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Global Drivers of Morphological Variation in Grey Wolves

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ABSTRACT

Aim: To investigate the ecological and evolutionary drivers of morphological variation in grey wolves (*Canis lupus*) across their global range:

Location: The entire Holarctic distribution of grey wolves, from Greenland to New Mexico in North America, from Norway to Israel in Eurasia, including several samples from Russia and India.

Methods: We analysed 227 wolf skulls using high-resolution 3D geometric morphometrics (585 cranial and 96 mandibular landmarks) to assess the influence of continental separation, latitude, prey mass and population history on skull (cranium and mandible) size and shape.

Results: Skull size was primarily influenced by population identity, increasing with average prey mass and latitude up to roughly 65°, with minimal differences between continents. Skull shape was mainly determined by population identity, with minor contributions from skull size, continent, and latitude; prey mass had no detectable effect. Average crania differed in the length-to-width ratio, shape and relative position of the frontal bones and zygomatic arches. Populations with the most distinct skull shapes included Modern Scandinavian wolves, Arctic wolves (East Greenland and Ellesmere Island), Italy and Coastal Alaska. These disparities are consistent with expected changes associated with long-term isolation, demographic events (e.g., bottlenecks, founder effects), human-driven fragmentation and extirpation of wolves, shifts in prey availability, and possible hybridization.

Main Conclusions: Morphological variation in wolves is shaped by a combination of ecological pressures, geography and human impacts. Past isolation and human-induced declines have increased divergence, emphasizing the importance of considering ecomorphological patterns when assessing evolutionary resilience and informing conservation planning for large carnivores.

Laura Kvist and Christy Anna Hipsley are joint senior authors.

1 | Introduction

The grey wolf (*Canis lupus*) historically occupied nearly the entire Holarctic region, spanning Arctic tundra and boreal forests, temperate ecosystems and deserts (Mech and Boitani 2003). However, intense persecution during the 19th and 20th centuries caused severe population declines and widespread local extirpations (Chapron et al. 2014; Mech and Boitani 2003). By the mid-20th century, wolves were eradicated from most of the contiguous United States, Western and Central Europe, eastern China, the Korean Peninsula and Japan (Mech and Boitani 2003). Despite mounting anthropogenic stress, some populations in Mexico, Iberia, Italy, the Carpathians and later Scandinavia persisted in isolation from larger populations. Recently, wolf numbers have rebounded in parts of Europe and North America through protection, recolonization and reintroductions (Di Bernardi et al. 2025; Phillips and Smith 1997; Publications Office of the European Union 2023).

Parallel to this, the main prey of wolves, that is, ungulates, also declined across Europe and North America during the 19th and early 20th centuries (Deinet et al. 2013; Hanberry and Hanberry 2020), yet wolves continue to display ecological and dietary flexibility. Their diet spans from small mammals (rodents and lagomorphs) to large ungulates such as deer (*Cervus*, *Odocoileus*), moose (*Alces*), muskox (*Ovibos*) and bison (*Bison*) (Table 1) (Mech and Boitani 2003; Newsome et al. 2016). They also consume plant material and anthropogenic food sources (Evavold et al. 2024; Fritts and Mech 1981; Mech and Boitani 2003). This dietary breadth contrasts with their carnivorous skull morphology, marked by enlarged carnassials, reduced molars and robust jaws (Van Valkenburgh 1991, 2007).

Such flexibility likely enabled wolves to survive centuries of persecution and suggests that they can adapt to diverse ecological and anthropogenic pressures, potentially driving morphological divergence among populations. North American and Eurasian wolf populations were last connected via the Bering Land Bridge approximately 24–34.4 k years ago, before the Bering Strait opened 11 k years ago (Jakobsson et al. 2017; Koblmüller et al. 2016; Pacheco et al. 2022). Since then, continental populations have likely followed independent evolutionary trajectories, causing genetic (Pacheco et al. 2022; Sinding et al. 2018) and potentially phenotypic diversification. However, similar niches and prey may drive convergent evolution across continents (Meloro et al. 2015), while phenotypic plasticity can further limit divergence at smaller scales (Crispo 2008). Wolf populations vary in coat coloration, coat density (Castelló 2018) and skull morphology (Ketchen 2020; Milenković et al. 2010; Mulders 1997; Wiwchar and Mallory 2012). For example, Arctic wolves are white for snow camouflage, while Arabian wolves have a thin coat adapted to desert heat. Such population differences are likely maintained by wolves' preferential dispersal within similar habitats (Geffen et al. 2004; Pilot et al. 2006; Sanz-Pérez et al. 2018), which also shapes genetic structure (Pilot et al. 2006).

These observations raise key questions about the drivers of wolf morphology, particularly for the skull, which not only reflects overall phenotype and can serve as a proxy for body size, but also represents a highly specialized integrated structure for prey acquisition and feeding (Ito et al. 2024; Meloro and Tamagnini 2022; Van Valkenburgh 1991, 2007), as well as the housing of the sensory systems, respiration, protection of the brain and more. As such, we aimed to explore the drivers of variation in grey wolf skull morphology by addressing the following questions: (1) To what extent have human persecution, ecological pressures, continental separation and geography shaped wolf skull morphology (cranium and mandible)? (2) Are intercontinental differences more pronounced than those observed along latitudinal gradients, distinct biomes or across populations? (3) How strongly is skull morphology influenced by local prey composition and ecological specialization? To investigate these questions, we have analysed cranial and mandibular morphological variation in more than 200 wolf specimens using high-resolution 3D geometric morphometrics combined with both ecological and population-level data.

2 | Methods

2.1 | Sampling and Data Collection

For the global analysis, we examined 227 three-dimensionally digitized adult grey wolf specimens to compare skull (cranial and mandibular) morphology across continents and along latitudinal gradients (Figure 1). The dataset comprised 125 crania and 117 mandibles from North America, and 100 crania and 98 mandibles from Eurasia (213 individuals with both elements, 12 with only crania, 2 with only mandibles). Missing elements reflected damage or loss in museum specimens, meaning those specimens could not be fully analysed. For population-level analyses, we restricted the dataset to populations with ≥ 4 specimens, yielding 201 crania and 192 mandibles (Table 1; Appendix S1). Populations were defined by continent and country of origin or major geographic landmarks (e.g., mountain ranges, national parks), with detailed sampling locations listed in Appendix S2.

Only adults, identified by fully erupted permanent dentition, including canines with a distinct neck, were included. The dataset included males, females and individuals of unknown sex (Appendix S1). Although wolves exhibit sexual dimorphism in skull size and shape (Bujnáková et al. 2025; Ketchen 2020; Milenković et al. 2010), this appears to account for significantly less variation than differences among populations (Bujnáková et al. 2025). Sex ratios may influence average centroid size (CS) within small datasets, but such effects are diluted in global-scale analyses. Given our focus on population-level variation, sexual dimorphism was not analysed further.

2.2 | Prey Data

For each of the 16 wolf populations, we compiled diet data from the literature, focusing on the most frequently reported wild prey species (Table 1; Appendix S2). Mean body mass per species was calculated by averaging male and female weights, and population-level prey mass was estimated as the mean across all prey species contributing $>1\%$ of the diet. Both wild prey and domestic livestock were included in the primary models, which may have biased results toward larger prey weights in populations that scavenged livestock rather than hunted it. We

TABLE 1 | Population details and sample sizes.

	No. crania	No. mandibles	Location	Timeframe	Main prey
Eurasia total	**100** (86)[a]	**98** (83)[a]			
Israel	5	5	Israel	2004–2015	Cattle, wild boar, poultry, gazelles (Reichmann and Saltz 2005)
Italy	16	15	Central Italy	15 from 1972 to 2010, one from 1913	Livestock, wild boar, red deer, roe deer, European brown hare, rodents (Meriggi et al. 2011; Patalano and Lovari 1993)
Balkan	4	4	Dinaric-Balkan	1908–1918	Livestock, wild boar, roe deer, red deer, European brown hare (Ćirović and Penezić 2019; Koychev and Uzunowa 2023; Trbojević et al. 2020)
Carpathians	15	15	Carpathian Mountains	13 from 2015 to 2019, one from 1909, one from 1966, and one unknown	Red deer, roe deer, wild boar, European brown hare, livestock (Kutal et al. 2024; Nowak et al. 2005; Sin et al. 2019)
Modern Finland	16	15	Modern Population in Finland	1976–2018	Moose, wild forest reindeer, European brown hare, white-tailed deer (Gade-Jørgensen and Stagegaard 2000; Kojola et al. 2004; Tammela 2008)
Modern Scandinavia	15	15	Modern Population in Scandinavia	1991–2015	Moose, roe deer, wild boar, fallow deer, cattle, red deer (Zumbach 2023)
Historical Scandinavia	15	14	Historical Population in Scandinavia	1831–1952	Roe deer, moose, European brown hare, mountain hare, birds, livestock (Kardell and Dahlström 2013; Lykke 2005; Thulin et al. 2015)
North America total	**125** (115)[a]	**117** (109)[a]			
New Mexico	19	17	Historical population from New Mexico and Arizona, before reintroduction	16 from 1899 to 1947, 3 unknown years, likely pre-reintroduction individuals	Mule deer, white-tailed deer, rodents, cattle (Reed et al. 2006; Smith et al. 2023)

(Continues)

TABLE 1 | (Continued)

	No. crania	No. mandibles	Location	Timeframe	Main prey
Great Lakes	6	6	Around Great Lakes, Canada	Three from 1960 to 1966, and three with unknown year	White-tailed deer, moose, snowshoe hare, American beaver (Fritts and Mech 1981; Fuller 1989)
Yellowstone	15	13	Yellowstone (descendants of the reintroduced wolves from Alberta and British Columbia, Canada)	2000–2016	Elk, mule deer, moose, bison (Lodberg-Holm et al. 2021; Metz 2021; Tallian et al. 2017)
British Columbia	7	5	British Columbia	5 from 1904 to 1950, 2 from unknown year	Elk, moose, Stone's sheep, mountain caribou (Bergerud and Elliot 1986; Milakovic and Parker 2011)
Coastal Alaska	12	12	Southern coastal Alaska	1961–2017	Sitka black tailed deer, American beaver, black bear, North American river otter (Massey et al. 2021; Roffler et al. 2021)
Interior Alaska	17	17	Inland Northern Alaska, between Brooks Range and Southern Alaska	1933–1999	Moose, Grant's caribou, American beaver (Ballard et al. 1987)
Brooks Range	10	10	Brooks Range up to the North Coast of Alaska	1961–1991	Grant's caribou, moose, Dall sheep (Dale et al. 1995)
Ellesmere Island	13	13	Ellesmere Island	13 from 1900 to 1949, two from 2015 and 2016	Muskox, Arctic hare (Mech et al. 2025)
Eastern Greenland	16	16	Coastal East Greenland	1899–1998	Muskox, geese, Arctic hare, lemmings (Dawes et al. 1986; Marquard-Petersen 1998, 2021)
World total[b]	**225**	**215**			

Note: Scientific names: American beaver—*Castor canadensis*, Arctic hare—*Lepus arcticus*, Bison—*Bison bison*, Black bear—*Ursus americanus*, Birds—*Aves*, Cattle—*Bos taurus*, Dall sheep—*Ovis dalli dalli*, Elk—*Cervus canadensis*, European brown hare—*Lepus europaeus*, Fallow deer—*Dama dama*, Gazelles—*Gazella* spp., Geese—Anserini, Grant's caribou—*Rangifer tarandus granti*, Lemmings—*Lemmus*, *Dicrostonyx*, Livestock—*Bos taurus*, *Ovis aries*, *Capra hircus*, *Sus scrofa domesticus*, *Gallus gallus domesticus*, Moose—*Alces alces*, Mountain caribou—*Rangifer tarandus caribou*, Mountain hare—*Lepus timidus*, Mule deer—*Odocoileus hemionus*, Muskox—*Ovibos moschatus*, North American river otter—*Lontra canadensis*, Poultry—*Gallus gallus domesticus*, Red deer—*Cervus elaphus*, Rodents—Rodentia, Roe deer—*Capreolus capreolus*, Sitka black-tailed deer—*Odocoileus hemionus sitkensis*, Snowshoe hare—*Lepus americanus*, Stone's sheep—*Ovis dalli stonei*, White-tailed deer—*Odocoileus virginianus*, Wild boar—*Sus scrofa*, Wild forest reindeer—*Rangifer tarandus fennicus*.

[a]Number of individuals assigned to populations.

[b]Total wolf skull samples = 227 (213 included both cranium and mandible, 12 only cranium, 2 only mandible).

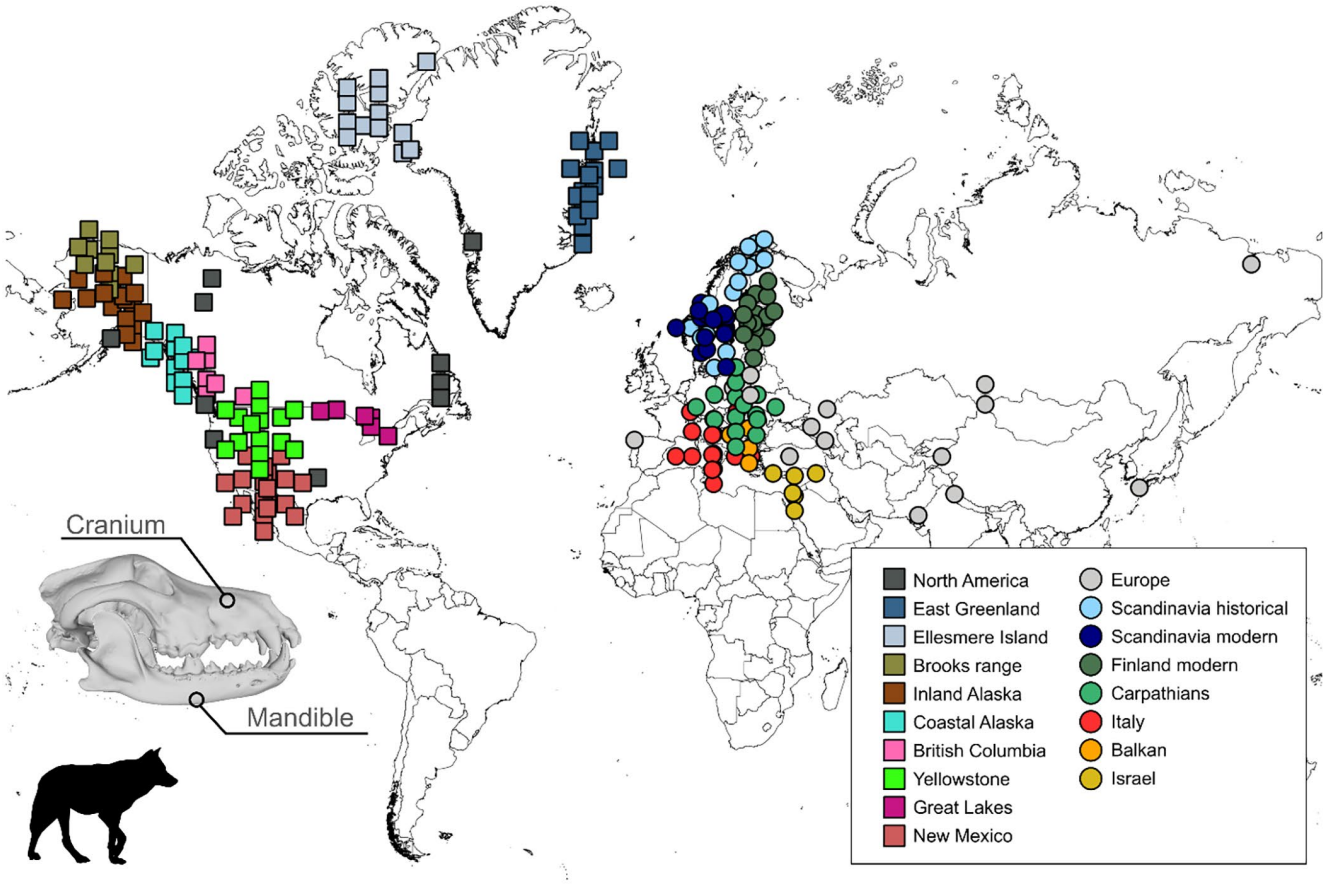

FIGURE 1 | Map of wolf skull samples used in this study. Sample points are displaced around their geographic locations for better visibility and are colour-coded according to populations reflecting their genetic or biogeographic relationships. Square symbols represent North American and circles Eurasian samples.

also incorporated frequency of occurrence of prey or estimated biomass percentage to calculate the mean prey weight for each population and ran the analyses using the same models. Note that these measures can be biased if they represent only a narrow time frame in the wolf's diet, which changes rapidly with the seasons (Mech et al. 2025; Mech and Boitani 2003). Full prey datasets, including species, weights and proportions per population, are provided in Appendix S2.

Prey data was available only at the population level and not for individual specimens. Consequently, analyses including average prey weight as a predictor were conducted at the population level ($n = 16$). Morphometric variables (shape and CS) were therefore summarized as population means to match the resolution of the ecological predictor. This approach ensures consistency in sampling units between response and predictor variables and prevents pseudo-replication that would arise from assigning identical prey values to multiple individuals within a population, which would otherwise inflate degrees of freedom and violate independence assumptions (Hurlbert 1984).

2.3 | Geometric Morphometric Analyses

We developed dense landmarking schemes to capture cranial (585 landmarks) and mandibular (96 landmarks) morphology, enabling visualization of fine-scale, within-species variation in skull shape (Appendix S4, Figure S4.1). Landmarks were placed to ensure homology among specimens, particularly for type 1 landmarks representing discrete anatomical features. Semi-landmarks positioned along curves and surfaces were distributed equidistantly, with surface configurations anchored to type 1 landmarks, thereby maintaining correspondence among specimens. All specimens were landmarked by a single researcher (D.B.) using STRATOVAN CHECKPOINT v.2024.03.07.4:35 (Stratovan Corporation, Sacramento, USA) to minimize observer bias. Figure 2 illustrates landmark placement. Left mandibles were prioritized, as mandibles were often separated at the symphysis, and ~30% of right mandibles were damaged; intact right mandibles were digitally mirrored to create the left mandible when necessary. Missing landmarks on damaged bones, which comprised 0.6% of the cranium and 0.1% of the jaw datasets, were estimated using thin-plate spline interpolation (Gunz et al. 2009) in the R package 'geomorph' v 4.0.10 (Adams et al. 2024; Baken et al. 2021), R v 4.4.3 (R Core Team 2024).

We extracted shape and size variables using a generalized Procrustes analysis with the *gpagen* function in 'geomorph'. Procrustes analysis standardizes specimens by translation, rotation and scaling to unit centroid size (CS); CS was log-transformed in subsequent analyses. As asymmetric shape variation is not considered adaptive in wolves and is instead an indicator of developmental stress (Van Valen 1962), we used only the symmetric shape component for further cranial analyses

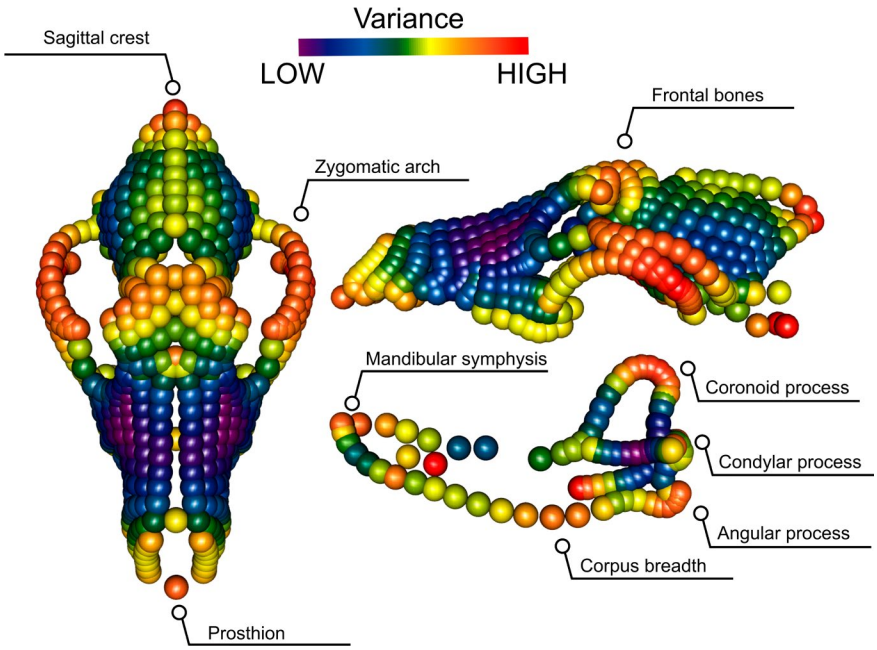

FIGURE 2 | Cranial and mandibular shape variation visualized as colour-coded landmarks, based on log-transformed Procrustes variance, a landmark-specific measure of shape variability across specimens. For the cranium, log-variance values range from −6.06 to −5.19, and for the mandible from −5.05 to −4.37. Note that the variance is dimensionless and meaningful only for relative comparisons between landmarks or regions. In the colour scheme, red indicates the most variable regions of the skull across global wolf populations, while violet denotes the most structurally conserved regions.

using *bilat.symmetry*. Shape and size variation were analysed with Procrustes ANOVA implemented in *procD.lm*, with inferential tests and significance assessed by residual randomization in permutation tests ($n = 1000$ permutations) in the R package 'RRPP' v 2.1.2 (Collyer and Adams 2018, 2024). Unlike classical MANOVA, RRPP does not rely on inversion of a pooled covariance matrix for hypothesis testing, instead, it uses residual randomization to generate an empirical null distribution of test statistics. This framework helps mitigate limitations associated with high-dimensional covariance estimation and matrix inversion in likelihood-based multivariate inference, particularly when trait dimensionality is high relative to sample size (Adams and Collyer 2018; Collyer and Adams 2018). Although *procD.lm* is designed for multivariate data, it can also accommodate univariate CS, providing a consistent analytical framework across shape and size. In such cases, the analysis is equivalent to a standard univariate linear model. This is because it implements the RRPP framework, which reduces to a linear model with residual randomization when applied to univariate data (Collyer and Adams 2018). We also used linear models, ANOVA and the Wilcoxon test for univariate factors. For analyses including CS with latitude as a predictor, we fitted quadratic regression models, which are not supported by *procD.lm*.

We tested multivariate models including CS, continent, latitude and population, entering predictors in a fixed order (Type I sums of squares). Prey mass, available only at the population level, was modelled separately with population shape and size averages (16 populations). To complement these, we ran models for each predictor separately; in shape models, we also included CS as a first predictor to account for allometry. These models assessed the independent contribution of each ecological or geographic variable to shape and size without the influence of other correlated predictors. For example, latitude, population and prey are partially associated with one another, and shape variation related to one factor could otherwise be partially attributed to another in multi-predictor models. Using both multi- and single-predictor models allowed us to evaluate shared versus independent contributions of predictors to morphological variation in shape and size.

Linear measurements were included to complement and contextualize geometric morphometric analyses by providing directly interpretable anatomical dimensions (i.e., lengths and widths) that can be readily compared with previous studies using traditional metrics. This approach also allows to associate shape differences to directly interpretable cranial dimensions and to complement rather than replace 3D geometric morphometrics. For this, we calculated inter-landmark distances using the *interlmkdist* function, including skull and jaw length and width (Appendix S2). These included the total cranial length (the greatest length of the cranium), condylobasal length (CBL, i.e., distance between the prosthion and condyles), cranial width (measured between the lateralmost points of the zygomatic bones, comparable but not identical to exact zygomatic breadth), mandibular length (from the mandibular symphysis to the posterior-most point of the angular process) and jaw width at the level of the condylar process. Normality of all variables was confirmed with the Shapiro–Wilk test ($p > 0.05$). All measurements are presented in centimetres (Appendix S2).

2.4 | Visualization of Morphological Differences

We visualized cranial and mandibular shape variation using Principal Component Analysis (PCA, *gm.prcomp* in 'geomorph'),

projecting Procrustes-aligned coordinates onto principal components to summarize major axes of variation.

To visualize group-level patterns, we used between-group PCA (*groupPCA* in 'Morpho' v 2.12) (Schlager 2017) and Linear Discriminant Analysis (LDA, *prep.lda* in 'RRPP'). Group PCA is an ordination method that rotates the data space to emphasize differences among group means rather than overall variation, while LDA provides ordination that maximizes separation among the 16 populations, providing clearer visualization of fine-scale population differences. Because LDA is sensitive to high dimensionality, the analysis was conducted on a PCA-reduced shape space retaining 99% of total variance, following the RRPP-based Procrustes ANOVA. We acknowledge that LDA can be sensitive in high-dimensional settings where the number of variables exceeds the sample size; however, in this study, LDA was used solely for visualization of group structure and not for statistical inference or hypothesis testing already assessed using RRPP models, which are appropriate for high-dimensional data.

Variance partitioning within cranium and mandible datasets was quantified using the *per_lm_variance* function in the R package 'hot. dots' (Felice 2024) and visualized with *spheres3d* from the 'rgl' package (Murdoch and Adler 2025). Graphs were created using the *ggplot* function in the R package 'ggplot2' (Wickham 2016). Shape extremes along the LD1 and LD2 axes and population means were reconstructed using the *plotRefToTarget* function in 'geomorph', and visualized as wireframes and point-displacement plots, with differences magnified three- to fivefold for interpretability. Population means were colour-coded based on Euclidean distance from the grand mean (grey).

GitHub Copilot and ChatGPT were used to assist with code writing and debugging, and ChatGPT was used for minor language refinement. Neither tool was used to generate text content or design the analyses.

3 | Results

Our high-density landmark scheme enabled a fine-scale reconstruction of wolf skull morphology based on 227 specimens (Figure 1; Appendix S1), identifying regions of greatest variability (Figure 2). In the cranium, variation was concentrated in the anterior prosthion, frontal bones, sagittal crest and zygomatic arches. In the mandible, these areas included the coronoid, condylar and angular processes, as well as the mandibular symphysis region and the mandibular corpus breadth below the molars. These regions correspond to major muscle attachment sites and structures critical for prey processing.

Both single- and multiple-predictor models (Appendix S3) identified population identity as the strongest driver of cranial and mandibular morphology. Averaged across the single and multiple-predictor models, populations explained 23% of shape and 44% of size. Prey mass had little (5%) and non-significant effect on shape but exerted a strong influence on size (31%) and thus overall morphology (18%). Latitude showed moderate effects (5% of shape, 21% of size, 13% of overall), while centroid size (CS, describing the dispersion of landmarks around their centroid and summarising overall skull size) explained 7% of shape. Continental affiliation contributed minimally (5% of shape, 3% of size, 4% of overall). Below, we present results from single-predictor models.

3.1 | Centroid Size

Based on individual models and total sample sizes (cranium = 225, mandible = 215), CS explained a small but significant proportion of shape variation in wolf skulls, averaging 5% (cranium: $R^2 = 6\%$, $Z = 6.9$, $p = 0.001$; mandible: $R^2 = 3\%$, $Z = 5.4$, $p = 0.001$). However, in population-level models based on population averages (16 data points), CS accounted for a larger proportion of variation, averaging 12% (cranium: $R^2 = 10\%$, $Z = 1.8$, $p = 0.038$; mandible: $R^2 = 13\%$, $Z = 2.1$, $p = 0.014$) (Appendix S3).

3.2 | Continents

The first two principal components together explained ~30% of the total cranial and mandibular variation. Eurasian and North American specimens overlapped broadly in morphospace, particularly for crania. Cranium size did not differ between continents ($R^2 = 0.6\%$, $Z = 0.8$, $p = 0.229$), but cranium shape, after accounting for size, differed between North American and Eurasian wolves ($R^2 = 3\%$, $Z = 4.5$, $p = 0.001$). Mandible size also differed modestly ($R^2 = 4\%$, $Z = 2.3$, $p = 0.005$), with North American wolves averaging 3% larger (CS = 56.4 vs. 54.9). Mandible shape was also significantly different ($R^2 = 3\%$, $Z = 5.7$, $p = 0.001$) (Appendix S4, Figure S4.2, Appendix S3).

3.3 | Latitude

Multivariate linear models of the full shape data revealed small, yet significant latitudinal effects (cranium: $R^2 = 4\%$, $Z = 4.8$, $p = 0.001$; mandible: $R^2 = 2\%$, $Z = 3.8$, $p = 0.001$). CS increased with latitude up to ~65°, then declined again toward the highest latitudes. A quadratic model captured this non-linear trend, explaining substantial variation in CS (cranium: $R^2 = 35\%$, Cohen's $f^2 = 0.53$, $p < 0.001$; mandible: $R^2 = 30\%$, Cohen's $f^2 = 0.43$, $p < 0.001$) (Figure 3A,B). This quadratic model provided a better fit to the data, outperforming the linear model without the quadratic term (cranium: $R^2 = 20\%$, $Z = 4.9$, $p = 0.001$; mandible: $R^2 = 16\%$, $Z = 4.4$, $p = 0.001$).

3.4 | Prey

Average prey mass (Appendix S2) did not significantly explain skull shape variation after accounting for CS (cranium: $R^2 = 8\%$, $Z = 0.6$, $p = 0.286$; mandible: $R^2 = 4\%$, $Z = -1.0$, $p = 0.834$). However, it was a strong predictor of centroid size (cranium: $R^2 = 30\%$, $Z = 1.9$, $p = 0.021$; mandible: $R^2 = 32\%$, $Z = 2.0$, $p = 0.020$; Figure 3C,D). At the extremes, average prey weight was highest in Yellowstone (~329 kg) and lowest in coastal Alaska (~37 kg), while the largest overall skulls (total cranial length ~26.4 cm, cranium width ~13.9 cm, total jaw length ~19.7 cm) were in Interior Alaska. The smallest skulls (with above measurements of ~22.8 cm, ~11.7 cm and ~16.3 cm, respectively) were observed in Israel (Appendix S2). Models using weighted averages based

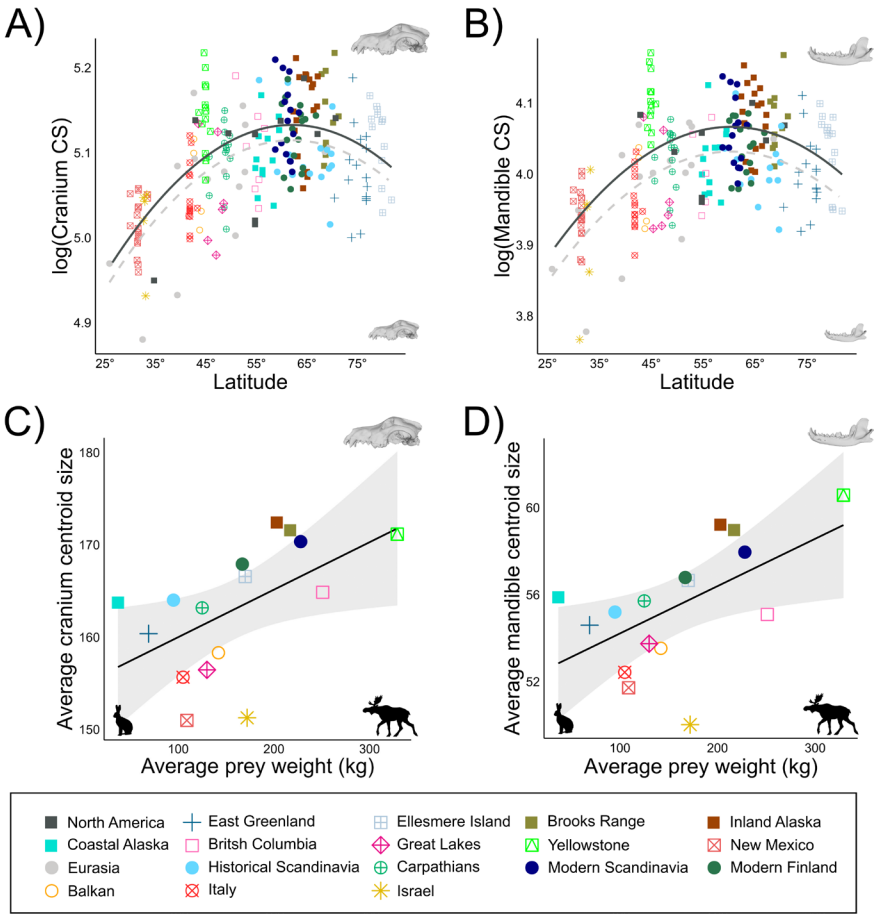

FIGURE 3 | Model fits illustrating the relationship between centroid size and latitude (A and B) and centroid size and average prey weight (C and D), with populations denoted by different colours and symbols. While shape variation along latitude was weak (cranium: $R^2 = 4\%$, $p = 0.001$; mandible: $R^2 = 2\%$, $p = 0.001$), latitude strongly explained variation in cranial and mandibular size (cranium: $R^2 = 35\%$, $p < 0.001$; mandible: $R^2 = 30\%$, $p < 0.001$). Average prey mass accounted for a significant proportion of variation in centroid size, explaining (C) 30% of the variance in cranial CS and (D) 32% in mandibular CS.

on frequency of occurrence or biomass consumed were not significant (cranium: $p = 0.082$; mandible: $p = 0.148$). Importantly, average prey mass remained a consistent predictor of CS even in extended models that included continent and latitude as preceding predictors.

3.5 | Populations

After controlling for CS, population identity explained substantial cranial ($R^2 = 27\%$, $Z = 10.9$, $p = 0.001$) and mandibular ($R^2 = 23\%$, $Z = 9.8$, $p = 0.001$) shape variation. Most pairwise population comparisons were significant, although effect sizes varied (Appendix S3A). The most distinct populations, based on mean permutation test statistics (Z values) calculated by averaging results from pairwise comparisons of cranial and mandibular shapes (Appendix S3C), were Modern Scandinavia ($Z = 4.2$), East Greenland ($Z = 3.7$), Italy ($Z = 3.4$), Coastal Alaska ($Z = 3.2$), Ellesmere ($Z = 3.2$), and the Carpathians ($Z = 3.1$). Although morphospaces of the first principal component axes did not indicate population-level differences (Appendix S4, Figure S4.3A,B), linear discriminant analysis (LDA) revealed clearer separations, highlighting the distinctiveness of Arctic populations' cranial shape (East Greenland and Ellesmere, Figure 4A,C). Other distinctive populations based on LDA of the cranium included Modern and Historical Scandinavia, the Carpathians, and Interior Alaska, and for mandibular shape, Arctic populations, modern Scandinavia, Italy and Yellowstone. Population identity accounted for more than half of CS variation (cranium: $R^2 = 51\%$, $Z = 10.3$, $p < 0.001$; mandible: $R^2 = 53\%$, $Z = 9.4$, $p < 0.001$). Based on Wilcoxon tests, size differences were absent between populations inhabiting similar types of biomes across continents (Interior Alaska and Scandinavia—Taiga; British Columbia and Carpathians—Temperate coniferous forests, New Mexico and Israel—Deserts and xeric shrublands and the Mediterranean, Figure 4B,D). We used biome categories as defined in a previous global assessment (Olson et al. 2001).

Shape visualizations (Figure 5, Appendix S4, Figure S4.4A,B) further illustrate population-specific deviations from the mean. For example, Israel, Brooks Range, Coastal Alaska and the Carpathians exhibit narrow crania, whereas others like Ellesmere, East Greenland and Interior Alaska display broader cranial shapes than average wolves. Additional variation is observed in the width of the frontal bones relative to the rest of the cranium and in the shape of the sagittal crest, further highlighting population-specific differences (Figure 5, Appendix S4, Figure S4.4A). In the mandible, differences between populations

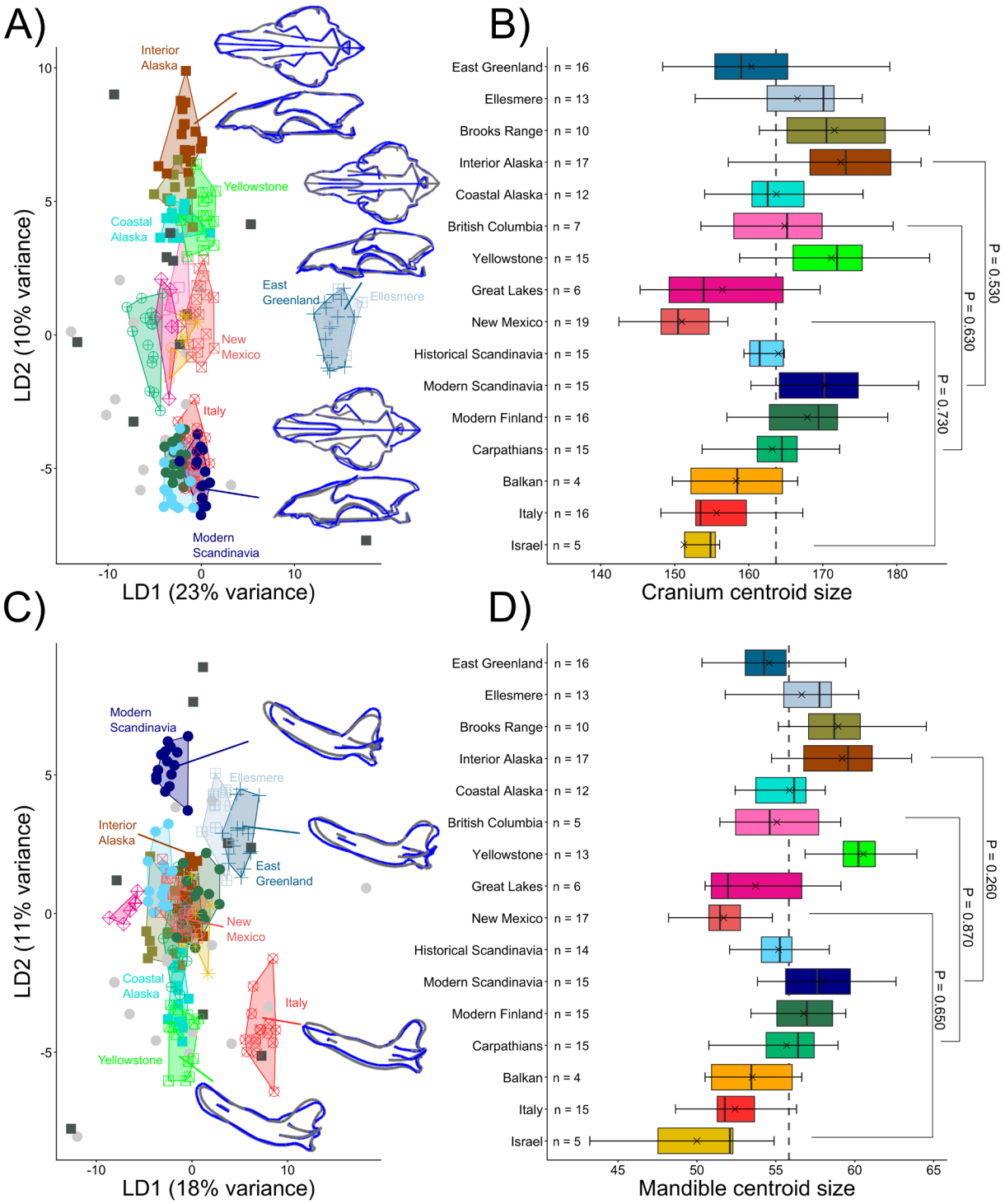

FIGURE 4 | Linear Discriminant Analysis (LDA) of shape data and centroid size for wolf crania (A and B) and mandibles (C and D). The wire-frame graphs show the overall mean shape of the dataset in grey and population means in blue, magnified 3.5 and 4-fold for better visualization. Populations accounted for more than half of the variation in CS (cranium: $R^2 = 51\%$; mandible: $R^2 = 53\%$). Wilcoxon tests revealed no significant size differences between populations inhabiting similar biomes across continents.

involve the height and width of the coronoid process, with overall smaller ones in Israel, Coastal Alaska, the Balkans and Italy, and more pronounced ones in Modern Scandinavia, Interior Alaska and Ellesmere. Further deviations from the mean shape include the width at mid-mandible length beneath the molars and the position of the angular and condylar processes (Appendix S4, Figure S4.4B).

Linear distance measurements (cranial length, cranial width, Appendix S2) showed similar patterns across populations inhabiting broadly similar biomes (Appendix S4, Figure S4.5–9) as CS (Figure 4B,D). However, significant differences were observed for cranial width/length ratio for Israel and New Mexico populations (New Mexico wolves displayed broader crania for their observed length), and for mandibular length between Modern

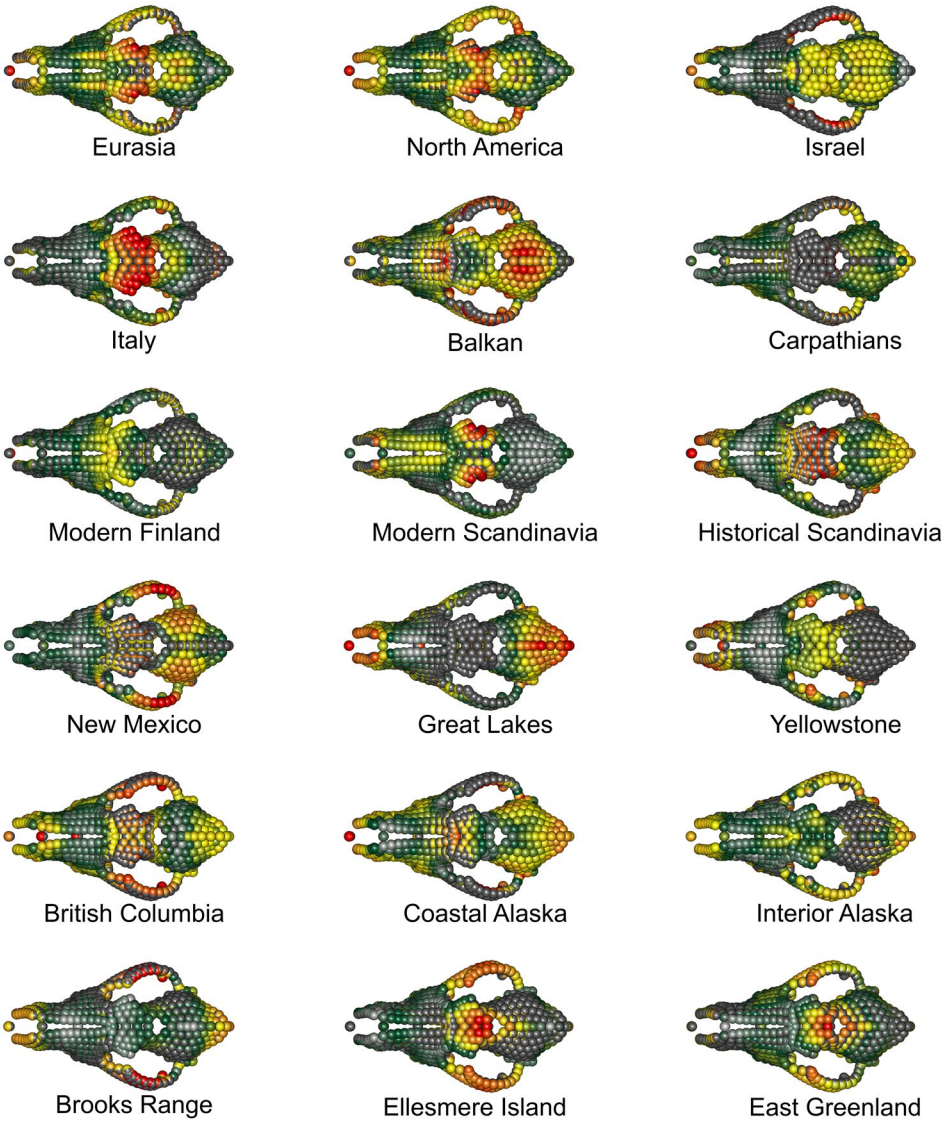

FIGURE 5 | Population cranial shape distances from the overall mean. The mean shape is represented by grey landmarks, whereas each population mean is depicted using coloured landmarks. Colours indicate the magnitude of Euclidean distance differences from the mean, with warmer (red) hues representing larger deviations and green to dark grey indicating smaller differences. Regions where coloured landmarks are more prominent correspond to areas that are larger or wider than the mean, whereas regions where coloured landmarks are obscured by grey correspond to smaller or narrower areas relative to the mean.

Scandinavia and Interior Alaska (Interior Alaskan wolves displayed, on average, longer jaws).

4 | Discussion

In this study, we demonstrate that morphological variation in wolves is concentrated at key functional regions, that is, muscle attachment sites and prey-processing areas (Figure 2). These sites provide a useful proxy for estimating relative muscle size and potential force generation, where larger or more pronounced attachment areas generally correspond to greater muscle development (Ito et al. 2024; Ketchen 2020). Centroid size explained a small proportion of skull shape variation, similar to previous findings (Bujnáková et al. 2025), indicating that other ecological and biogeographical factors tend to exert a stronger influence on morphology. We further found that skull morphology is mostly shaped by geography (latitude, geographic distance), prey and population history (founder effects, bottlenecks and isolation).

4.1 | Geography

Eurasian and North American wolves broadly overlapped in morphospace along the first two principal component axes, which together represented approximately 30% of total shape variation (Appendix S4; Figure S4.2). Significant differences were observed in cranial and mandibular shape and size between the continents, although the proportion of variation explained by continent was low ($R^2 = 3\%–4\%$), indicating that continental affiliation accounts for only a modest component of overall morphological variation. Therefore, these differences should be interpreted cautiously, particularly given

the uneven geographic sampling and the absence of Arctic Eurasian populations in the dataset. Nonetheless, the overall low morphological divergence is striking given 24–34.4 k years of evolutionary separation (Koblmüller et al. 2016; Pacheco et al. 2022). Latitude explained only modest proportions of shape variance, yet it exerted a strong influence on centroid size. Skull size increased with latitude up to ~65°, with peaks in Yellowstone, Scandinavia and Interior Alaska—consistent with Bergmann's rule (Bergmann 1847), assuming that skull size reflects body size. However, wolf skull size declined at the highest latitudes (Brooks Range, Ellesmere Island, East Greenland), in contrast to Bergmann's rule. A quadratic model captured this non-linear pattern, explaining 35% of cranial and 30% of mandibular size variation. In the study by O'Keefe et al. (2013), latitude explained 26% of morphological variance, likely underestimating the full trend due to limited representation of Arctic wolves ($n = 2$). Populations inhabiting extreme northern environments may experience resource-mediated stress, such as limited prey availability, which results in energetic challenges. Such stress can lead to overall smaller bodies despite colder climates. It has been suggested that Bergmann's rule does not apply universally (Meiri and Dayan 2003), and here we show that other ecological pressures, such as diet or local resource availability, can override climate effects. Mixed patterns in other Arctic mammals underscore this complexity, for example Arctic hares (*Lepus arcticus*) and polar bears (*Ursus maritimus*) are larger than their temperate relatives, whereas Arctic foxes (*Vulpes lagopus*) are smaller than red foxes (*Vulpes vulpes*).

Allen's rule, on the other hand, predicts shorter appendages in cold environments (Allen 1877). Extending this principle to cranial proportions, which can be shaped by similar thermoregulatory pressures, we observed that Arctic wolf populations (East Greenland and Ellesmere) exhibited generally shorter and broader crania (Appendix S2). Similar patterns have been reported in Himalayan wolves, which exhibit shorter snouts relative to Holarctic and Indian wolf lineages (Viranta et al. 2025).

Island effect may also partly explain the observed centroid size patterns in East Greenland and Ellesmere wolves inhabiting islands, as these wolves displayed a decreased centroid size in the north. In general, large-bodied mammals often undergo dwarfism in insular settings, whereas small-bodied species tend to increase in size (Benítez-López et al. 2021; Whittaker and Fernández-Palacios 2007). Carnivores, however, appear to deviate from the island rule and are thought to be more constrained by prey (Meiri et al. 2006), which is scarce in the Arctic.

Rather than fitting wolves into a universal ecogeographic rule, our findings emphasize the interplay of several latitude-linked factors. Multiple factors that can affect morphology change with latitude, including temperature and precipitation, which influence prey biomass and ecosystem provisioning (Berzaghi et al. 2024), and prey size, which also scales latitudinally (Ashton et al. 2000; He et al. 2023). Furthermore, human presence often overrides ecosystem provisioning locally, either through habitat destruction and prey elimination or through direct hunting and persecution (as discussed in the Populations section).

4.2 | Prey

Our results indicate that average prey mass is a strong predictor of wolf skull size, explaining roughly one-third of the size variation in the cranium and mandibles. This suggests that population-level differences in the average size of consumed prey are directly reflected in overall skull dimensions. A previous study reported an even higher variance (> 65%) explained by average prey size, reinforcing its influence on wolf cranial size (Ketchen 2020). Prey density may also contribute to size variation: for example, moose, the main prey of wolves in the taiga zone, are more abundant in Scandinavia and parts of Interior Alaska (0.6–> 1 moose/km^2) (Boertje et al. 2009; Hörnberg 2001; Kalén et al. 2022; Keller et al. 2009) than in Finland (0.3–0.7 moose/km^2) (Luonnonvarakeskus 2025; Nygrén 1984; Nygrén and Pesonen 1994), which could explain why wolves from Finland exhibit smaller skulls than populations in Scandinavia and Alaska, despite occupying broadly similar taiga biomes. Comparisons of modern and historical Scandinavian populations revealed differences in frontal bone width, rostrum slope and slightly smaller centroid size historically, likely reflecting both genetic factors and limited prey availability during periods when moose and roe deer (*Capreolus capreolus*) were scarce (Bujnáková et al. 2025). Yellowstone wolves, which prey on highly abundant elk (*Cervus canadensis*), exhibit cranial sizes comparable to northern populations, despite being ~20° south of Interior Alaska and elk being smaller than moose, a main wolf prey in Alaska. This pattern holds even when considering the source population of Yellowstone wolves in Alberta and British Columbia (Phillips and Smith 1997). In contrast, Coastal Alaska wolves, which feed predominantly on small prey, show smaller centroid sizes, even though they are north of the Yellowstone population. These patterns indicate that while latitude provides a coarse predictor of skull size, prey mass and, potentially, prey density exert a stronger influence at smaller regional scales.

In contrast, prey mass does not significantly explain cranial or mandibular shape after accounting for centroid size. This is consistent with the expectation that shape variation within a species is less sensitive to prey differences than interspecific comparisons, where diet strongly influences skull morphology (Meloro and Tamagnini 2022). Nevertheless, visual comparisons of population means reveal subtle trends, i.e., populations feeding on smaller prey (Israel, Coastal Alaska) tend to have narrower crania and mandibles, while populations reliant on large ungulates (Modern Scandinavia, Modern Finland, Interior Alaska) exhibit broader crania and mandibles (Figure 5; Appendix S2).

4.3 | Populations

While latitude and prey strongly influence skull size, and continent has only minor effects on shape, population identity explains 25% of shape and 52% of size variation in single-predictor models. Populations, which are shaped by latitude, climate, prey communities, human interference and genetics, therefore represent a key axis of divergence.

Not all populations follow broad latitudinal trends, highlighting population- or biome-specific influences, as seen in Coastal

Alaska or Historical Scandinavia. However, some populations converge on similar sizes across similar biomes on different continents (e.g., Modern Scandinavia–Interior Alaska, Carpathians–British Columbia, Israel–New Mexico; Figure 3), suggesting ecological convergence or prey limitations. Linear measurements largely mirrored patterns observed in centroid size, with a few exceptions in specific cranial proportions, suggesting localized deviations in skull shape that were not fully captured by overall size trends, but may be represented as shape differences between populations and continents. Shape variation is most pronounced in muscle attachment sites (Figures 2 and 5, Appendix S4, Figure S4.4), but population differences extend to the slope of the rostrum, especially evident in the Balkan versus Carpathians, Modern versus Historical Scandinavian populations, and the Arctic populations (Ellesmere and East Greenland) versus Brooks Range. Other populations, such as those from New Mexico, the Great Lakes and Coastal Alaska, vary in the shape of the brain vault compared to the mean. Such heterogeneity may indicate population-specific adaptations rather than uniform scaling effects.

Genetics and isolation may reinforce these differences, that is, related individuals resemble one another, and geographically or demographically isolated populations often display distinctive morphologies (e.g., Modern Scandinavia, East Greenland and Ellesmere, Italy, Coastal Alaska). Modern Scandinavia, with extreme founder effects and restricted gene flow, has diverged from Historical Scandinavia in both genetics (Stenøien et al. 2021) and morphology (Bujnáková et al. 2025), which has possibly also been influenced by prey availability (Bujnáková et al. 2025). Arctic populations (Ellesmere, East Greenland) remain small, isolated and shaped by harsh climates. Italian wolves, long isolated and bottlenecked (Battilani et al. 2025), retain low genetic diversity and distinct cranial morphologies despite their demographic recovery (Fabbri et al. 2025). Coastal Alaska wolves also diverge morphologically from nearby Interior Alaska and British Columbia populations (Pacheco et al. 2022), reflecting both genetic distinctiveness and prey specialization. Carpathian wolves, though geographically central in Europe, remain genetically (Hulva et al. 2018) and morphologically (Milenković et al. 2010) differentiated from neighbouring populations. New Mexico wolves, which represent the historical Mexican wolf population, show a small size likely linked to both prey size and prey depletion at that time, underscoring the value of comparisons with reintroduced Mexican wolf populations. Reintroduced Mexican wolves now prey more on the Rocky Mountain Elk, a relatively large animal, than the historical Mexican wolves did (Reed et al. 2006; Smith et al. 2023).

Hybridization brings additional nuance to this picture. Dogs tend to display broader frontal bones and generally exhibit a higher cranial width-to-length ratio than wolves (McGreevy et al. 2013). Both traits were observed in Italian and Balkan wolves, where wolf-dog introgression is well-documented (Kusak et al. 2018; Moura et al. 2014; Randi et al. 2014; Santostasi et al. 2021). In contrast, only the elevated cranial width-to-length ratio was observed in Ellesmere and East Greenland wolves. If dog introgression occurred in these regions, it may trace back to the Thule people, ancestors of today's Inuit, who arrived in Ellesmere Island and Greenland around 1200 AD and kept dogs, or to later sporadic Inuit expeditions with sled dogs to Ellesmere Island (Lund Jensen and Sinding 2024). For East Greenland, no genetic records of dog-wolf introgression exist. Although Greenlandic sled dogs were at times intentionally bred with Arctic wolves to improve sled dog qualities, there is no genetic evidence of such hybridization in present-day Greenlandic sled dogs (Lund Jensen and Sinding 2024). An alternative explanation is that the higher cranial width-to-length ratio in Arctic wolves reflects adaptation to extreme cold, as discussed above, rather than hybridization.

4.4 | Conservation Implications

Our findings carry several important conservation implications. First, populations shaped by founder effects or long-term isolation (e.g., Scandinavia, Italy, East Greenland, Ellesmere, Coastal Alaska) show distinct morphologies paralleling to their genetic uniqueness, underscoring the need to protect such reservoirs of evolutionary diversity. Second, wolf morphology is also strongly coupled with prey, that is, populations track both prey size and availability, linking their form and function to ecosystem productivity. Securing robust prey communities is thus fundamental for sustaining wolf populations and their ecological roles. Third, latitudinal trends further reveal that climate interacts with prey and geography in shaping morphology. As anthropogenic climate change and habitat alteration reshape prey distributions and ecosystem dynamics, wolves may face novel selective pressures, particularly in small, isolated Arctic populations. Taken together, these results caution against treating wolves as morphologically uniform in conservation planning, including reintroductions. Effective management must be population-specific, integrating local ecology, prey dynamics, genetics and anthropogenic pressures to preserve both the functional and evolutionary potential of wolves across their entire range.

5 | Conclusion

This research demonstrates that wolf skull morphology varies widely across populations, reflecting ecological, geographical and demographic histories. The most pronounced morphological divergences among populations reflect long-term isolation, demographic events (e.g., bottlenecks or founder effects), human impacts, including extirpations and limited connectivity, geographic constraints, prey specialization and potential hybridization. Collectively, these findings highlight that wolf skull morphology emerges from the interplay of evolutionary history, ecological context and anthropogenic influence. Our results also demonstrate the power of dense landmark analyses in detecting fine-scale morphological variation across a species' global range.

Author Contributions

Dominika Bujnáková, Jouni Aspi, Laura Kvist and Christy Anna Hipsley contributed to conceptualization and analyses. Dominika Bujnáková led the analyses and writing of the manuscript. Data acquisition and/or processing were contributed by Dominika Bujnáková, Sarah J. du Plessis, Daniele Falcinelli, Carsten Gundlach, Katja Holmala, Jonathan S. Keller, Mohammed Khumri, John Korbin, Robert W. Mysłajek, Sabina Nowak, Ladislav Paule, Katrine Raundrup, Madeline

K. Rowland, Mikkel-Holger S. Sinding, Davide Tamagnini and Mia Valtonen. All authors contributed to interpretation of the data, critically revised the manuscript, approved the final version, and agreed to be accountable for all aspects of the work.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Appendices S1 and S2 provide all covariate and prey data used in the analyses. The full dataset, including raw landmark files, a complete R script and the cranium and mandible landmarking templates used in Stratovan Checkpoint, is archived on Figshare: https://doi.org/10.6084/m9.figshare.30746732.

Peer Review

For transparency, the peer review documents associated with this article are available at https://doi.org/10.1111/ddi.70228.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Sample information, including museum source, specimen ID, collection locality, collection year, CT/3D scanning institution, model covariates and, where applicable, usage rights and licensing information for online data sources. **Appendix S2:** Prey data for 16 wolf populations, including the most common prey species, male and female prey weights, mean prey weight, weighted mean prey weight by frequency of occurrence and population-specific linear measurements of the cranium and mandible. **Appendix S3:** Results of statistical models for cranial and mandibular shape and size, including individual predictor models, multiple predictor models and the overall results summarized as average contribution of predictors to wolf skull shape and size. **Appendix S4:** Additional supporting figures showing landmark configurations, principal component analyses, additional cranial and mandibular comparisons among populations and continents, and linear measurement analyses, such as cranial length, cranial width, cranial width/length ratio, mandibular length and mandibular width.