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Long-term dietary shifts in a generalist predator, the wolverine (*Gulo gulo*)

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Over the last hundred years, many large carnivore species have suffered range
contractions, population losses, and habitat alterations that may be influencing
their dietary preferences. To identify shifting isotopic niches and reconstruct past
and present diets from species of high conservation concern, stable isotope
analysis (SIA) of δ^{13}C and δ^{15}N values of tissue from museum collections and
ongoing non-invasive monitoring programs offers an effective approach. Here,
we assessed the long-term alterations in the trophic structure of a generalist
large carnivore over a time of population loss and recovery. Wolverine stable
carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes were measured in hair samples
collected from 44 individuals in Finland for the period 1905–2020, and
potential dietary were quantified using isotopic niche metrics shifts in two
study areas. We provide evidence of a long-term diet shift in Finnish
wolverines, with a temporal depletion of hair's δ^{13}C (β = −0.016‰, R^2 = 0.46,
p < 0.001). Correspondingly, there was a shift in the isotopic niches of the
Historical population (before the year 2000) and *Recent* population (after 2000),
with the niche overlap between the *Historical* and *Recent* periods being only 33%
throughout Finland, and even lower in the two study areas (22% to 24%). The
breadth of the isotopic niche, however, did not significantly differ between the
two periods, suggesting that despite a change in diet composition, wolverines
did not specialize more. The trophic level of wolverines in Finland was stable
throughout the study period, with no significant change in δ^{15}N with time (β =
0.0055‰, R^2 = 0.043, p = 0.17). In summary: A) the strong trophic resilience of
this top predator was shown by the stability of its niche breadth and trophic level
feeding regime during periods of population decline and recovery as well as
during a period of major anthropogenic alterations in their environment; B) the
use of SIA methods on historical and recent hairs provided a unique tool to
unravel long-term changes in wolverine feeding strategies.

KEYWORDS

stable isotope analysis, SIA, large carnivores, diet switch, diet niche, isotopic niche

1 Introduction

Terrestrial food webs are often considered to be structured by large carnivores (Wilson and Wolkovich, 2011; Allen et al., 2017; Buskirk, 2023). The top-down control of predators on prey cascades to various taxa through multiple food-web pathways, impacting ecosystem processes at all levels from nutrient cycling to landscape features (Ripple et al., 2014; Winnie and Creel, 2017; Peziol et al., 2023). Despite their crucial ecological function, large carnivore populations have experienced a global decline and range contractions throughout the last century (Wolf and Ripple, 2017; Wolf and Ripple, 2018). Meanwhile, habitat alteration and fragmentation together with climate change have led to modifications in prey species richness and distribution (Christian et al., 2009; Schwensow et al., 2022). The persistence of a predator in an altered ecosystem is then partly predicted by its resilience to changing habitats and prey populations (Hempson et al., 2017). Given the time scale of these alterations and the long generation time of many large carnivore species, the predator's trophic adaptations to changes in the food web may only be observable in the long term, i.e. several decades (Beckmann and Berger, 2003; Moreno et al., 2013).

Stable Isotope Analysis (SIA) is a valuable tool for studying food web ecology, including reconstructions of large carnivores' diets (Rogers et al., 2015; Newton, 2016; Stanek et al., 2017; Stanek et al., 2019). As an organism consumes and assimilates resources, the stable isotope ratios of the food sources will be reflected in the consumer's tissues (DeNiro and Epstein, 1978; DeNiro and Epstein, 1981; Ben-David and Flaherty, 2012). A change in a consumer's carbon ratio value (δ^{13}C) is a proxy for processes such as changes in carbon source, i.e. a diet shift toward an alternative prey (DeNiro and Epstein, 1978; Kaczensky et al., 2017; Reynolds et al., 2019). The nitrogen ratio value (δ^{15}N) on the other hand is typically enriched relative to its food source, thus a high δ^{15}N value indicates a higher trophic level (DeNiro and Epstein, 1981; Layman et al., 2007; Jennings and Van Der Molen, 2015).

Sequentially grown tissues (e.g. hair, bone, feather) encapsulate long-term information about a consumer's diet by retaining the δ^{13}C and δ^{15}N isotopic values from the time of growth and remaining metabolically inert afterward (Rogers et al., 2020; Hamstrom, 2023). Moreover, a tissue such as hair does not degrade as fast as soft organs after death and can be preserved for decades in museum collections, on naturalized specimens or pelts. Hair also has the advantage of being easily sampled non-invasively on living individuals, e.g. using hair traps (Barja et al., 2016). Yet, only a few diet studies have seized the opportunity of using carbon and nitrogen SIA on museum and recent hair samples in terrestrial ecosystems (Walker et al., 1999; Dalerum and Angerbjörn, 2005).

Isotopic values measured in consumers' hair samples can be used as a proxy to assess and compare diet breadth at different spatial and temporal scales (Nilsen et al., 2012). The diet breadth of a consumer determines its position on the generalist–specialist continuum, with generalists having a more diverse diet and thus a larger breadth than specialists (Jedrzejewska and Jedrzejewski, 1998). The trophic niche of generalist consumers, i.e. their position in the food web of a community, can be especially

dynamic (Balza et al., 2020). Generalists may switch between alternative prey items, e.g. during a seasonal peak in food availability (Ben-David et al., 1997; Djagoun et al., 2016), or shift their diet in the long term to either cope with the loss of resources or take advantage of newly available supplies (Buelow et al., 2018). While long-term dietary studies inferred by SIA have increasingly been used in aquatic ecosystems (Thompson et al., 1995; Farmer and Leonard, 2011; Moreno et al., 2013; Mariano-Jelicich et al., 2017; Reynolds et al., 2019; Carney et al., 2023), it has been sparsely applied on terrestrial food webs (Hilderbrand et al., 1996; English et al., 2018), and essentially at a scale of a few years to three decades in mammalian studies (Galicia et al., 2016; Carbonell Ellgutter et al., 2020).

The wolverine (*Gulo gulo*) is a large carnivore inhabiting the tundra and boreal forest of the circumpolar north (MacDonald et al., 2017). Like other boreal large carnivores, wolverines disappeared from the southernmost parts of their range due to persecution, overhunting, habitat loss, and human development (Landa et al., 2000; Kyle and Strobeck, 2002). Wolverines are facultative scavengers and generalist predators feeding on diverse prey ranging from small rodents to large ungulates (Myhre and Myrberget, 1975; Magoun, 1987; Koskela et al., 2013a). They adapt to food scarcity by foraging opportunistically, i.e. switching their diet toward occasionally available food sources (Samelius et al., 2002; Shardlow, 2013). In Alaska, for example, Dalerum et al. (2009b) showed that wolverines switched their diet between moose (*Alces alces*) and caribou (*Rangifer tarandus*) depending on the ungulate's population abundance and availability. The diet switch happened on an annual scale and was also observed over six years using SIA of multiple wolverine tissues (Dalerum et al., 2009a).

Despite the global range contraction, local wolverine populations in northern Europe are currently stable or increasing (Abramov, 2016). In Finland for example, wolverines underwent a severe population and genetic bottleneck during the 20th century (Lansink et al., 2020; Sugiyama et al., 2022). After a critical low in 1973, the population entered a slow recovery phase followed by faster growth in the last decade (Mykrä and Pohja-Mykrä, 2015). In 2022, Finland counted 400 individuals split into a Scandinavian and Karelian genetic population (Kojola et al., 2022; Lansink et al., 2022). The species is classified as *Endangered*, protected nationwide, and therefore qualifies for conservation actions (Nature Conservation Act, 1996; Hyvärinen et al., 2019). However, In Northern Finland where semi-domesticated reindeer (*R. t. tarandus*) are herded extensively, the wolverines' predation on livestock results in a typical human–wildlife conflict that negatively affects its conservation (Rasmus et al., 2020). Although previous studies have suggested diet differences between wolverine populations within Finland (Koskela et al., 2013a; Koskela et al., 2013b), little is known about the long-term dynamics of their trophic niches nor about the relevance of potential niche variations for conservation (The Finnish Ministry of Agriculture and Forestry, 2014; Fisher et al., 2022).

In this study, we aimed to detect possible long-term alterations in the diet of a terrestrial generalist predator, the wolverine, by using stable isotope analysis of δ^{13}C and δ^{15}N. We applied SIA on hair samples from modern and museum collections, and assessed

changes in carbon source and trophic level over the last 100 years. We specifically quantified isotopic niche position, breadth, and relative overlap of historical and recent wolverine populations, while considering their population structure. Finally, we discussed the overall suitability of SIA for gaining information on the trophic ecology of past and present populations of wolverines, and its implications for large carnivores' conservation.

2 Materials and methods

2.1 Study area

The study was conducted in Finland, covering the eastern and northern parts of the Finnish wolverine range (Figure 1). The whole study area was defined as *Finland* and further divided into *Northern* and *Eastern* study areas, based on their distinct ecological communities and genetic population structure. The *Northern* study area is within the reindeer management area (RMA), where about 190,000 semi-domesticated reindeer are extensively herded (The Finnish Reindeer Herding Association, 2021). It consists of various alpine, sub-arctic, and boreal ecosystems, with high plateaus and hills (maximum elevation 1,365 meters above sea level). The snow cover period extends from October/November until May/June

(Koskela et al., 2013a). The *Eastern* study area, outside the RMA, consists mainly of boreal pine forests dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), though mixed forests can be found as a result of felling and clear-cuttings. There, the rugged terrain reaches an elevation of 300 masl, and snow cover usually lasts from November/December until April, with a peak in March. In contrast to the *Northern* region, other large carnivores are present in high densities in the *Eastern* study area (the grey wolf [*Canis lupus*; Heikkinen et al., 2021a], the Eurasian lynx [*Lynx lynx*; Holmala et al., 2021], and the brown bear [*Ursus arctos*; Heikkinen et al., 2021b]).

2.2 Sampling

Wolverine hair samples were obtained from 44 individuals from the period 1905–2020. All samples (N = 52) were collected using non-invasive methods, from an ongoing DNA-monitoring project (N = 27), museum specimens (N = 16), and individuals found dead or legally culled independently from our research (N = 9). Baited hair snags were used to collect hair samples over the period 2016–2019 (Lansink et al., 2020). The hairs are plucked by metal brushes, collected in paper envelopes and analyzed for individual identification (see for details on the microsatellite genotyping:
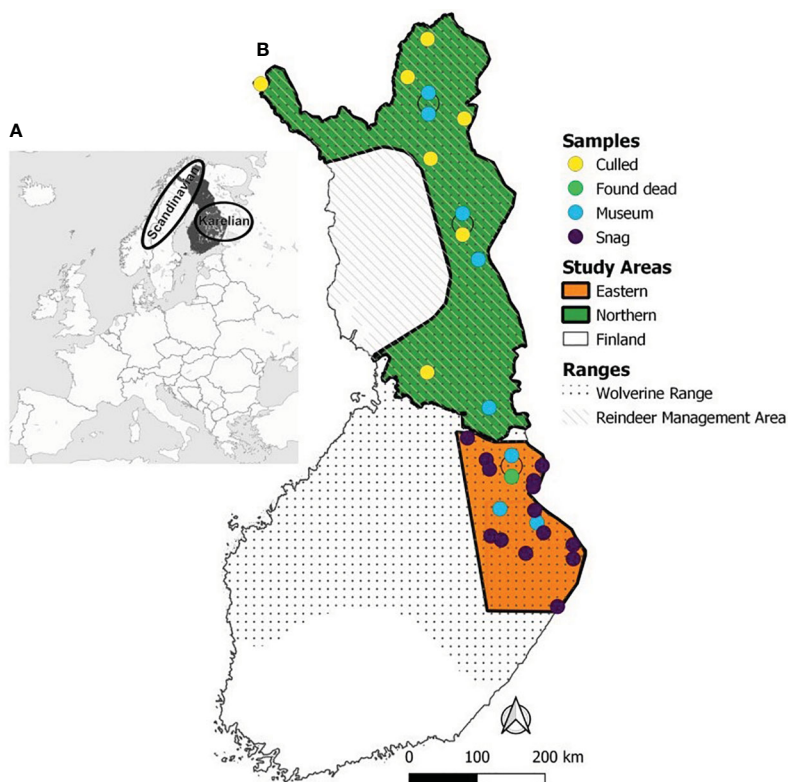
FIGURE 1
Wolverine sample locations in Finland and the two study areas. **(A)** In the insert, Finland is coloured dark grey and the two wolverine populations of Fennoscandia (Scandinavian and Karelian; Lansink et al., 2020) are roughly marked with ellipses. **(B)** Sampling sites were grouped into *Northern* (green polygon) and *Eastern* (orange polygon) study areas within the Finnish wolverine range (dots; Abramov, 2016; Kaczensky et al., 2017; The Finnish Natural Resources Institute, 2022). The *Northern* study area overlaps with the Reindeer Management Area (dashed). Samples (circles) were either collected from museum specimens (blue), hair snags (purple), or from found dead (light green) and legally culled individuals (yellow).

Lansink et al., 2020). While most individuals were sampled once, four individuals were sampled on several occasions due to the opportunistic nature of the sampling method. From three individuals sampled three times within the same year, samples were pooled per individual and labeled with the respective collection year. One individual was sampled on three occasions, each in a different year. Given the strong inter-annual variation in wolverines' diet (Myhre and Myrberget, 1975; Dalerum et al., 2009b), we treated each sample from this individual as independent. Additional hair samples were collected from one individual found dead in 2020 and from eight legally culled individuals in 2019–2020 (Appendix 1). Museum hair samples from similar regions as the other individuals were taken from skins and stuffed specimens from Finnish natural history museums.

2.3 Sample preparation

Hair samples were washed in a solution of 2:1 chloroform/methanol overnight on an orbital shaker at 180 rpm to remove lipids. Samples were rinsed once with fresh 2:1 chloroform/methanol, twice with 96% ethanol, twice with distilled water, and dried in an oven at 50°C for 24 hours. For each hair sample, 15 of the longest guard hairs were cut with a surgical scalpel into 2 cm sections from the follicle to the tip (Careddu et al., 2021). Each hair sample's section was weighed (0.8–1.2 mg) into a 5×9 mm tin capsule (Elemental Microanalysis [UK]).

2.4 Stable isotope analysis

Carbon ($^{13}C:^{12}C$) and nitrogen ($^{15}N:^{14}N$) stable isotope ratios were measured in each sample with a mass spectrometer at the Environment and Natural Institute Stable Isotope Laboratory at the University of Alaska Anchorage (Rogers et al., 2020). Ratios were measured as a deviation from international reference standards (Vienna Pee Dee Belemnite for carbon and air for nitrogen), expressed as δ in per mil (‰). The internal laboratory standards were BWBII keratin, peach leaves, moose, and three-spined stickleback (Gasterosteus aculeatus). Measurement errors were found to be typically smaller than $\pm$ 0.02‰ for both $\delta^{13}C$ and $\delta^{15}N$. In addition, the carbon to nitrogen concentration ratio (C:N) was measured to assess possible contamination or alteration of the samples (DeNiro, 1985).

2.5 Data preparation

2.5.1 Suess effect

Correction of isotopic values is required on large temporal ranges, as changes in the natural occurrence of stable isotopes can be gradually integrated into the tissues of primary producers and may propagate along the food web to higher-level consumers (Long et al., 2005; Kumar, 2011; Newton, 2016). Increasing atmospheric

CO_2 emission and its associated depletion in ^{13}C, called the "Suess effect", is the main known long-term change in the isotopic baseline (Keeling et al., 2017). As CO_2 emissions accelerated after 1960, $\delta^{13}C$ measured in hair samples was corrected using equation (1) for samples between 1960 and 2019, and equation (2) for samples prior to 1960 (Francey et al., 1999; Chamberlain et al., 2005; Ben-David and Flaherty, 2012). The most recent sampling year (i.e. 2020) was taken as the reference year and thus not corrected.

$$\delta^{13}C_{corrected} = \delta^{13}C_{raw} - ((2020 - Year_{sampling}) \times -0,022\,‰) \quad (1)$$

$$\delta^{13}C_{corrected} = \delta^{13}C_{raw} - (59 \times 0,022 + ([1960 - Year_{sampling}] \\ \times 0,005)) \quad (2)$$

Temperature and rainfall could also influence the carbon isotopic baseline of primary producers, but the scale of these changes is far smaller than the Suess effect (Marshall et al., 2007) and becomes negligible when moving up in the food web (English et al., 2018). Values were not corrected as there is no strong evidence of global atmospheric NO_3^- depletion being integrated into the ecosystem (Felix and Elliott, 2013). Moreover, local processes of soil $\delta^{15}N$ depletion due to agricultural fertilization (Bol et al., 2005) are likely irrelevant in the soils of the boreal forest (Liu et al., 2022).

2.5.2 Periods

Samples from before the year 2000 were grouped as Historical (N = 13), and samples taken after 2000 as Recent (N = 33). The Historical-Recent division reflected the wolverine population history in Finland (i.e. the bottleneck and a period of low population densities vs. population recovery and growth; Lansink et al., 2020; Kojola et al., 2022) as well as the carnivores guild recolonization history in Finland (i.e. absent or in low numbers during the Historical, and rapidly increasing or stabilizing during the Recent period; Pohja-Mykrä et al., 2005; Heikkinen et al., 2021b; Holmala et al., 2021). Moreover, the groups ensured that the sample sizes were large enough for the later analysis (N ≥ 3; Jackson et al., 2011). The sample size of Recent individuals was larger than the Historical one in the Eastern region (N = 26 and N = 6, respectively). Any bias attributed to this difference in sample size was ruled out by running all analyses with equal Historical and Recent sample sizes (N = 6). Six Recent individuals from the Eastern study region were randomly selected, with replacement, and the process was repeated 10 times. Results from the random samplings were similar to the original results (Appendix 2).

2.6 Data analysis

Long-term shifts in isotopic niches between the Recent and Historical wolverine populations were evaluated for the study areas (Northern and Eastern) and pooled together as Finland. The isotopic niches were reconstructed for each group by fitting ellipses encompassing 95% of the data using the R package SIBER

(Stable Isotope Bayesian Ellipses in R package; version 2.1.6; Jackson et al., 2011). The similarity in isotopic niches between the two groups was quantified by their overlap, expressed as a percentage of the overlapping area over the total area covered by the two ellipses (Krumsick and Fisher, 2019). Niche breadths were quantified by their Bayesian standard ellipse area (SEA_B), calculated by fitting Bayesian multivariate normal distributions to the data (Catry et al., 2016). We used JAGS (Just Another Gibbs Sampler) parameters as: iterations = 130.000, burn-in = 5.000, thin = 50, chains = 4, and applied a correction for small sample size (Jackson et al., 2011). To compare the niche breadth extent between the two periods, the posterior probability of *Historical*'s SEA_B being larger than *Recent*'s SEA_B was calculated ($PP_{H>R}$). *Historical*'s SEA_B was considered significantly larger where $PP_{H>R} \geq 0.95$.

3 Results

The $\delta^{13}C$ stable isotopes values of wolverine hairs in Finland ranged from −24.7 to −21.3 ‰ (mean= −23.3‰, SD = 0.8, Suess corrected) and $\delta^{15}N$ values fell between 5.1 and 8.8 ‰ (mean = 6.5 ‰, SD = 0.9). The carbon to nitrogen ratio was consistent throughout the study period (max = 3.1, min = 2.8, mean = 2.9, SD = 0.1), falling in the expected range for unaltered tissue samples (DeNiro, 1985). Detailed isotopic values are given for each sample in Appendix 1.

During the last century (1905–2020), the $\delta^{13}C$ values of wolverine hairs became depleted in *Finland* (Figure 2A; estimated slope β = −0.016‰, R^2 = 0.46, p-value < 0.001), and within both study areas (Figure 2B; *Northern*: β = −0.015‰, R^2 = 0.76, p < 0.001; *Eastern*: β = −0.012‰, R^2 = 0.17, p = 0.031). For the $\delta^{15}N$, although the *Eastern* study area showed a slight temporal enrichment with a minor correlation (β = −0.013‰, R^2 = 0.12, p = 0.046), no significant correlation between years and the $\delta^{15}N$ values was found in the *Northern* study area (Figure 2D, R^2 = 0.085, p = 0.31) nor overall in *Finland* (Figure 2C, R^2 = 0.043, p = 0.17).

The isotopic niche of the overall *Historical* population was significantly different from the *Recent* populations (Overlap$_{Finland}$ = 33%, Figure 3A), though there was no significant difference in the niche breadth extent ($PP_{H>R}$ = 0.32, Figure 3B). When divided between study areas, isotopic niche overlaps between *Historical* and *Recent* populations were small, ranging from 22% in the *Eastern* to 24% in the *Northern* region. In the *Northern* region, the SEA_B of the *Historical* population was 1.40 ‰² (95%CI: 1.08–1.95 ‰², N = 7) and of the *Recent* population 2.00‰² (95%CI: 1.43–2.82‰², N = 7). SEA_B values of a similar range were found in the *Eastern* region (*Historical*: 1.37‰², 95%CI: 1.00–1.97‰², N = 6; *Recent*: 1.35‰², 95%CI: 1.17–2.57‰², N = 26). Differences in SEA_B between the *Recent* and *Historical* populations were not statistically significant in Finland or in the regions (*Northern*: $PP_{H>R}$ = 0.60; *Eastern*: $PP_{H>R}$ = 0.33).
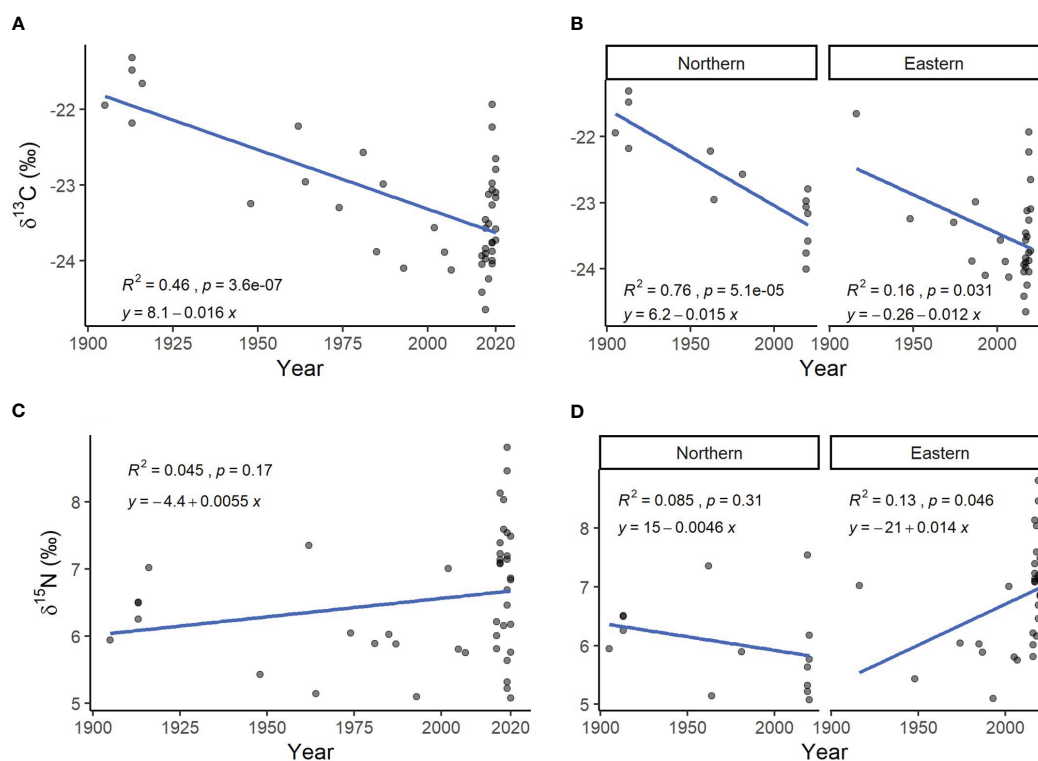
FIGURE 2
$\delta^{13}C$ **(A, B)** and $\delta^{15}N$ **(C, D)** isotopic values over the years 1905–2020 of hair samples (N = 44) from wolverines in Finland **(A, C)** and per study region **(B, D)**. Linear regression equations are given 'y = α+ βx' and shown as a blue line, the coefficient of determination is given as 'R²', and the p-values as 'p'. Overlapping points are shown as darker grey. $\delta^{13}C$ values prior to 2020 were corrected to account for the Suess effect.

FIGURE 3
Reconstructed isotopic niches for ellipses and standard ellipses area (SEA) of Historical and Recent wolverine hair samples throughout Finland and divided over two study areas. **(A)** Bivariate plots of $\delta^{13}C$ and $\delta^{15}N$ showing the SIBER 95% standard ellipse areas surrounding the reconstructed isotopic niche spaces of Historical (dark grey) and Recent (light grey) wolverines in Finland and in the study areas. Overlap between Historical and Recent population's ellipses are given as percentages. $\delta^{13}C$ values prior to 2020 were corrected to account for th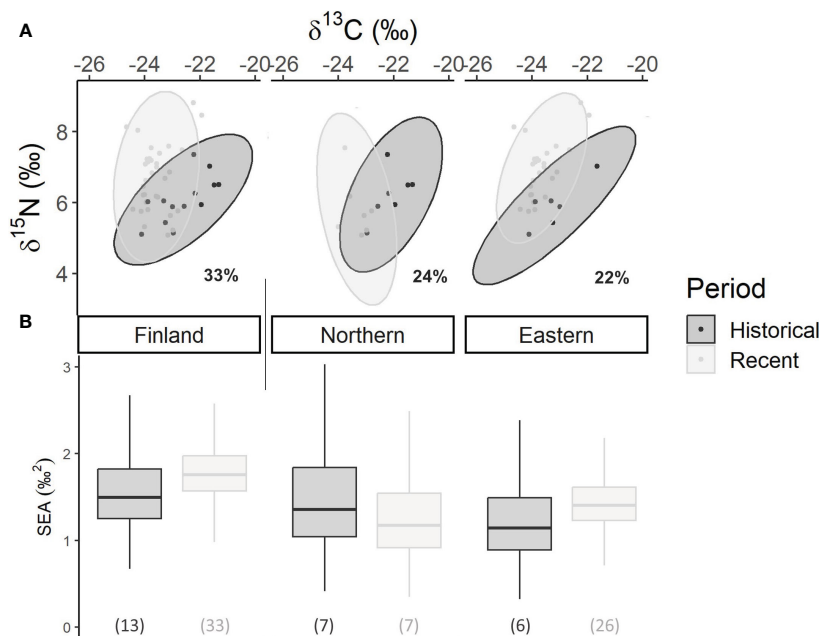e Suess effect. **(B)** Boxplots of the posterior predictive estimates of the Bayesian standard ellipse areas (SEA_B) modeled in SIBER comparing Historical (dark grey) and Recent (light grey) wolverines in the study areas. Sample sizes are given in brackets for each period and study area.

4 Discussion

4.1 Long-term diet shift of wolverines in Finland

The $\delta^{13}C$ values of wolverine hairs became depleted during the last 100 years in both *Eastern* and *Northern* study areas of Finland. $\delta^{13}C$ shifts in generalist predators are often linked with the predator shifting its diet toward an alternative prey type, e.g. from planktivorous to benthic-feeding prey (Hempson et al., 2017), or herbivorous to detritivorous prey (Wise et al., 2006). Interestingly, our results are consistent with Dalerum et al. (2009a), who observed similar patterns of isotopic values from various tissues of Alaskan wolverines over a shorter period (6 years). In Alaska, this change in $\delta^{13}C$ values was associated with a shift in their diet composition from caribou toward moose (Dalerum et al., 2009b). Our results suggest a possible change in the diet composition of Finnish wolverines, shifting towards an alternative prey, though without a change in trophic level.

Our results further support a possible diet shift by the small overlap between the *Historical* and *Recent* wolverine population's reconstructed isotopic niches (Figure 3). Small overlaps in isotopic niches have been shown to reflect for example long-term shifts in the diet of aquatic consumers (Secchi et al., 2017; Reynolds et al., 2019). For another boreal large carnivore, Hilderbrand et al. (1996) found a long-term shift (1916–1994) in the diet of grizzly bears (*Ursus arctos horribilis*) in North America by comparing the isotopic values of tissues from a historical and a modern

population. In this case, the difference in isotopic niches between the temporal populations was linked to a change in the grizzly's diet from salmon toward terrestrial prey, as increased damming negatively affected salmon availability.

In the current wolverine study, the enriched $\delta^{15}N$ values and the variance observed were typical of a generalist consumer at a high trophic level (DeNiro and Epstein, 1981). Nonetheless, the absence of a clear trend in $\delta^{15}N$ values indicates a lack of a significant diet switch towards an alternative trophic level during the study period (Stanek et al., 2017). Thus, the trophic level of wolverines in Finland during the last century was likely stable despite an alteration of habitat, climate and an associated change in prey community. This is consistent with SIA of Alaskan wolverines (Dalerum et al., 2009a) and has also been observed in other generalist consumers, such as marine birds or fur seals (Ceia et al., 2012; Vales et al., 2020).

Despite the shift in the isotopic and dietary niche, there was no significant temporal variation in the niche breadth of wolverines. In Norway, Van Dijk et al. (2008) suggested that the niche breadth of wolverines would decrease with grey wolf recolonization, as wolves provide moose carrion which the wolverine can specialize on. However, in our *Eastern* study area, where wolves recolonized their former range after 1990 (Kojola et al., 2006; Mykrä et al., 2017; Heikkinen et al., 2021b), we did not observe a significant difference between the isotopic niche breadth of the *Historical* and *Recent* wolverine populations. A possibility is that coexistence with wolves might not be the sole driver of the wolverine niche breadth extant, especially in a community of several other large carnivores. The Eurasian lynx also recolonized its former range and acts as a

carrion provider throughout Fennoscandia, making carcasses of diverse prey species available for wolverines (Sunde and Kvam, 1997; Andrén et al., 2011; Mattisson et al., 2011). Thus, the overall long-term stability of the wolverine niche breadth might be partly caused by wolverines scavenging from carrion made available by several coexisting large carnivores (Magoun, 1987).

Considering other generalist consumers and predators, long-term diet shifts have typically been associated with changes in prey communities (Farmer and Leonard, 2011; Secchi et al., 2017) resulting from multiple factors such as overharvesting (Reynolds et al., 2019), habitat degradation (Hempson et al., 2017), or anthropogenic disturbances (Hilderbrand et al., 1996). The Finnish boreal forest in our study areas is known to have largely lost its ecosystem integrity over the past century (Grantham et al., 2020). Factors such as climate change (Fraixedas et al., 2015), the intensification of forestry practices (Järvinen et al., 1977; Vasander, 2006), urbanization (Scrafford et al., 2018), and fluctuation in ungulate populations (Nygrén, 1987; Luoma, 2002) could all have led to changes in the wolverine's prey communities, resulting in the observed diet shift. In any case, the remarkable stability of the Finnish wolverine's niche breadth through a century of habitat modification and dietary shift may indicate the resilience to trophic alteration (Jenkins and Davoren, 2021), with subsequent conservation implications for wolverines.

4.2 Implications for wolverine conservation

Generalists often respond the most successfully to trophic disturbances (Berumen and Pratchett, 2008; Peers et al., 2014), especially in cases of alterations of their prey community (Wilmers and Post, 2006; Christian et al., 2009). As the persistence of a consumer in a changing ecosystem is partly conditioned to its dietary plasticity (Silver and Marsh, 2003; Dunham, 2017), the wolverine might be particularly resilient to fluctuations in prey abundance and availability. The diet shift of wolverines in Finland over the last century confirms the versatility of this generalist consumer to adapt to long-term changes in its environment. Although our results indicate trophic resilience, preserving the boreal ecosystem remains highly important as food-web alterations can reach a tipping point after which the survival of consumers is put at risk (Llope et al., 2011; Griffith et al., 2019).

At a local scale, our results show that the current diet niche of wolverines in the *Northern* area is not smaller than the niche of the *Eastern* area. These results indicate that wolverines living within the reindeer herding area are as generalist predators as the wolverines living outside of it. Somewhat surprisingly the degree of specialization of wolverines in the *Northern* study area did not significantly change over time, even though the abundance of semi-domestic reindeer varied greatly (Helle and Kojola, 2006; Uboni et al., 2016). Previously, Koskela et al. (2013a) detected that reindeer accounts as a significant part of the wolverine diet. Additional wolverine diet studies in the RMA are thus necessary to assess if the current generalist population is composed of a few individuals that specialize on reindeer, i.e. specific individuals taking a

disproportionate reindeer toll, or if the majority of wolverines are generalists (Mcaulay et al., 2021).

4.3 SIA for diet studies of large carnivores

While the causality between diet shifts and observed long-term shift in stable isotopes values is supported by many studies (Chamberlain et al., 2005; Kaczensky et al., 2017; Mariano-Jelicich et al., 2017; Reynolds et al., 2019), there are other factors that could explain the changes in isotopic values. Metabolic processes, for example, can cause short-term and seasonal variation in isotopic values (Ben-David and Flaherty, 2012; Newton, 2016). However, our study encompasses 44 individuals sampled over a century, so the short-term and individual-specific variations are most likely not affecting the observed long-term trend (Post, 2002; Dalerum and Angerbjörn, 2005). Given this long study period, our results could be affected by background fluctuations in isotopic ratios. For example, the observed trend in carbon isotopic values of the wolverine tissues could be impacted by long-term changes in the isotopic values of the prey items themselves (Dalerum et al., 2009a). Nevertheless, the scale of this shift at a prey species level would not significantly impact the isotopic values of a predator at a higher trophic level (Calandra et al., 2015). Hypothetically, even if there were a strong shift in the isotopic values of a dietary source, its effect on the consumer's values would likely be reduced by the diverse diet composition of wolverines. Although a unidirectional shift in isotopic values across all dietary sources cannot be ruled out, this explanation is of little parsimony and is not supported by long-term SIA studies to our knowledge (Balčiauskas and Balčiauskienė, 2022). Therefore, the observed shift in isotopic niche and trend in hair isotopic values are best explained by the hypothesis of a long-term diet shift of the wolverine.

Our study further demonstrates the potential of using SIA on museum and recent samples to infer changes in the trophic ecology of large carnivores, particularly in the long term. Fisher et al. (2022) noted that as research on wolverines started decades after their range collapse, ecological investigations are limited to the remaining present populations. Our results nonetheless suggest that SIA can shed light on the trophic ecology of past and extinct populations of wolverines, and could easily be extended to other species with key trophic roles. For extinct populations with only museum samples left, SIA provides the only record of dietary change over historical time scales of range contraction and population collapse. Remarkably, the samples collected for SIA studies also open up ways for complementary studies, e.g. on population genetics (Lansink et al., 2020).

5 Conclusion

We were able to identify a long-term diet shift of wolverines in Finland. There was, however, no change in the degree of specialization nor in the trophic level of the wolverine, thus

suggesting a high dietary resilience and adaptation to multiple alterations in their food web. Overall, SIA proved to be a suitable tool to study long-term diet trends in top consumers of terrestrial food webs, especially when hair samples from both museum collections and modern studies are available. We thus encourage further long-term stable isotope analysis on large carnivores to assess their past diet niches and to provide a better understanding of their ecological context for the conservation of present populations. Finally, as the diet of carnivores is considered an indicator of the overall status of biodiversity within an area (Sergio et al., 2008; Reynolds et al., 2019), reconstructing their past and present trophic niches could help to detect signs of temporal changes in biodiversity.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author/s.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because we used historical hair samples from museum skins and stuffed specimens. I used modern samples by re-using leftover hair samples from a previous study on wolverine genetics, and from individuals found dead or legally culled independently from our research. As no animal was handled or killed in link with this research, no ethical approval was required.

Author contributions

CM: Conceptualization, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft. TH: Investigation, Methodology, Software, Writing – original draft. GL: Conceptualization, Investigation, Resources, Writing – original draft. KH: Resources, Writing – review & editing. MI: Resources, Writing – review & editing. IK: Resources, Writing – review & editing. JA: Project administration, Supervision, Writing – review & editing. JW: Conceptualization, Funding acquisition,

Investigation, Project administration, Resources, Supervision, Writing – review & editing.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1284901/full#supplementary-material

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