; Child et al. 2010). Hunting regulations for moose in Poland, prior to the ban, treated males with cervine antlers with a maximum of 4 tines as selective, but also allowed decisions to be made



Fig. 5 Regional variation in number of tines (A), and antler size index (B) in moose in Poland in 2005–2021. Whiskers denote 95% CI. Results of GLMs (Model 2 and 3)

regarding the shooting of non-selective males with intermediate and palmated antlers. Less controlled and excessive culling at low population size most likely led to the rejuvenation of the population and the disappearance of the stronger antler types. Under these conditions, most males probably met the selection criteria, as evidenced by the low number of tines at the beginning of the period analysed. The cervine type is the most common antler type in young age classes and its proportion decreases with population ageing, while the opposite relationship is observed for intermediate and palmated forms. In fact, the ageing of moose populations in Poland resulted in a shift of antler types from the predominance of cervine to intermediate forms at the beginning of the hunting ban. The appearance of more palmated antlers and their relatively high proportion after 20 years of hunting ban is particularly interesting, as many specialists claimed that the cervine form was a typical antler type in Poland. (Dzięciołowski and Pielowski 1993).

Variation in antler size in cervids is density-dependent (Torres-Porras et al. 2009; Vanpé et al. 2007; Peláez et al. 2018; Smolko et al. 2022). It was shown that antler size increases with decreasing population densities, which was attributed to enhanced nutrition at low population densities (Schmidt et al. 2007). We observed the reverse pattern of increase in antler size with growing moose population and presumably moose densities. This can be explained by the high availability of vacant areas to be settled by moose at the beginning of studied period when the ban on moose hunting was introduced which could relax competition for food resources. Most probably, most of the moose subpopulations in Poland were much below ecological capacities of inhabited areas, hence density-dependent mechanisms in antler size have been not observed yet. However, observed stabilization of antler size in recent years, may indicate that density-dependant mechanisms have started operating or the quality of antlers reached its maximum allowed by foraging conditions. It was found that environmental conditions influence size of cervids antlers (Smolko et al. 2022), because forage availability and quality, influencing body mass and related antler size, is crucial for antler development (Horrell et al. 2015).

Furthermore, we found significant differences in the antler size between studied regions. Smallest size of moose antlers in newly colonised areas is probably an effect of younger moose populations created mainly by migrating individuals. In the remaining regions, the most plausible explanation behind the observed differences is an availability of high quality habitats. The Biebrza and Kampinos areas are less diverse and they are dominated by pine tree stands, which offers lower quality forage (Borowik et al. 2020). The remaining areas, where moose antlers were of the highest quality, offer more diversified environments dominated with rich in undergrowth mixed and deciduous forests (Niedziałkowska et al. 2010; Borowik et al. 2020) and are characterised by higher densities of ungulates (Borowik et al. 2013). In addition, moose populations from Biebrza and Kampinos most probably occur at higher densities, as those areas served as refugia during collapse of moose population in Poland in 1990s (Świsłocka et al. 2013).

It is difficult to say if the quality of moose antlers is an effect of genetic structure, which was found as one of the factors responsible for large scale patterns in phenotypic characters in moose (Herfindal et al. 2014). The lowest quality antlers were found in the populations in Biebrza and Knyszyn characterised by the lowest genetic diversity and they are the most divergent from other moose populations

(Świsłocka et al. 2013). Biebrza population is a relict one with very limited immigration level (Świsłocka et al. 2015) and the Kampinos population arose from an introduction of several individuals from Belarus in 1950s (Niedziałkowska et al. 2014). Thus, partial isolation of this populations and limited immigration rate may influence size and lower change of antlers.

Interestingly, moose antler size after recovery in Poland was smaller than observed in northern latitudes. The median number of antler tines was 4.0 (max. 11), while in Scandinavia and North America it is 8.7-9.0 (max. 25) (Stewart et al.2000; Nygrén et al. 2007). This may result from smaller body size of moose in Poland (Dzięciołowski and Pielowski1993), occurring on the southernmost edge of distribution, as body size of this species follows Bergmann's rule (Sand et al. 1995; Herfindal et al. 2014).

After 20-years of hunting ban we observe recovery of moose populations in Poland and significant strengthening of the quality of their antlers. This may have further consequences, as ageing of the population and growth of antler size may influence the reproductive success of males. Positive correlations between horns on antlers size and male breeding success have been found in several species of cervids and bovids (Coltman et al. 2002; Kruuk et al. 2002; Robinson et al. 2006; Willisch et al. 2015). Moose males with larger antlers probably benefit more, as their lifetime breeding success is expected to be higher (Kruuk et al. 2002). In white-tailed deer (*Odocoileus virginianus*), antler size had the greatest effect on male reproductive success within older male age structures (Newbolt et al. 2017).

Conclusions

Our study is another example how passive citizen science can be used to help understand ecological trends and impact of game management on wildlife. The growing interest in nature and visitation to wilderness, including national parks (Burivaloba et al. 2018; Adach et al. 2023), combined with the development of photo equipment and social media results in increasing participation of citizen science in wildlife monitoring. Thus, crowdsourced data have become an important component in various research projects (Ghermandi and Sinclar, 2019). In case of charismatic species, additionally equipped with impressive antlers, being a subject of nature photography and collection of cast antlers, such as moose, it is possible to collect robust amount of records to quantify species or population patterns.

Our findings has important implications for management of species affected by trophy hunting as it demonstrates how release from hunting influence quality of male secondary sexual weapon in a wild populations. When mortality due to hunting increases, as it was the case of overhunted moose populations in Poland, the direct effects of hunting on antler size is becoming evident (Pozo et al. 2016). The increase in moose antler quality may further impact mating competition and the breeding success of males.

In Poland, there is an increasing pressure to resume moose hunting due to increasing conflicts caused by recovered populations of this large herbivore. As trophy hunting is the main motivation for hunting male cervids in Poland, the reopening of moose hunting may quickly reverse the observed pattern of antler quality growth.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10344-024-01811-5.

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Author contributions "RK conceived the study and designed methodology. RK, PD, KG, SK, RM, PS, and PT collected the materials, RK and NK determined the parameters of moose antlers, TB performed statistical analyses, RK and TB wrote the manuscript and prepared Figs. 1-5; other authors provided editorial advice."

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Data availability The data was deposited in the Open Forest Data repository and can be publicly accessed at https://doi.org/10.48370/ OFD/BNCAOL (Kowalczyk et al. 2023).

Declarations

Ethics approval Not applicable.

Conflict of interest The authors declare no competing interests.

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