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Dietary innovations spurred the diversification of ruminants during the Caenozoic

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Global climate shifts and ecological flexibility are two major factors that may affect rates of speciation and extinction across clades. Here, we connect past climate to changes in diet and diversification dynamics of ruminant mammals. Using novel versions of Multi-State Speciation and Extinction models, we explore the most likely scenarios for evolutionary transitions among diets in this clade and ask whether ruminant lineages with different feeding styles (browsing, grazing and mixed feeding) underwent differential rates of diversification concomitant with global temperature change. The best model of trait change had transitions from browsers to grazers via mixed feeding, with appreciable rates of transition to and from grazing and mixed feeding. Diversification rates in mixed-feeder and grazer lineages tracked the palaeotemperature curve, exhibiting higher rates during the Miocene thermal maxima. The origination of facultative mixed diet and grazing states may have triggered two adaptive radiations—one during the Oligocene–Miocene transition and the other during Middle-to-Late Miocene. Our estimate of mixed diets for basal lineages of both bovids and cervids is congruent with fossil evidence, while the reconstruction of browser ancestors for some impoverished clades—Giraffidae and Tragulidae—is not. Our results offer model-based neontological support to previous palaeontological findings and fossil-based hypothesis highlighting the importance of dietary innovations—especially mixed feeding—in the success of ruminants during the Neogene.

1. Introduction

Broad-scale habitat and environmental changes should have extensive macroevolutionary impacts [1–3]. For instance, diversification rates in both marine and terrestrial mammals may have shifted in concert with global climatic shifts and continental drift [4–6]. Additionally, the acquisition of novel traits may mediate a connection between habitat change and macroevolutionary patterns. In particular, this connection may be stronger for highly habitat-sensitive groups, for example the ruminant herbivores [7], where the evolution of novel herbivorous feeding modes—often used as indicator of past habitat

changes [8]—may be related to both lineage persistence and diversification into newly created niches.

For this reason, the members of the suborder Ruminantia—today including giraffes, mouse-deer, deer, buffaloes, antelope, etc.—provide an ideal system for testing the macroevolutionary link between climate, diet and diversification in a neontological modelling framework. There are rich complementary palaeontological data [9–13], as well as a history of work drawing on the comparative method [14–16]. Ruminant species can be readily categorized into three broad categories of feeding behaviour: browsing (eating dicotyledonous plants; including leaves, stems, bark, fruits, etc.), grazing (grass eating) and mixed feeding (both browsing and grazing) [17]. The ancestral ruminant diet is generally thought to be browsing, evolving towards pure grazing via mixed feeding with the opening of C_4 grasses-dominated habitats during the Late Miocene, around 8 Ma [12,18–20]. In this model, mixed feeding is a transitional step leading from a hypothesized ancestral browsing state to derived pure-grazing state, concomitant with the cooling and drying trend from the Late Miocene onwards [16,21]. This simple ‘towards grazing’ scenario (browsing to mixed feeding to grazing) is common in the palaeontological literature [16,22,23] but has not been formally tested for more than a decade [16]. This is surprising because recent fossil analyses raise the possibility that mixed feeders may be the ancestral condition for several families of ruminants [24,25]. In addition, species with mixed feeding seem to dominate the Neogene fossil record [26–30], suggesting that it may have been a ‘key innovation’ associated with high diversity. An early appearance of facultative mixed feeding is probable, given that heterogeneous and dynamic grass-browse ecosystems may have been in place well before the C_3/C_4 transition in the Late Miocene [31,32]. However, despite the rich palaeontological literature, there have been no explicit tests of predictions linking dietary transitions to diversification rates in a context of global climate change through the Tertiary. This is the goal of this contribution.

More specifically, we extend recent comparative techniques to explore the role of climate and diet shifts in ruminant diversification while testing between two broad hypotheses for feeding mode evolution. We simultaneously compare different scenarios of dietary transitions and explore the importance of dietary innovations (mixed feeding and grazing) on ruminant evolution by testing for an association between diet and diversification rate. We also test the prediction that feeding strategies may represent a connection between habitat change and macroevolutionary patterns by adding palaeoclimatic information to the model. Finally, we study the timing of appearance of facultative mixed-feeding and pure-grazing states and estimate the ancestral diet of the ruminant families.

2. Material and methods

(a) Feeding modes

Extant herbivorous ungulates, primarily ruminants, have traditionally been placed in three broad dietary categories proposed by Hofmann & Stewart [17] based on which predominant type of forage they prefer. We performed an extensive review of the ecological literature (see figure 1*a* and the electronic supplementary material) to classify each of the 197 extant and recently extinct

taxa. Browsers feed primarily on herbaceous and woody material, such as forbs, leaves and fruits (e.g. mouse-deer *Tragulus napu*, moose *Alces alces*, giraffe *Giraffa camelopardalis*). Grazers concentrate feeding on grasses, rushes and sedges (e.g. hartebeest *Alcelaphus buselaphus*, sable antelope *Hippotragus niger*). Mixed (intermediate) feeders have a composite diet of grasses, rushes and sedges, and browse (e.g. impala *Aepyceros melampus*, sambar *Cervus unicolor*). While different classification schemes have been proposed [35–37], Hofmann & Stewart’s [17] categorization, which is based on observations of the natural feeding behaviour, is almost universally accepted.

(b) Phylogenetic data

The basis of our analysis is a supertree of all 197 extant ruminant species, including those that became extinct in historical times [33]. This supertree is a consensus from 124 trees published from 1970 to 2003, including morphological, ethological and molecular information. It was constructed using matrix representation with parsimony. The tree is extensively time-calibrated; 80% of the nodes on the tree were originally dated using a large compendium of molecular and fossil data, with the remaining 20% of the nodes being interpolated using a pure birth model. Polytomies (approx. 12% of the nodes) in this supertree are ‘soft’—representing missing data rather than true multifurcations—and would bias almost any statistic that draws on tree shape, as we do here. We therefore resolved polytomies and recalibrated the tree nodes using the fossil and molecular data available in the original paper in a Bayesian framework [38,39] (for further information, see the electronic supplementary material). A distribution of these resolved trees is available in the TreeBase repository, <http://purl.org/phylo/treebase/phyloids/study/TB2:S11461>.

(c) Comparative analyses

We tested different evolutionary scenarios of dietary transitions and the association between diet and diversification rates using the Multi-State Speciation and Extinction (MuSSE) model [40]. This is a multi-state extension of the Binary State Speciation and Extinction (BiSSE) model of Maddison *et al.* [41]. MuSSE is a likelihood method that computes the probability of a tree, including branch lengths and character states, under a model where speciation and extinction rates may vary with the state of character. The character is modelled as evolving under a constant rate Markov model of evolution [42], and as such we can simultaneously explore the evolution of diet and the association between diet and diversification.

The first step was to explore three scenarios regarding the transitions among the three dietary states while also estimating the speciation rates of lineages exhibiting each of the three states. Because state-dependent speciation rate differences can appear as asymmetries in character evolution rates [43], the framework is designed to fit these models while simultaneously modelling the effect of these traits on speciation rates. To do so, we allowed speciation rates to vary with diet. We tested three *state transition* models that differ in the number of parameters that must be estimated.

- (1) *Unconstrained*: a free model where all transitions between browser, grazer and mixed-feeder states were allowed; 12 free parameters.
- (2) *Flexible*: a bidirectional linear model where transitions between browser and grazer states were forbidden, forcing those transitions to be made through the mixed-feeder state; 10 free parameters ($B \leftrightarrow M \leftrightarrow G$).
- (3) *Towards grazing*: a unidirectional linear model where only transitions from browser to mixed feeder and from mixed feeder to grazer were allowed [16]; eight free parameters ($B \rightarrow M \rightarrow G$).

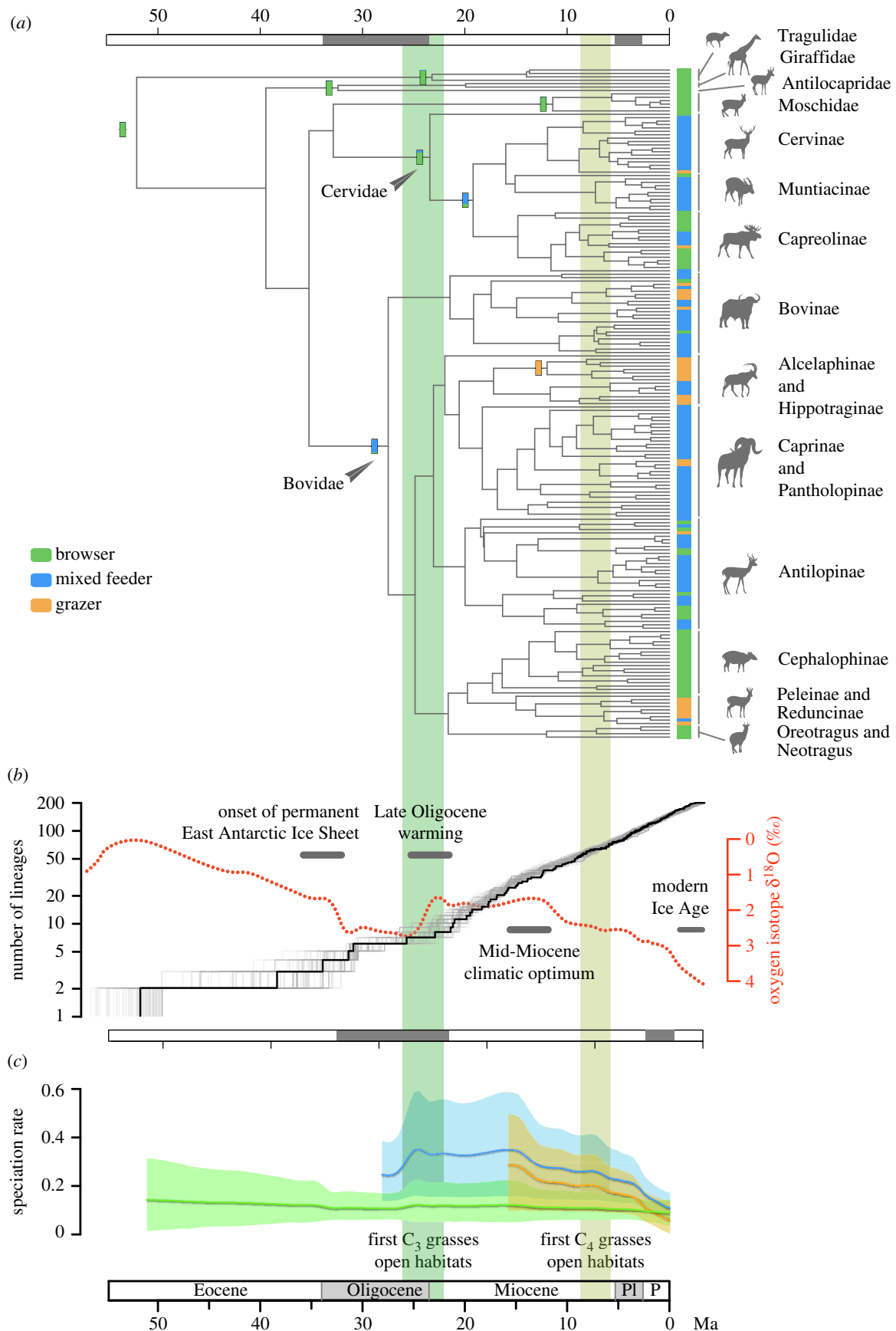


Figure 1. (a) Summary of our tree distribution and dietary categories for the 197 living ruminant species. Families (black) and subfamilies (grey) are shown. Ancestral diet reconstructions based on the best MuSSE model are depicted for each family and also for Cervidae without *Hydropotes*. First robust reconstruction of a grazing diet is also depicted. (b) Cumulative number of lineages against time for the supertree of ruminants published by Hernández Fernández & Vrba [33] (black line) and the distribution of 100 resolved trees (grey lines). The dotted smoothed curve represents the mean global temperature for the past 50 Myr [34]. (c) Diversification profiles for the different dietary strategies according to the best-fit model. Solid lines represent the average speciation rate across the 100 trees. Shaded areas represent the 95% credibility intervals for the 2000 MCMC steps on every tree. Vertical bars represent the estimated times of expansion of C_3 grass-dominated patches in the Late Oligocene–Early Miocene [32] and the major expansion of C_4 -dominated grasslands in tropical regions around 8 Ma [18]. Pl, Pliocene. P, Pleistocene. Ma, million years before present. (Online version in colour.)

Based on these models, we also developed three novel *climatic models* where rates of speciation not only varied among diets but were also allowed to vary as a function of the global temperature profile. While previous work has used global palaeoclimate records to fit diversification models based on the use of time windows [4,44], the palaeotemperature information itself has rarely been included directly in evolutionary models. To construct our *climatic models*, we drew on the complete record of deep-sea oxygen isotopic values ($\delta^{18}\text{O}$) as a proxy for the global palaeoclimate during the Tertiary [34]. We fitted models where speciation rates can vary proportionally with palaeotemperature curve. To do this, we first fitted a smoothing spline through the raw isotopic data (with a smoothing parameter of 0.8; see figure 1b) [45] and scaled this so that the response varied from 0 to 1. We then parametrized the speciation rate as a function of time as

$$\lambda_i(t) = \lambda_{0i} + (\lambda_{1i} - \lambda_{0i}) \cdot \delta^{18}\text{O},$$

where $\lambda_i(t)$ is the speciation rate over time for state i , $\delta^{18}\text{O}$ is the smoothed and scaled $\delta^{18}\text{O}$ function (lower values for higher temperature), and λ_{0i} and λ_{1i} are the speciation rates corresponding to the minimum and maximum values of $\delta^{18}\text{O}$. Where $\lambda_{0i} = \lambda_{1i}$, this reduces to the time-constant MuSSE model (i.e. $\lambda_i(t) = \lambda_{0i}$). This model focuses on testing whether ruminant clades with different feeding styles diversified more during warm or cold periods. MuSSE models were run over 100 resolved tree topologies. The estimate of parameters was assessed from the 100 trees distribution and models were compared using their Akaike Information Criterion (AIC) [46].

Finally, after comparing the six models described above (table 1), we used the best-fit model (the *flexible + climate* model) to assess the timing of appearance of facultative mixed-feeding and pure-grazing states and to estimate the ancestral diet for the basal node of the families Bovidae, Cervidae, Moschidae (musk deer), Tragulidae (mouse-deer) and Giraffidae, as well as for the root of the tree of the ruminants.

For each tree, distributions of parameters were computed over 10 000 steps of a Markov chain Monte Carlo (MCMC) simulation starting from the maximum-likelihood (ML) point. For all parameters, we used an exponential prior; for speciation and extinction rates, this had a mean of twice the ML net diversification rate, and for character transition rates the prior had a mean of half the ML net diversification rate. The marginal probabilities of ancestral state reconstructions were computed for each sample of the chain and the first 500 steps were discarded as burn-in. This means that our ancestral states are marginalized over the distribution of parameter states and phylogenetic uncertainty (while being conditional on the best-fit *flexible + climate* MuSSE model).

3. Results

Across the six ruminant families (Antilocapridae $n = 1$; Bovidae $n = 137$; Cervidae $n = 47$; Giraffidae $n = 2$; Moschidae $n = 6$ and Tragulidae $n = 4$), we classified 13.71% of species as grazers, 31.47% as browsers and 54.82% as mixed feeders (figure 1a and electronic supplementary material, table S1).

Estimated diet transition parameters best support the *flexible* model; maximum *a posteriori* estimates of transitions between browsing and grazing without passing through mixed feeding were essentially zero, suggesting that direct transitions are unlikely. There was little support for the directional *towards-grazing* evolution model (browsing to mixed feeding to grazing) with estimates for the reverse transitions rates mixed \rightarrow browsing and grazing \rightarrow mixed being significantly greater than zero (table 1). To test this further, we compared models fitted with ML and found that using AIC

the *flexible* model was preferred over the *unconstrained* and *towards-grazing* models for all 100 trees (table 1).

Different speciation rates were associated with different diets (fixing evolutionary rates to be equal across diets resulted in approx. 4 AIC units drop of the fit; see the electronic supplementary results, table S2) and varied significantly with the inferred climate (the *flexible + climate* model was preferred for 92 trees); not all diets were affected equally (figure 1c; table 1). We inferred relatively low speciation rates for browsing lineages, but these were constant over time. By contrast, lineages associated with mixed-feeding and grazing diets have higher inferred speciation rates that are positively correlated with temperature, such that speciation rates tended to decrease over time as temperatures decreased (figure 1c). This tendency to decrease is pronounced when looking over the region where a state is inferred to be present. Simulation-based tests suggest a climate-dependent trend, where decelerating speciation rates correlate to low temperatures, is unambiguously recovered by MuSSE (see the electronic supplementary material).

Our reconstruction of the ancestral diets based on the best-fit model (*flexible + climate* model) is consistent with a mixed-feeding style at the basal node of Bovidae and browser diets at the basal nodes of Giraffidae, Moschidae, Tragulidae and Cervidae (figure 1a), and at the root of the entire sub-order Ruminantia. Interestingly, though the ancestral state of the Cervidae was inferred to be a browser, we inferred mixed-feeding states for the ancestor of all the cervids except the genus *Hydropotes*.

4. Discussion

Our analysis suggests that ruminants did not follow a simple unidirectional model of evolution from browsing towards grazing through mixed feeding: mixed feeding seems indeed to be an intermediate step between browsing and grazing but transitions between diets are highly reversible, especially between grazing and mixed feeding (table 1). The acquisition of both mixed feeding and grazing diets was associated with elevated diversification rates, which in turn were associated with a period of high temperature (from the Late Oligocene–Early Miocene onwards). Finally, our reconstruction of ancestral diet supports widespread mixed feeding among early bovids and cervids.

(a) A flexible evolutionary model for the ruminant diets

The evolutionary flexibility in diet (transitions between pure browser and grazer and mixed-feeding ecologies) that we report is consistent with previous studies that have suggested lineages may change their dietary strategy towards a mixed leaf–grass intake as a response to adjustments in vegetal resource abundance during episodes of climatic forcing and habitat change [12,13,24,47]. As we develop further below, the existence of rapid transition rates between mixed feeding and grazing highlights the mixed-feeding diets (and the ability for lineages to evolve this strategy) as the real innovation driving the success of the ruminant clade through the Tertiary.

(b) Diet and evolutionary patterns through time

The appearance of dietary innovations is associated with high diversification rates (figure 1c). We found that diversification rates in mixed feeding and grazing lineages were higher

Table 1. Summary of the fit (ΔAIC) and ML parameter estimates of the six competed models. Under each category (constant and climatic models), models are ordered by mean ΔAIC rank. The best-fit model is shown in bold. The number of parameters in each model is given (P). Parameters include speciation rates (λ), extinction rates (μ) and transition rates between states (q_{ij} , transition rates from state i to state j). B, browser; M, mixed feeder; G, grazer. In the climatic models, λ is a function of the temperature, where λ_0 is the midpoint of λ around which the climate effect wobbles and $\lambda_1 - \lambda_0$ is the amplitude of the climate effect (T ; oxygen isotopic values). Note that negative values of $\lambda_1 - \lambda_0$ imply negative correlation with $\delta^{18}O$ and positive correlation with temperature.

MusSE models	P	speciation rates				extinction rates				transitions					
		λ_B	λ_M	λ_G	λ_{1G}	μ_B	μ_M	μ_G	μ_{1G}	q_{BM}	q_{MB}	q_{MG}	q_{GM}	q_{BG}	q_{GB}
flexible	10	0.077	0.138	0.111	0.111	0.006	<0.001	<0.001	<0.001	0.005	0.020	0.011	0.029	0	0
unconstrained	12	0.077	0.137	0.111	0.111	0.006	<0.001	<0.001	<0.001	0.004	0.020	0.011	0.029	<0.001	<0.001
towards grazing	8	0.097	0.139	0.079	0.079	<0.001	<0.001	<0.001	<0.001	0.031	0	0.023	0	0	0
speciation rates ($\lambda = \lambda_0 + (\lambda_1 - \lambda_0) \cdot T$)															
MusSE + climate models															
		λ_B	λ_M	λ_G		μ_B	μ_M	μ_G		q_{BM}	q_{MB}	q_{MG}	q_{GM}	q_{BG}	q_{GB}
flexible + climate	13	0.063	0.086	0.730	0.107	0.459	0.021	0.021	0.021	0.014	0.011	0.007	0.050	0	0
unconst. + climate	15	0.064	0.086	0.740	0.107	0.457	0.021	0.021	0.021	0.013	0.011	0.006	0.050	<0.001	<0.001
twr-grazing + climate	11	0.146	0.072	0.361	0.106	0.740	0.002	0.002	0.002	0.171	0	0.032	0	0	0

during the Miocene thermal maxima (25–13 Ma; figure 1*b,c*), and decreased towards the present in association with lower temperature values. This conclusion contrasts with the classic view—mainly based on raw diversity patterns—of increasing diversification of facultative mixed feeders and pure grazers as global temperature dropped and aridity reached its apex from the End-Miocene onwards (the last 9 Myr) [16,48,49]. Potentially, the decreasing speciation profiles we document correspond to the latter periods of a classic adaptive radiation [50]. In this scenario, dietary innovations permitted the use of new food resources, typically rendering high initial speciation followed by a decline [51]. In turn, such radiations were modulated by several other ecological factors, including the Early and Middle Miocene warm and highly productive terrestrial ecosystems with complex habitat structures and niche partitioning [22].

The timing of appearance of mixed feeders and pure grazers largely predates the Late Miocene C₃/C₄ transition (figure 1*a*). According to our results, mixed-feeding diets could have evolved as early as the Late Oligocene and have been widespread in ruminant lineages in the Early Miocene (around 24 Ma; [24,27,31]; figure 1*a,c*). We suggest that relying on both browse and grass probably permitted ruminants to radiate as a new type of highly seasonal, grass-patched ecosystems progressively spread around this time [32,52,53]. Furthermore, such diets may increase the ‘threat tolerance’ of isolated populations during habitat fragmentation in relation to such climatic shifts [47,54] and represent a favourable strategy during episodes of faunal turnovers, when changes in habitat and faunas may offer not only new ecological opportunities but also the appearance of unexpected competitors [12,47]. Tolerance of isolated populations to habitat fragmentation and resource limitation in turn may be associated with increased survival and speciation [54]. This is also consistent with the abundance of mixed-feeding ruminants (inferred from dental micro- and mesowear) of diverse ruminant clades [25,27,55,56] in the fossil record of the Early to Middle Miocene. The ruminant radiation during the Oligocene–Miocene boundary not only involved innovations in diet, but it is also associated with changes in body size and, likely, social behaviour and physiology [21,57,58].

According to our MuSSE model, the first shifts towards grass-dominated diets would have taken place in the Late Middle Miocene (earliest robust reconstruction around 13 Ma in bovid lineages; figure 1*a*). Accelerating diversification of ruminants adapted to open grass-covered habitats—based on fossil tooth hypsodonty—has been previously reported around 12 Ma [59]. This timing also agrees with palaeobotanical and isotopic data [60,61]. Taken together, these suggest that extensively established non-C₄ grass-dominated patches could have maintained grazer diets before the major expansion of C₄ grass-dominated ecosystems (approx. 8 Ma) [18,19]. However, despite a very good fossil record for the Middle Miocene, relatively very few direct estimates of diet—using tooth wear or isotopic analyses—are available for extinct ruminant taxa of this period. The inference of a grass-dominated mixed-feeding diet is particularly common among fossil forms of the Middle Miocene [25,62,63], and some evidence suggests that the existence of grazing ruminants around 14 Ma should not be wholly rejected [64]. In this regard, a deeper characterization of ruminant diets based on micro- and mesowear as well as isotopic data will be crucial to unveil the timing and nature of the appearance of grass-dominated dietary strategies through the Middle Miocene.

(c) Ancestral diets: phylogenetic and fossil evidence

Our phylogenetic reconstructions of ancestral diet both agree (for Bovidae, Cervidae and Moschidae) and disagree (for Giraffidae and Tragulidae) with evidence from fossil micro- and mesowear. Our reconstruction is consistent with a mixed-feeding style at the basal node of Bovidae. A facultative mixed diet very likely evolved deep within the cervid lineages, being reconstructed as widespread in basal forms of Cervidae (figure 1*a*). These estimates are congruent with the fact that the earliest known bovids could already have incorporated grass in their diet [47,64]. Therefore, a wide spectrum of feeding strategies is not unexpected among basal bovid forms (see [24]). The early acquisition of the mixed-feeding state in the cervid lineage (during the Early Miocene) is also congruent with the recent findings by DeMiguel *et al.* [24,25] that mixed feeding evolved in the early stages of deer evolution. Our phylogenetic reconstruction of browsing also agrees with fossil evidence of a fruit-browsing ancestor for Moschidae [29,65]. Furthermore, studies for earlier species attributed to this family (e.g. Late Oligocene *Dremotherium* and *Bedenomeryx*, and Early Miocene *Pomelomeryx*) reveal both browsing and grazing strategies [28,63], although these ‘moschids’ may be more related with other pecoran groups [66].

For Giraffidae and Tragulidae, our estimate of a browsing ancestral diet conflicts with fossil evidence. The diet of extinct Giraffidae was until recently thought to be similar to that of the living members, the giraffe (*Giraffa camelopardalis*) and the okapi (*Okapia johnstoni*); both species of Giraffidae have been commonly described as browsers [67]. However, Solounias *et al.* [26,56] found a higher heterogeneity (browsing, mixed feeding and grazing) in early species than previously thought. As a consequence, we consider that an ancestral mixed-feeding condition should be considered as plausible for this group. Living tragulids have a varied diet [11], even including animal matter [68]. New dental microwear texture analyses on fossil tragulids reveal that primitive representatives of this clade were mixed feeders 22 Ma [27] and signify that the high species diversity of tragulids during the Late Oligocene to Early Miocene was coupled with a wide variety of dietary strategies [27]. Giraffidae and Tragulidae are two impoverished clades (two and four species, respectively) which today represent but a vestige of their taxonomic and ecological diversity. Such examples, in which ancestral reconstruction and the fossil evidence disagree, highlight a need for an inference framework where fossil, contemporary and phylogenetic data can be integrated.

5. Conclusion

Past adaptation may impose limits on the response to selection for new dietary choices. Such constraints will involve at the least dietary anatomy ([69–71]; but see ref. [72]), but also dietary physiology [73] and social behaviour [14]. However, past adaptation need not impose powerful constraints. For example, the pronghorn—*Antilocapra americana*—has the signature high teeth anatomy of a grazer, yet browses, whereas David’s deer—*Elaphurus davidianus*—has the low teeth of a browser, yet grazes, suggesting that diet can be modulated by other factors, such as biogeographic history [74,75] or niche dynamics [76]. Indeed, present-day diet may be the best integrator of the varied responses to selection on diet through the entire history of a lineage. Our new evolutionary model with reversible transitions among dietary strategies for the ruminants suggests that both the ancestral dietary strategy of several ruminant

families should be reconsidered and that dietary innovations and perhaps evolutionary flexibility (the ability to transition among diets) may have interacted with global climate change to lead to the diversification and ecological success of the ruminants during the Neogene.

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