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Evolutionary causes and consequences of ungulate migration

Joel O. Abraham [1✉], Nathan S. Upham [2,3,4], Alejandro Damian-Serrano[3,5] and Brett R. Jesmer [3,4,6]

Ungulate migrations are crucial for maintaining abundant populations and functional ecosystems. However, little is known about how or why migratory behaviour evolved in ungulates. To investigate the evolutionary origins of ungulate migration, we employed phylogenetic path analysis using a comprehensive species-level phylogeny of mammals. We found that 95 of 207 extant ungulate species are at least partially migratory, with migratory behaviour originating independently in 17 lineages. The evolution of migratory behaviour is associated with reliance on grass forage and living at higher latitudes wherein seasonal resource waves are most prevalent. Indeed, originations coincide with mid-Miocene cooling and the subsequent rise of C_4 grasslands. Also, evolving migratory behaviour supported the evolution of larger bodies, allowing ungulates to exploit new ecological space. Reconstructions of migratory behaviour further revealed that seven of ten recently extinct species were probably migratory, suggesting that contemporary migrations are important models for understanding the ecology of the past.

The scientific community and public imagination have long been captivated by ungulate migrations. Migrations, like those of wildebeest in the Serengeti, have been referred to as one of the natural wonders of the world[1] and continue to demonstrate their value, both via ecotourism revenue to local economies[2] and as the focus of critical ecological research[3]. By tracking plant quality and quantity across space and time—a behaviour known as 'green wave surfing' (hereafter referred to more generally as 'resource tracking'[3-5])—migratory ungulates can sustain much larger populations than their resident counterparts[6-8]. Since ungulates track spatio-temporally variable forage across landscapes (that is, 'resource waves'), they also serve as important vectors of nutrients, seeds, spores and diseases along migration corridors and between seasonal ranges[9,10], thus linking ecosystem processes across large spatial scales. However, despite their cultural, economic and ecological importance, large gaps remain in our knowledge of ungulate migrations[8,11-13]. Both resource tracking and avoidance of predators, parasites and pathogens have been identified as proximate drivers of migration[13,14] but scant evidence exists regarding the evolutionary origins of this behaviour[11,12]. Classically, migratory behaviour is thought to have evolved via natural selection on genetic variation directly associated with a migratory phenotype[11,15,16]. However, recent evidence suggests that ungulate migrations may be a cultural phenomenon, wherein socially learned information about spatio-temporal patterns of plant quality (that is, 'resource waves') is transmitted across generations and improved on via asocial learning within generations—a process known as cumulative cultural evolution[17]. In either case, migratory behaviour is thought to emerge from a combination of physiological, morphological and cognitive traits[11,18-20], suggesting that genetics at least partially underpin the evolution and maintenance of migratory behaviour (that is, 'migratory genes' might be reinforced by cultural transmission of migratory knowledge[16,21]). Altogether, understanding the role that ungulate traits (for example, body size, digestion, metabolic physiology) and environmental factors (for example, latitude, resource waves) play in the evolution of migratory behaviour will bring clarity to the mystery of why some ungulates migrate while others do not.

Extant migratory ungulates are hypothesized to share a 'migratory syndrome', a common suite of environmental, morphological and behavioural characteristics that interact to form a migratory phenotype[11,19]. Environmentally, migratory behaviour is prevalent in seasonal environments where predictable resource waves are present[3,12,20]. Because the seasonality of grass growth in the tropics and subtropics tends to be more pronounced than that of trees[22,23], migration at lower latitudes is largely restricted to grazing ungulates that depend primarily on grasses to meet their nutritional needs[20,24]. In contrast, all plants in temperate and mountainous regions are seasonally variable in their nutritional quality and quantity (not just grasses)[25], which drives the seasonal migrations of browsers, mixed feeders and grazers alike[20]. Nevertheless, the most consistent migrants are grazers even in these seasonal systems[3,5,26]. Grass dependence may therefore be tied to the evolution of migration inside and outside the tropics (Fig. 1). Morphologically, larger body size may also be a key component of a migratory syndrome in ungulates[27,28] (Fig. 1). Migratory mammals tend to be larger than non-migratory taxa and larger species undertake longer migrations[28-30]. Such allometry in migratory behaviour may stem from the ability of large-bodied species to accumulate greater nutritional reserves and thereby better tolerate the energetic demands of migration, reduced predation risk during their migratory journeys and lower reliance on high-quality forage[28,30-32]. Thus, we hypothesize that latitude, grass dependence and body size together may lead to a migratory syndrome and that these characteristics have jointly contributed to the evolution of migration (Fig. 1; see Supplementary Notes for additional justification of hypotheses).

To test the relative support for hypothetical models of how migratory behaviour evolved (Supplementary Fig. 1), we first estimated the evolution of migration across a species-level ungulate phylogeny and determined how the evolution of migration relates

[1]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA. [2]School of Life Sciences, Arizona State University, Tempe, AZ, USA. [3]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA. [4]Center for Biodiversity and Global Change, Yale University, New Haven, CT, USA. [5]Institute of Ecology and Evolution, University of Oregon, Eugene, OR, USA. [6]Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA, USA. ✉e-mail: joeloa@princeton.edu
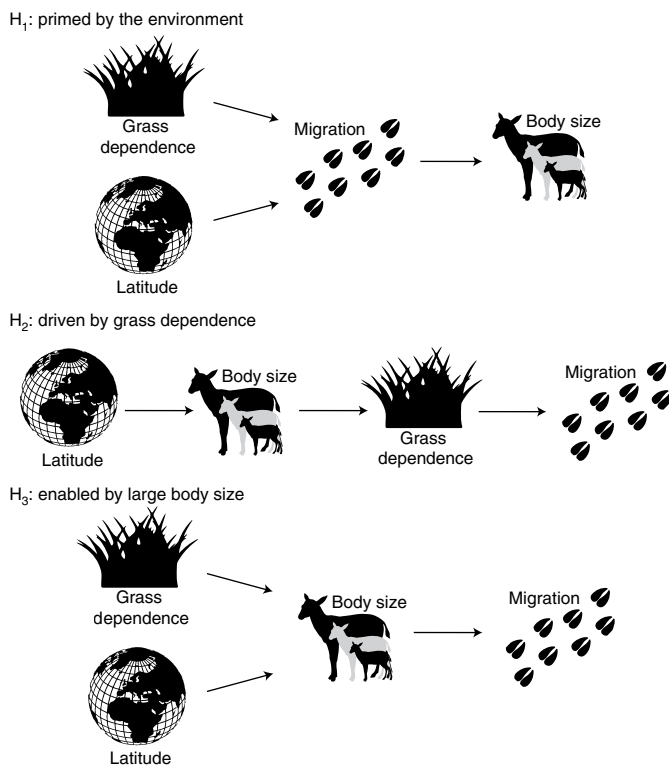
Fig. 1 | Hypothetical evolutionary models of migration. Migration may evolve in direct response to a spatio-temporally fluctuating resource environment, resulting both from living at high latitudes and being reliant on seasonally variable grasses (**H₁**); alternatively, migration might evolve in large-bodied, grass-dependent ungulates as a consequence of their particular need to track grass productivity across large spatial scales (**H₂**) or migration might evolve when ungulates get large enough to where migration is energetically feasible (**H₃**).

to the evolution of other ungulate characteristics, namely species mean adult body size, latitudinal centroid of species' geographical range and degree of grass dependence. We then applied phylogenetic path analysis, a method for determining the underlying causal structure in phylogenetically structured comparative data[33], to determine the evolutionary causes and consequences of ungulate migration. Next, we used a global dataset of the normalized difference vegetation index (NDVI) to assess the role that resource waves played in promoting the evolution of migration. Finally, we used the relationships between migration and other ungulate characteristics to reconstruct the migratory behaviour of recently extinct ungulates. Overall, we found evidence that migratory behaviour in ungulates evolved in response to relying on grass forage and living at high latitudes, which in turn drove the evolution of large body sizes, and that migration may have been more widespread historically than it is today.

Results

A migratory syndrome. Extant ungulates are highly variable with regard to migratory behaviour, body mass, grass consumption and latitude (Fig. 2). Compiling data from a range of literature sources, we found that 95 of 207 (45.9%) extant ungulate species are at least partially migratory. Ungulate body masses span more than 3 orders of magnitude, from 2.78 to 2,950 kg. Likewise, ungulates range from pure grazers, consuming entirely grass, to pure browsers, consuming entirely trees and forbs, with yet others (mixed feeders) eating intermediate amounts of both grass and trees. Furthermore, ungulates

can be found across latitudes, residing in the tropics through to the Arctic (up to nearly 75° N).

Amid this ecological variation, and in accordance with the existence of a migratory syndrome, we recovered consistent differences between the characteristics of migratory and non-migratory ungulates. We found that migratory ungulates are larger, inhabit higF-Browninanher latitudes and are more grass-dependent on average than non-migratory ungulates (Fig. 2a–c and Supplementary Table 1). Likewise, we found that larger ungulates tend to consume more grass on average (Fig. 2d and Supplementary Table 1), although migratory ungulates are still more grass-dependent than non-migratory ungulates even accounting for differences in body size. However, contrary to expectations (Supplementary Notes), body size is not correlated with latitude across ungulates species (Fig. 2e and Supplementary Table 1). As such, the larger body sizes of migratory ungulates are not the direct result of their inhabiting higher latitudes.

We found that migratory ungulates inhabit distinctly seasonal environments compared to non-migratory species. Migratory behaviour is most prevalent among taxa whose ranges include highly seasonal resource waves (Extended Data Fig. 1). Specifically, resource wave seasonality, rather than wave magnitude or resource wave distance, best explains the observed interspecific variation in migratory behaviour (Extended Data Fig. 1). When added to the above model of migratory behaviour that includes latitude, grass dependence and body mass as covariates, resource wave seasonality loses its predictive power and becomes non-significant (Supplementary Table 1). This suggests that the predictive power of resource wave seasonality is obscured by its covariation with one or more other predictors. Unsurprisingly, we found that resource wave seasonality increases with both increased latitude but also with increased grass dependence (Extended Data Fig. 1), indicating that vegetation growth is more seasonal at higher latitudes and also that ungulates inhabiting landscapes with more seasonal resource waves are more grass-dependent (probably due to the inability of ungulates to specialize exclusively on a particular plant functional type in the face of seasonally variable plant availability[20,34,35]). Together, these results suggest that inhabiting higher latitudes and relying on grass for nutrition exposes ungulates to predictable spatio-temporal variability in resource quality and quantity, ultimately making migratory behaviour advantageous.

Dynamic evolution. Not only are extant ungulates ecologically variable but ungulate characteristics have also varied dynamically through evolutionary time (Fig. 3a-d). By estimating the evolution of migration, grass consumption, body size and latitudinal range centroid across the ungulate phylogeny (Supplementary Table 2 and Supplementary Fig. 2), we found phylogenetic evidence that the most recent common ancestor (MRCA) of extant ungulates was most probably a small-bodied mixed feeder living in the tropics to subtropics, although with marginal statistical support (Supplementary Table 3). Although the confidence intervals (CIs) on reconstructed states are broad and encapsulate a variety of ecologically disparate possibilities (Supplementary Table 3), these findings are consistent with previous reconstructions of ungulate evolution[34] and with fossil evidence[36,37]. Taken together, these lines of evidence suggest that some of the characteristics that define the present-day migratory syndrome—large body sizes, grass dependence and living at high latitudes—are derived relative to the MRCA. We also found that the MRCA was more likely non-migratory, although only by a small margin (Supplementary Table 3); therefore, this finding should be interpreted as inconclusive, as is often the case when reconstructing the evolution of binary traits with multiple independent transitions across the tree. Although the state of the MRCA as non-migratory is equivocal, we found 17 branches where transitions from non-migratory to migratory are supported (defined as a shift in the
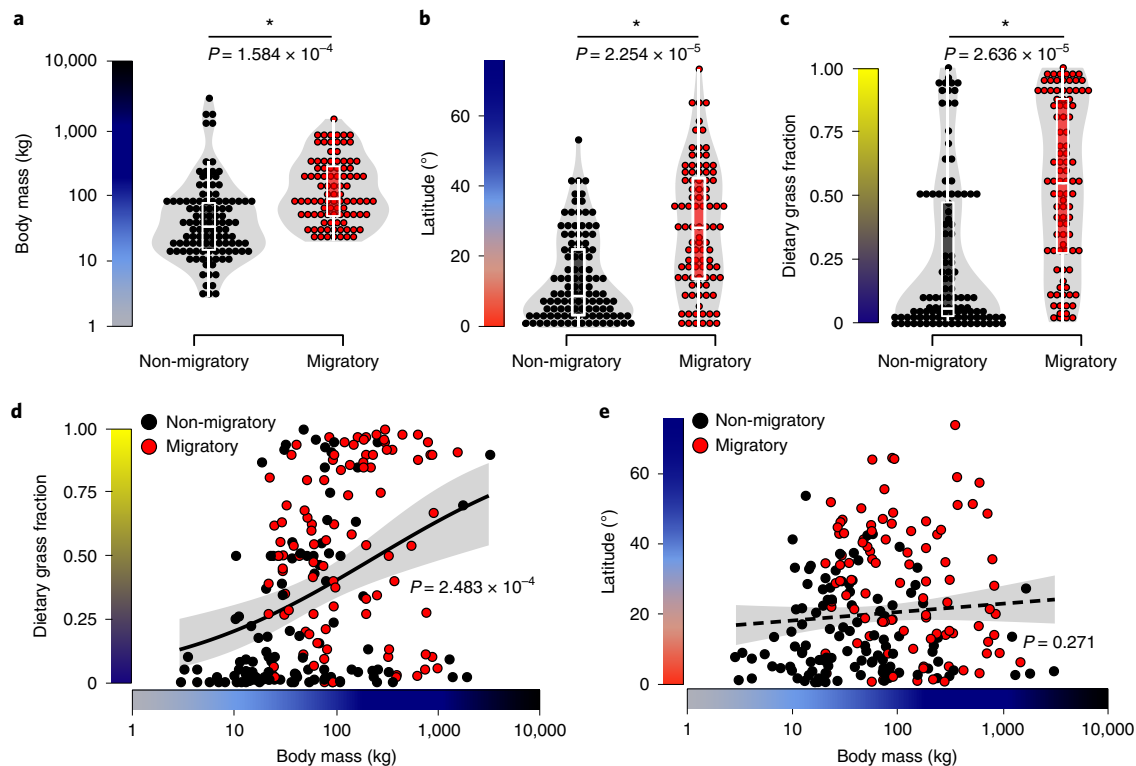
Fig. 2 | Evolutionary correlations between ungulate characteristics. a–c, Using phylogenetic modelling, we found that migration is positively correlated with body mass (**a**), latitude (**b**) and grass dependence (**c**), such that migratory ungulates tend to be larger, inhabit higher latitudes and consume more grass than non-migratory ungulates (two-sided PGLM; $n = 207$ species). **d,e,** Across all extant ungulate species, grass dependence (**d**) is positively correlated with body mass (two-sided PGLM; $n = 207$ species), such that larger ungulates tend to eat more grass on average, but latitude and body mass (**e**) are not significantly correlated (two-sided PLM; $n = 207$ species). The colour gradients along the axes correspond to those in Fig. 3. The asterisks in **a–c** and solid regression line in **d** denote a significant relationship ($P < 0.05$), whereas the dashed line in **e** denotes the lack of a clear relationship ($P \geq 0.05$), corrected for multiple comparisons. The white bands in **a–c** represent the median values, the coloured black and red bars represent the interquartile range and the white whiskers extend to $\pm 1.5\times$ the interquartile range. The grey shaded regions in **d,e** represent the 95% CIs on the regression. Full model details are available in Supplementary Table 1.

posterior probability of migratory behaviour from <0.5 to >0.5). By the same token, we estimate 23 branches along which the loss of migratory behaviour is supported (defined as a shift in the posterior probability of migratory behaviour from >0.5 to <0.5). Altogether, these findings suggest that migratory behaviour was highly labile across ungulate evolution, with a complex history of independent, and possibly convergent, gains and losses.

The evolution of migratory behaviour appears to have changed the evolutionary trajectories of several other ungulate characteristics. We modelled grass dependence, body size and latitude as continuous characters evolving within the discrete selective regimes of being migratory or non-migratory, finding that multi-optimum Ornstein–Uhlenbeck models are preferred almost every time (299 out of 300 iterations) for all characters (Supplementary Table 4). This suggests that not only do characters associated with migratory behaviour interact evolutionarily, but migratory behaviour is also associated with distinct evolutionary optima for these characteristics. Such results suggest that ungulate characteristics change directionally in response to evolving migratory behaviour, although the direction of causation cannot be ascertained from these results alone.

Altogether, our results provide evidence for the existence of a migratory syndrome within ungulates, characterized in part by large body sizes, grass dependence and living at high latitudes. Furthermore, this migratory syndrome appears to have evolved multiple times independently over the course of ungulate evolution.

Finally, our results suggest that the advent of migratory behaviour changed the adaptive landscape for other ungulate characteristics.

Causes and consequences. In accordance with the hypothesis that environmental factors motivated the evolution of migratory behaviour (H_1; Fig. 1), we found directional phylogenetic evidence that latitude and grass dependence underpinned the evolution of migratory behaviour, which in turn drove body size evolution. To do this, we used phylogenetic path analysis, a method that tests claims of conditional independence implied by various causal hypotheses to determine the most probable causal relationship between phylogenetically distributed characters. By comparing alternative models, we found that the most probable causal model for the evolution of migration (the average of all causal models with C statistic information criterion corrected for small sample sizes $(\Delta CIC)_c < 2$) shows that two characteristics—inhabiting higher latitudes and being highly dependent on grass—promoted the evolution of migratory behaviour. Migratory behaviour, in turn, promoted the evolution of large body sizes (Fig. 4a and Supplementary Table 5).

To further interrogate the hypothesis that resource waves mediate the relationship between latitude and grass dependence on migratory behaviour, we tested additional path models that included links between resource wave seasonality and both latitude and grass dependence (Supplementary Fig. 3). The average causal model (Fig. 4b) is structurally similar to the path model without data on
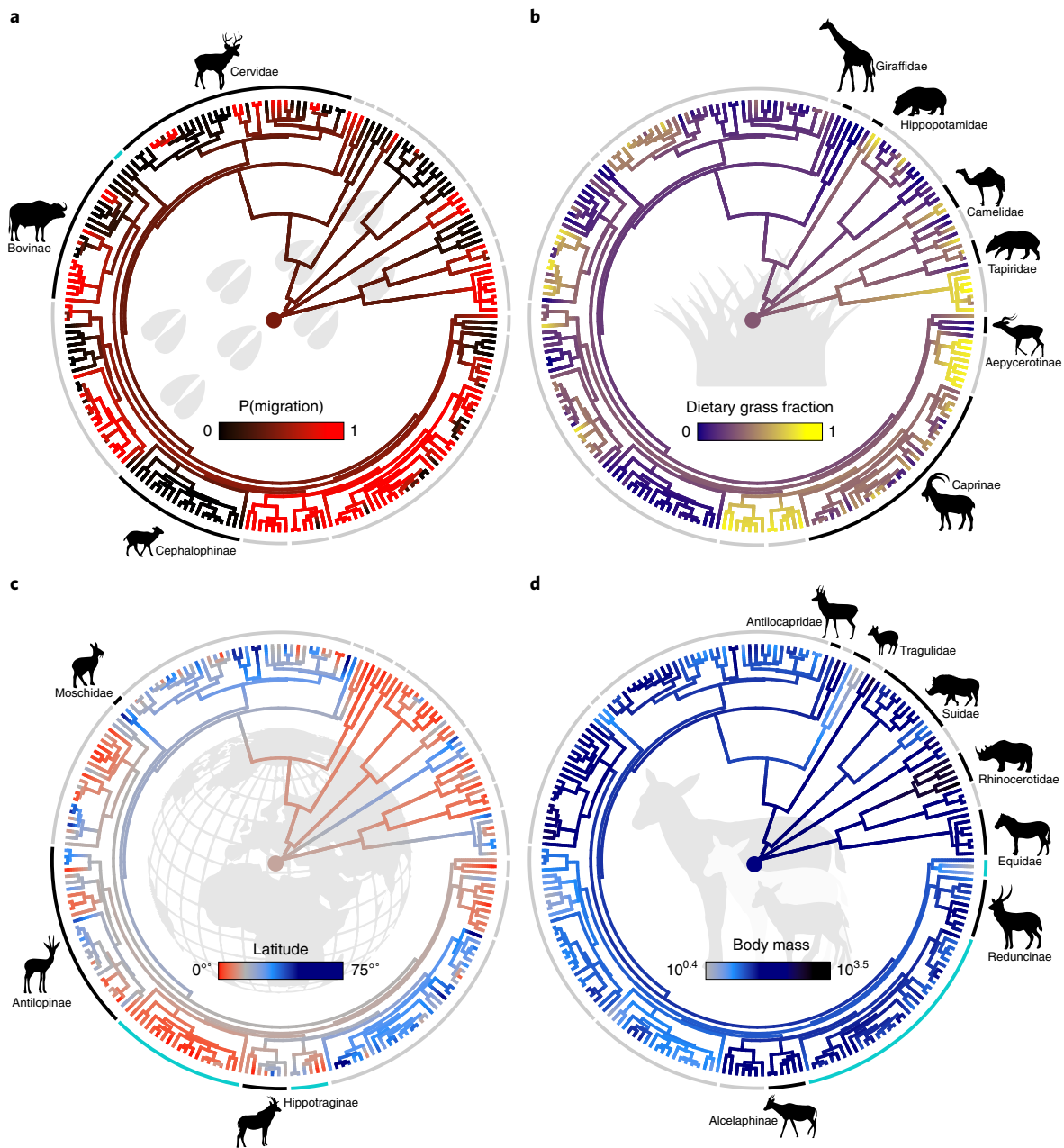
Fig. 3 | Ungulate character evolution. a–d, The evolution of migratory behaviour in ungulates was estimated using stochastic character mapping, whereas the evolution of dietary grass fraction (**b**), latitude (**c**) and body mass (**d**) in ungulates were each reconstructed using Ornstein–Uhlenbeck models of character evolution ($n = 207$ species). Branch colors represent reconstructed character values and color gradients correspond to those in Fig. 2. In **a**, branch colors correspond to P(migration), or the posterior probability (computed as the relative frequency across stochastic maps) of migration along the branch, where red indicates high posterior probability of migration. Ungulate families and Bovidae subfamilies[74] are denoted around the perimeter of the phylogenies, along with the silhouette of a representative from each group. The colour gradients correspond to those in Fig. 2.

resource wave seasonality (Fig. 4a): links are the same but additional links arise between latitude and green wave seasonality, green wave seasonality and migratory behaviour and green wave seasonality and grass dependence (Fig. 4). The most notable difference is that green wave seasonality mediates some of the effects of latitude on migratory behaviour (Fig. 4b). Altogether, this provides additional support for the hypothesis that latitude and grass dependence exposed ungulates to seasonal green waves and thereby selected for the evolution of migratory behaviour (Fig. 1). However, no causal model including resource waves is well supported (Supplementary Table 6). This suggests that all models we tested make claims of independence that are violated given our data; this is somewhat

unsurprising given our aforementioned findings that green wave seasonality covaries significantly with both latitude and seasonality.

Additionally, the origins of migratory behaviour may be temporally correlated with the mid-Miocene cooling of the Earth (and resultant increases in seasonality towards the poles[38]) and the consequent rise of C_4 grasslands[39]. Branches along which migration arose overlap the time intervals when these two changes to the Earth system occurred (Fig. 5). This suggests that these environmental changes may have contributed to the emergence of migratory behaviour, further emphasizing the central roles that living at high latitudes and relying on grass forage have played in the evolution of migratory behaviour.
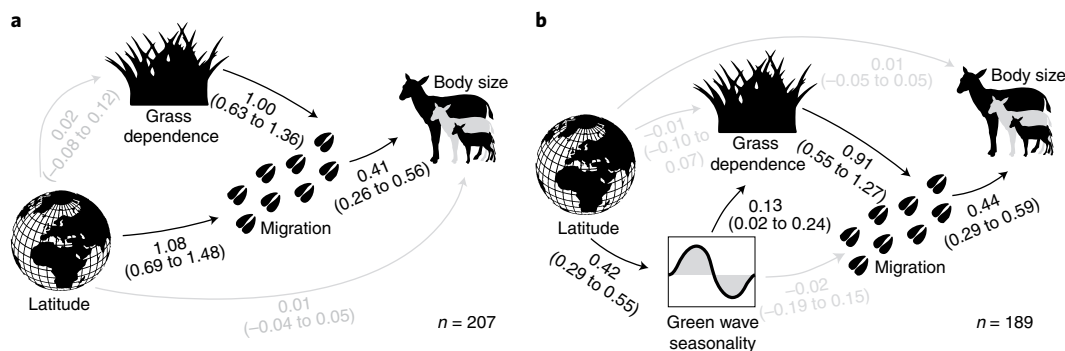
Fig. 4 | The causes and consequences of evolving migratory behaviour in ungulates. a, The average causal path model of migratory evolution demonstrates that migration evolved in response to living at high latitudes and being dependent on grass ($n = 207$ species). **b**, Causal path models incorporating green wave seasonality (NDVI semi-variance) suggest that green wave seasonality mediates some of the effects of latitude and grass dependence on migration ($n = 189$ species). The arrows are coloured by whether or not they are significant; the links for which the CIs of the regression coefficients overlap zero are depicted in grey since they cannot be taken to be significant. The numbers below the arrows represent the strength of the effects, along with the corresponding 95% CI (via bootstrapping).

Finally, we found evidence that now-extinct ungulates may have been disproportionately migratory. We reconstructed the migratory phenotype of ten recently extinct ungulates using phylogenetic imputation and found that seven out of the ten extinct taxa are supported as being migratory (Fig. 6 and Supplementary Table 7). Migration is significantly more prevalent among these extinct taxa compared to extant ungulates (phylogenetic generalized linear model (PGLM); $n = 217$, $z = 3.007$, $P < 0.001$; Supplementary Table 1); the proportion of extinct ungulates that were migratory was 1.52× that of extant taxa (70.0% for extinct taxa compared to 45.9% for extant taxa). However, this result is based on only ten extinct taxa that could be adequately placed in the ungulate phylogeny from existing genetic data and should therefore be interpreted with caution.

Discussion

Ungulate migrations are important for maintaining both robust population sizes and ecosystem dynamics[6,7,10], yet little is known about the ultimate drivers of migration and what the emergence of migratory behaviour has meant for ungulate evolution[11,12,16]. We used phylogenetic path analysis to evaluate the coevolution between migratory behaviour and ungulate characteristics, finding that: (1) migratory ungulates exhibit a migratory syndrome, tending to be larger, depending more on grass and inhabiting higher latitudes than their non-migratory counterparts; (2) migratory behaviour appears to have arisen 17 times independently across the ungulate phylogeny, contemporaneously with an increasingly seasonal climate and the subsequent spread of C_4 grasslands; and (3) migratory behaviour most likely evolved in response to selective pressures associated with being grass-dependent and living at high latitudes (or other highly seasonal environments), in turn enabling the evolution of large body sizes. Our work provides a causal explanation for the origin of migratory behaviour in ungulates and consequent evolution of large body sizes in grazing mammals.

These results illuminate the critical role that migratory behaviour has played in ungulate evolution. The evolution of migratory behaviour appears to have been driven, at least in part, by living at high latitudes and depending on grass for nutrition (Fig. 4). Both characteristics likely exposed ungulates to substantial resource variability; vegetation at high latitudes is highly variable across seasons and grass is both fast-growing and responsive to environmental variation relative to other plant functional groups[22,25,31,40]. In support of this hypothesis, most of the probable gains of migratory behaviour that we estimated are temporally coincident with two dramatic changes in the ecology of the planet: global cooling in the mid-Miocene[38] and the subsequent rise of C_4 grasslands[39] (Fig. 5).

Both of these changes drastically altered patterns of terrestrial resource availability and applied new selective pressures on the foraging ecology of ungulates[35,37]. Therefore, migratory behaviour likely evolved as a strategy to cope with this increasingly variable but also highly predictable vegetation growth (that is, resource waves). Recent work has similarly demonstrated that many (although not all) extant migratory ungulates track resource waves[3,5,8]. Thus, the environmental contexts that historically selected for migratory behaviour probably resemble those that continue to make this an adaptive strategy for nearly half of the ungulate species today.

We found evidence that these global shifts in climate and vegetation triggered the evolution of migratory behaviour multiple times across the ungulate phylogeny. Two compatible mechanisms may have contributed to the many independent origins of migratory behaviour (Fig. 5). First, ungulates and other migratory taxa use spatial memory to form cognitive maps that enable them to track resource waves across large spatial scales[8,41–43], which suggests that the ancestor of modern ungulates likely also possessed the cognitive capacity to remember and integrate spatial information at large scales[41]. This ability may have been subsequently co-opted by different lineages for the purposes of migration in response to local selection pressures. Second, cultural evolution may have facilitated the evolution of migratory behaviour, following evidence from contemporary migrations that knowledge of when and where to migrate results from the cumulative cultural transmission of social and asocial information about spatial patterns of plant phenology[17]. Cultural evolution can exert particularly strong selection on behaviour since culture can allow rapid diffusion of a particular behaviour through a population, accelerating its genetic fixation[16,21,44]. Nevertheless, some ungulate species appear unable to learn migratory behaviour, even under extreme conditions (like severe drought[31]). Thus, while the repeated evolution of migratory behaviour may have been facilitated by social learning and cultural evolution, our results indicate that other physiological, morphological and ecological characteristics likely constrained which species did and did not evolve migratory behaviour.

Our results suggest that the evolution of migratory behaviour precipitated the evolution of large body size in ungulates (Fig. 4). This finding is consistent with the Behavioral Drive hypothesis, which proposes that behaviour is not simply a product of morphology but rather a powerful selective force that shapes evolutionary trajectories, capable of initiating evolutionary shifts in morphology, physiology or ecology[44,45]. Accordingly, increases in body size after the emergence of migratory behaviour may have been the result of selection pressures to mitigate the costs of migrating. Although
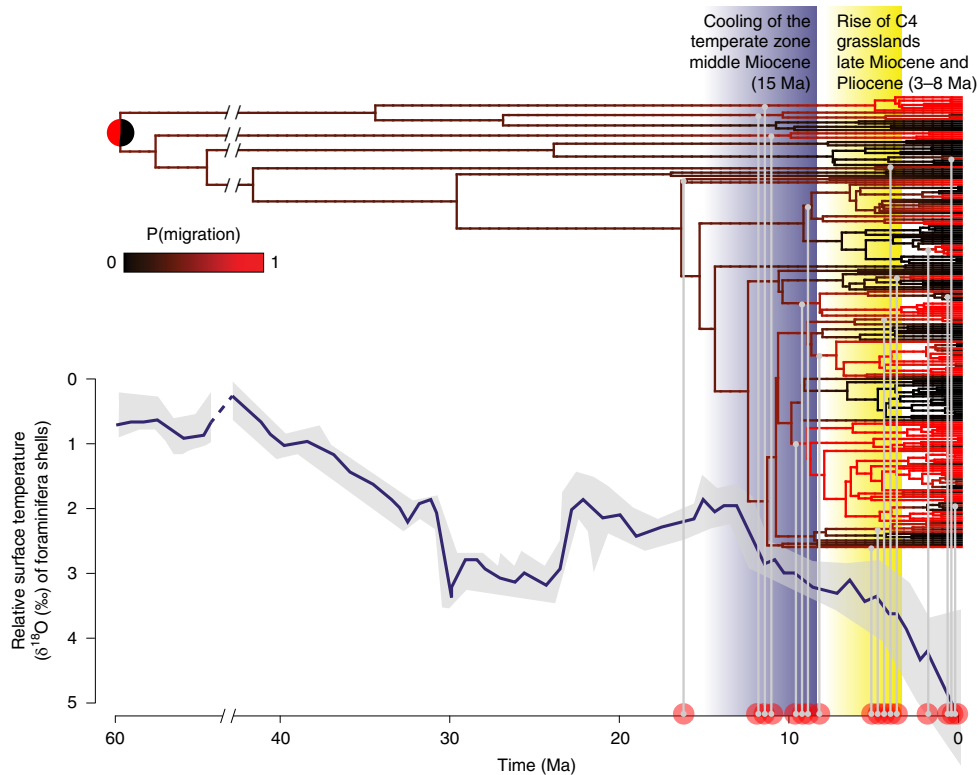
Fig. 5 | The Earth system context for the evolution of migratory behaviour. The evolutionary origins of migratory behaviour are temporally aggregated and are coincident with the onset of mid-Miocene cooling as well as the global proliferation of C_4 grasslands. The 17 branches along which the origins of migration are most likely are marked with grey circles along the branches of the phylogeny; the timing of these origins is depicted by the semi-transparent red circles along the x axis. The Cenozoic record of Earth surface temperature changes is derived from the $\delta^{18}O$ (‰) of foraminifera shells and is reproduced from Zachos et al.[38] and Edwards et al.[39]. The blue line represents the mean temperature over the last circa 60 Ma and the grey shaded region represents the variation around the mean.

long-distance migration is energetically intensive[30], larger organisms can move more efficiently and freely, such that large body sizes may reduce the energetic costs associated with migrating[26,30,46]. Additionally, evolving migratory behaviour may have freed ungulates from resource limitation by providing them access to a larger forage pool, thereby allowing them to evolutionarily explore a broader phenotypic space and exploit unoccupied niches[31,40,46]. Regardless of the mechanism, phylogenetic evidence suggests that migration changed the adaptive landscape for ungulate body size and this may have been the case for other mammal lineages also[47]. Some of the largest extant mammals are migratory: savanna elephants migrate seasonally in response to forage green-up[47] and blue whales, which share a common ancestor with artiodactyl ungulates[48], track resource waves in a manner similar to their terrestrial relatives[49]. Thus, migratory behaviour may have played a key role in the evolution of large body sizes in mammals more generally.

Our results suggest that migratory mammal species may have been more numerous in the Earth's past. Given that extant large-bodied grazing species tend to be migratory (Fig. 2) and that many such large grazing ungulate species roamed high latitude environments before the Pleistocene megafaunal extinctions[35,50–52], it follows that many of these extinct megafauna likely also exhibited migratory behaviour. Our results directly support this hypothesis, with seven out of ten ungulate species that went extinct within the past 1 Ma reconstructed as migratory (Fig. 6). As such, landscapes were probably more spatially connected before the Pleistocene extinctions, with migratory Pleistocene megafauna conveying nutrients, seeds, spores and diseases across vast distances much as they do today[9,10]. Indeed, the legacies of these lost migrations likely

continue to inform the ecology of modern ecosystems via persistent effects on soil properties, fire regimes and plant communities[35,53]. Hence, contemporary ecosystem dynamics may be somewhat anachronistic[54,55], informed by a past where migrations were more widespread. The few remaining ecosystems with intact migrations are therefore critical for understanding how these lost migrations continue to influence the dynamics of ecosystems today.

We also speculate that the disruption of migrations may have played a key role in the progression of the megafaunal extinctions in North America, Europe and Asia and the ongoing loss of ungulate migrations[56]. Expansion of humans out of Africa in tandem with changing environment conditions are chiefly implicated in megafaunal extinctions[50,57,58] but the precise mechanisms underlying these extinctions are unclear[28]. Migratory behaviour is currently under severe threat from global change[11,13] and many large-scale migrations have either already collapsed or are now imperilled by intensifying anthropogenic pressures from land use change, overhunting and the construction of physical barriers[11,56,59]. If similar drivers (a changing climate and human impacts) also caused the collapse of migratory behaviours during the Pleistocene[28,50], triggering associated population declines[7,24], then migratory species would have become more vulnerable to stochastic events, ultimately leading to extinction. Our findings that migratory ungulates generally occur at higher (especially northern) latitudes and are larger-bodied than non-migratory species (Fig. 2) may thereby account for the size-biased nature of the Pleistocene extinctions as well as their severity outside Africa[50,51]. The Pleistocene megafaunal extinctions and subsequent decline of ungulate diversity may thus serve as an analogue for contemporary and future loss of migratory
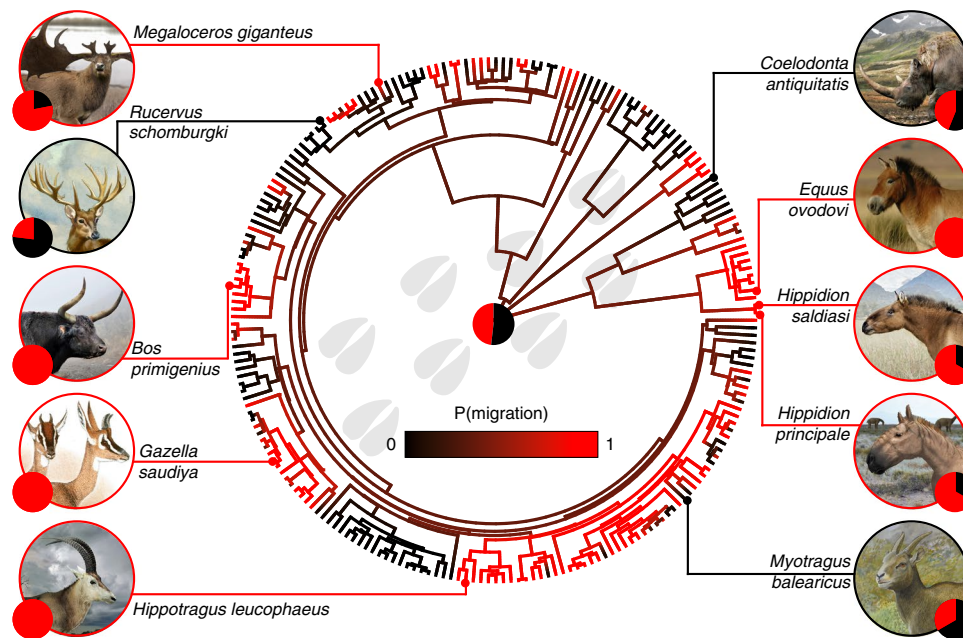
Fig. 6 | Reconstructed migratory behaviour in extinct ungulates. The pie charts represent phylogenetically imputed values of migration and reflect the likelihood that ten recently extinct ungulate species were migratory. These recently extinct ungulates are disproportionately migratory relative to extant taxa (two-sided PGLM; $n = 217$ species, $z = 3.007$, $P < 0.001$). The likelihood of migratory behaviour in these taxa was imputed from available data on grass dependence, body mass and latitudinal range centroid from the fossil record (see Supplementary Table 7 for further details). Images of extinct ungulates are courtesy of R. Uchytel and D. Boh and are reproduced with permission.

behaviour if ongoing trends of habitat fragmentation and degradation are not reversed.

Conclusions

Resource waves associated with mid-Miocene cooling and the spread of C_4 grasslands created widespread selective pressures that helped drive the repeated evolution of migratory behaviour in high-latitude, grass-dependent ungulates (Figs. 4 and 5). The widespread evolution of migratory behaviour across ungulate lineages was likely facilitated by a suite of cognitive or physiological preadaptations and possibly also cultural evolution. New migratory behaviour, in turn, resulted in the selection for larger body sizes (Fig. 4), which perhaps mitigated the energetic costs associated with migratory behaviour and leveraged the additional resources accessed by migrating. Dependence on migration for sustaining their populations may have exposed migratory ungulates to an increased extinction risk in the face of a changing Pleistocene climate and expanding human impacts, subsequently contributing to the extinction of many large-bodied grazing taxa (Fig. 6). By extension, we suggest that the Pleistocene megafaunal extinctions are both an analogue for the present and a warning for the future of ungulate species as threats to migrations continue.

Methods

Incidences of migratory behaviour. To determine the incidence of migratory behaviour in ungulates, we first made an operational list of all ungulate species to be included in our analyses. To do this, we used a recently constructed species-level mammal phylogeny[48], focusing all analyses on the node-dated DNA-only consensus tree (maximum clade credibility of 10,000 trees in the credible set). We pruned the whole mammal tree down to just ungulates (species in the orders Perissodactyla and Artiodactyla but excluding Cetacea). Therefore, our list of ungulates included 207 extant and 10 extinct species for which DNA sequence information was available (see Supplementary Dataset 1 and Supplementary Table 7 for the complete list of ungulate species and references consulted).

We then sought to determine which of these species were migratory. To curate a list of migratory behaviour in ungulates, we first compiled published syntheses of migratory species and performed an exhaustive literature review, searching

Web of Science and Google Scholar for any records of migratory behaviour for each ungulate species. For the purposes of this study, we reduced migration to a binary characteristic; ungulates were considered migratory if any population exhibited seasonal round-trip movements between discrete areas and/or if they were explicitly described as migratory in the published literature[13,59]; therefore, our categorization of migratory ungulates includes elevational and latitudinal migrants. We coded species as migratory if there was any record of the species having ever exhibited migratory behaviour in the past or present.

Covariates of migration. Next, we gathered data on the three ungulate characteristics we hypothesized to be relevant to the evolution of migration: body size; latitude; and grass dependence. Species mean adult body masses were assembled for all ungulate species from various mass datasets[60–62], which are themselves compilations from the primary literature. Body mass values were log-transformed for all analyses.

To summarize the latitudinal niche of each ungulate species, we calculated the latitudinal centroid of species' geographical ranges. For extant species, expert geographical range maps were downloaded from the International Union for the Conservation of Nature[63]; the mean latitude and longitude were calculated. For extinct ungulate species, the latitudinal centroids of their ranges were estimated based on known fossil localities (Supplementary Table 7).

Our final hypothesized driver of migration was ungulate grass dependence. Therefore, we performed a targeted literature search to determine the grass dependence of each species, defined in this study as the mean dietary grass fraction over the duration of each given study. As above, we searched Web of Science and Google Scholar for published studies that reported ungulate diet composition. For some understudied ungulates (29 out of 207 extant species), quantitative dietary data were not available. Thus, the dietary grass fraction for these understudied species was estimated from available qualitative information on their diets. Dietary data were even sparser for extinct ungulates and entirely lacking for many taxa. When diet data were absent, we used the degree of hypsodonty to estimate diet (for example, see Toljagić et al.[64]).

Resource seasonality. To quantify resource waves across the ranges of globally distributed ungulate species, we used metrics derived from spatial semi-variance and semi-variograms of the NDVI (8×8 km, 16-day composites, 816 composites spanning 34 years (1982–2015)) data housed in the Global Inventory Modelling and Mapping Studies database[65]. For each 16-day composite, we calculated the semi-variance among pairs of locations (NDVI pixels) across spatial scales ranging from 5 to 100 km. We used the maximum semi-variance (that is, the 'sill'; excluding the last 1/4 of each semi-variogram) to determine the magnitude of resource waves, and the distance lag of the peak semi-variance (that is, the 'range') to represent the

distance over which the resource wave travelled (Extended Data Fig. 2). We also estimated seasonal variation in resource wave strength by calculating the difference between maximum semi-variance throughout the annual cycle over the 34-year time series (Extended Data Fig. 2). By doing so, we identified which species ranges possessed the seasonal resource waves that would make migration a viable strategy. Note that the NDVI semi-variance data could only be derived for 189 of the 207 species in our dataset because the scale of semi-variance data was too coarse to be relevant for ungulates with small species ranges, such as small-island endemics.

Data analysis. Data were analysed in R v.3.6.1 (ref. [66]). All phylogenetic analyses used the consensus tree as described above. First, to test whether these characteristics are heritable across the ungulate phylogeny, we calculated multiple indices of phylogenetic signal for all characters using the packages phytools v.0.7-70 and adephylo v.1.1-11[67,68]. Then, to determine the manner in which these characters evolved, we fitted evolutionarily explicit and non-evolutionary models of character change across the phylogeny (white noise, star Brownian motion (BM), BM, early burst, Ornstein–Uhlenbeck) for each character using the package geiger v.2.0.7 and compared Akaike information criterion (AIC$_c$) support values to select the best-fitting model[69] (Supplementary Table 2).

Next, to evaluate how each of these characteristics changed over the course of ungulate evolution, we estimated ancestral character states across the tree from the species tip data (Supplementary Table 3). For continuous characters, we used maximum likelihood estimations implemented in phytools[67], employing the evolutionary model of character change with the lowest AIC$_c$ score based on the above model selection (Supplementary Table 2). Therefore, the best-fitting Ornstein–Uhlenbeck models from the above model selection were used to estimate grass dependence, body mass and latitude across the ungulate phylogeny (Fig. 3). To estimate migration (a binary character), we performed stochastic character mapping in phytools with 1,000 simulations[67].

To evaluate whether these characteristics coevolved, we used 100 stochastic character maps of migration as maps of different selective regimes on the tree and evaluated whether migration resulted in different evolutionary optima for each character. Using the package OUwie v.2.6[70], we fitted Ornstein–Uhlenbeck models with multiple optima and rates of evolution matched to the estimated migration regimes (Ornstein–Uhlenbeck$_{mv}$, Ornstein–Uhlenbeck$_{ma}$, and Ornstein–Uhlenbeck$_{mva}$), a single optimum Ornstein–Uhlenbeck model, a multi-rate BM model (BM$_s$) and a single-rate BM null model, following the analyses in Cressler et al.[71]. As above, we compared their corrected AIC$_c$ support values to select the best-fitting model (Supplementary Table 4).

Then, we used phylogenetic models to estimate the evolutionary correlations between characteristics with the phylolm v.2.6 package[72] (Supplementary Table 1). First, we used a binomial PGLM to determine if grass dependence and body mass are correlated across ungulates. We used a phylogenetic linear model (PLM) to evaluate whether body mass is related to latitude. Finally, we tested whether migration is related to body mass, grass dependence and latitude also using a binomial PGLM.

To investigate whether the presence of resource waves predicted migratory behaviour, we again used PGLMs to estimate the relationships between resource wave metrics and migratory behaviour (Supplementary Table 1). We tested how well each of the three resource wave metrics we calculated (that is, green wave sill, green wave range and green wave seasonality) predicted migration by constructing separate PGLMs for each metric, again using binomial distributions (Extended Data Fig. 1). Because green wave seasonality was determined to significantly predict migration, we then modelled how green wave seasonality predicted migratory behaviour in concert with latitude, grass dependence and body mass with a binomial PGLM. Finally, we modelled the relationship between green wave seasonality and grass dependence and latitude, employing separate PLMs (Extended Data Fig. 1).

Next, to evaluate the directionality of these relationships (that is, whether migration is the cause or consequence of inferred relationships), we performed phylogenetic path analysis[73]. Based on the plausible relationships between the characteristics outlined above, we defined a list of probable candidate path models (Supplementary Fig. 1). We compared the support for these different candidate models using the CIC$_c$ with the package phylopath v.1.1.2[73] (Supplementary Fig. 4). All models with a ΔCIC$_c$ < 2 were weighted and averaged (with full averaging) to yield the average path model (Fig. 4a).

We sought to determine whether resource wave metrics mediated the causal relationships between environmental predictors and migration. Because the seasonality of the green wave was identified to be a significant predictor of migration, we defined another set of candidate models that included green wave seasonality as an additional independent variable (Supplementary Fig. 3). As above, we compared support for the candidate models using the CIC$_c$ (Supplementary Fig. 5) and computed the weighted average of all models with a ΔCIC$_c$ < 2 to yield the average path model (Fig. 4b). This analysis included only the 189 taxa for which we could calculate the NDVI semi-variance data.

Finally, to illuminate migration's role in the ecology of Earth's past, we performed phylogenetic imputation with the phytools package[67] to reconstruct the migratory phenotype of ten extinct ungulates included in our phylogeny from data on body mass, grass dependence and latitude (Fig. 6). After reconstructing the migratory behaviour of these extinct species, we compared the imputed migration phenotypes of extinct species with observed migration among extant species using a PGLM (with phylolm[72], as above) to evaluate if the prevalence of migration differed significantly between extinct and extant ungulates (Supplementary table 1).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

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Author contributions

J.O.A. conceived the study. J.O.A. compiled the underlying ungulate trait data from the literature and B.R.J. calculated the green wave metrics for all species. J.O.A. and A.D.-S. designed the analyses, with significant contribution from N.S.U. J.O.A. and B.R.J. wrote the initial manuscript drafts with significant input from N.S.U. and A.D.-S. All authors discussed and provided feedback on subsequent manuscript drafts.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Joel O. Abraham.

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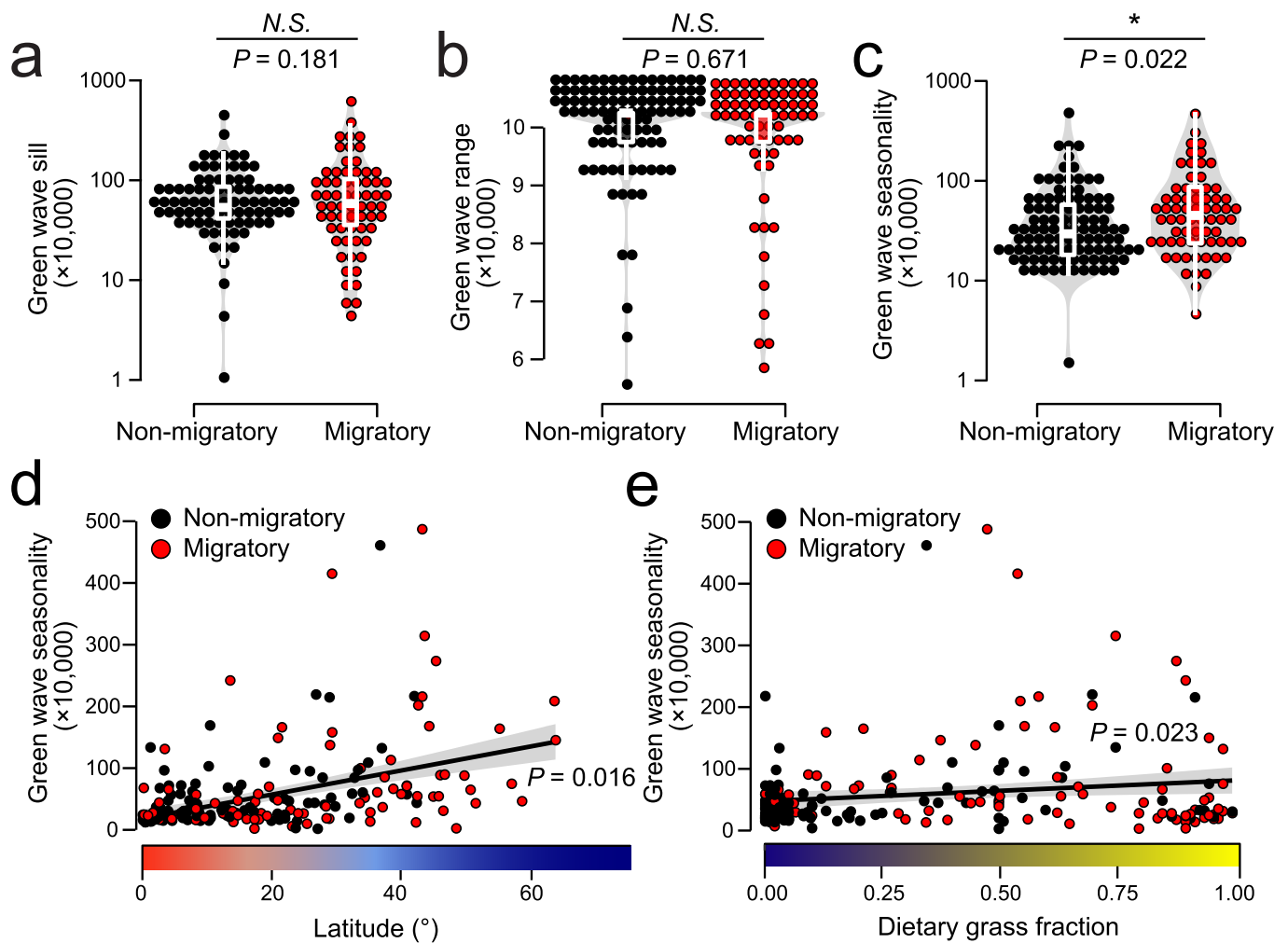
Extended Data Fig. 1 | The role of green wave tracking in the evolution of migration. Relationships between (**a**) green wave sill, (**b**) green wave range, and (**c**) green wave seasonality and migration are depicted, as well as between (**e**) green wave seasonality and latitude and (**f**) green wave seasonality and grass dependence. Of the green wave metrics we calculated, only green wave seasonality significantly predicts migration (two-sided PGLM; $n = 189$ species), with migratory behavior more prevalent amongst taxa exposed to more seasonal green waves. Green wave seasonality is likewise positively correlated with latitude and dietary grass fraction (two-sided PLMs; $n = 189$ species). The asterisks (*) in (c) and solid regression lines in (**e, d**) denote a significant relationship ($P < 0.05$), whereas the '*N.S*' in (a,b) denotes the lack of a clear relationship ($P \geq 0.05$), corrected for multiple comparisons. White bands in (a-c) represent median values, the colored bars represent the interquartile range (IQR), and white whiskers extend to $\pm 1.5 \times$ IQR. Grey shaded regions in (d,e) represent 95% confidence intervals on the regression. Full model details are available in Supplementary table 1.
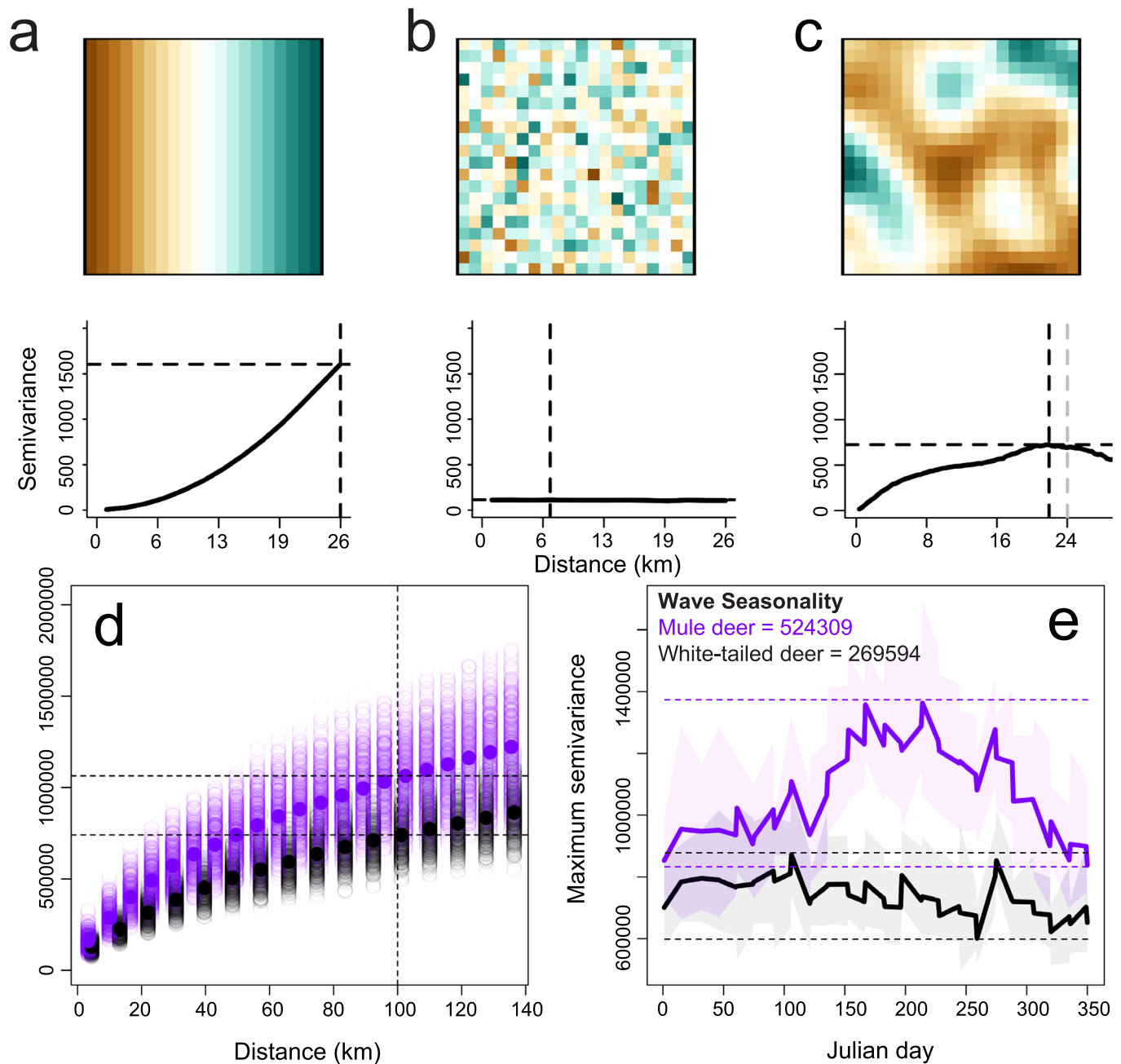
Extended Data Fig. 2 | Measuring landscape suitability for migration. A simulated (a) perfect resource wave, (b) heterogeneous landscape with no resource wave, and (c) landscape intermediate to (a) and (b). *Brown* pixels represent areas where the date of peak NDVI occurred early, whereas *green* pixels represent relatively late peaks NDVI. (**a**-**c**) The x-axis represents the distance travelled by resource waves (distance lag in km) and y-axis represents magnitude of the green wave (semivariance). Dashed lines illustrate maximum semivariance (horizontal) and maximum distance lag (vertical). (**d**) Empirical variograms for mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*), depicted in *purple* and *black* respectively. Vertical and horizontal dashed lines represent maximum semivariance (horizontal) and maximum distance lag (vertical) just as in panels (a-c). (**e**) Illustration of how seasonality in resource waves varied among the geographical ranges of mule deer (*O. hemionus*) and white-tailed deer (*O. virginianus*). Horizontal dashed lines depict the minimum and maximum magnitude of resource waves throughout the annual cycle. Note that the distance between *purple* dashed lines for mule deer (*O. hemionus*) is much larger than the distance between *black* dashed lines for white-tailed deer (*O. virginianus*), indicating greater seasonality in resource waves across the geographic range of mule deer (*O. hemionus*).

Corresponding author(s): Joel O. Abraham, NATECOLEVOL-211014922A

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Data collection	No software was used for data collection.
Data analysis	Data were analyzed in R statistical software version 3.6.1

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We compiled existing data on the incidence of migratory behavior within ungulates to evaluate how migratory behavior evolved.
Research sample	Our study focused on species-level variation in migratory behavior. As such, we sought to include all extant species of ungulates and to characterize migratory phenotype at the species level.
Sampling strategy	We included all 207 extant ungulate species that were included in the species-level mammal phylogeny of Upham et al. (2020) in our analyses.
Data collection	To curate a list of migratory behavior in ungulates, we first compiled published syntheses of migratory species and performed an exhaustive literature review, searching Web of Science and Google Scholar for any records of migratory behavior for each ungulate species. For the purposes of this study, we reduced migration to a binary characteristic; ungulates were considered migratory if any population exhibited seasonal round-trip movements between discrete areas and/or if they were explicitly described as migratory in published literature.
Timing and spatial scale	We coded species as migratory if there was any record of any population within the range of the species having ever exhibited migratory behavior in the past or present. This approach enabled us to capture any evolutionary history of migration, and therefore control against the confounding influence of anthropogenic impacts. As such, our study is global in scale and extends as far back as there are publicly accessible published records documenting ungulate behavior.
Data exclusions	No ungulate species present in the species-level mammal phylogeny of Upham et al. (2020) were excluded from the study. We were not able to derive NDVI data for some species, however, as their species ranges smaller than the spatial scale of NDVI data and/or species range maps did not exist for these species. These species (n = 18) were excluded from analyses that incorporated NDVI data, but we indicate this in the text where applicable.
Reproducibility	All underlying data are provided in a supplementary data file and are also available via Dryad Data Repository, and we cited the R packages (and the specific functions) used for all analyses.
Randomization	We incorporated all extant ungulate for which phylogenetic data were available in our study, precluding the need for a randomized sampling design.
Blinding	Though it was impossible to truly blind our data collection (we employed the species name of each ungulate in our literature search), our data collection protocol was designed to control against canonized notions of what defines a migratory ungulate. We were systematic in our literature review and had objective criteria for classifying an ungulate as migratory or not.

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