



Drivers of the artiodactyl turnover in insular western Europe at the Eocene–Oligocene Transition

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Simultaneously investigating the effects of abiotic and biotic factors on diversity dynamics is essential to understand the evolutionary history of clades. The Grande Coupure corresponds to a major faunal turnover at the Eocene–Oligocene transition (EOT) (~34.1 to 33.55 Mya) and is defined in western Europe as an extinction of insular European mammals coupled with the arrival of crown clades from Asia. Here, we focused on the species-rich group of endemic European artiodactyls to determine the drivers of the Grande Coupure during the major environmental disruptions at the EOT. Using Bayesian birth–death models, we analyzed an original high-resolution fossil dataset (90 species, >2,100 occurrences) from southwestern France (Quercy area) and estimated the regional diversification and diversity dynamics of endemic and immigrant artiodactyls. We show that the endemic artiodactyl radiation was mainly related to the Eocene tropical conditions, combined with biotic controls on speciation and clade-related diversity dependence. We further highlight that the major environmental changes at the transition (77% of species became extinct) and the concurrent increase in seasonality in Europe during the Oligocene were likely the main drivers of their decline. Surprisingly, our results do not support the widely-held hypothesis of active competition between endemic and immigrant artiodactyls but rather suggest a passive or opportunistic replacement by immigrants, which is further supported by morphological clustering of specific ecological traits across the Eocene–Oligocene transition. Our analyses provide insights into the evolutionary and ecological processes driving the diversification and decline of mammalian clades during a major biological and climatic crisis.

biological crisis | biotic interactions | diversity dynamics | trait evolution | Grande Coupure

Studying the evolutionary dynamics of biological diversity over time is a central topic in evolutionary biology and paleontology (1–3). Changes in species richness are measured by the balance between speciation and extinction rates, which vary over time and lead clades to diversify, prosper, or decline (4–6). These rates are further influenced by multiple—often intertwined—factors, whether biotic (predation, competition for resources) (7–13) or abiotic (temperature, sea level, continental fragmentation) (14–18). Understanding the role and contribution of these drivers on diversity dynamics represents one of the main current challenges in macroevolutionary studies (12, 19–21).

Estimating the drivers shaping clades' diversification recently benefited from methodological developments of specific birth–death models allowing for the identification of key factors acting over long time scales (9–11, 13, 22). However, studies investigating simultaneously the effects of abiotic and biotic factors in driving diversity dynamics remain scarce (7, 10, 11, 13, 18). They highlighted a combined role of these two types of factors on diversification. These recent works call for additional macroevolutionary studies integrating the role of environmental parameters and biotic interactions over large time scales, both of which are now essential to understand the evolutionary history of clades (19, 20). This is especially true for biological systems experiencing a strong biotic crisis that can reset evolutionary processes and ecological constraints on diversity dynamics (23).

The Eocene–Oligocene transition (EOT, ~34.1 to 33.55 Mya) is now considered as one of the major extinction events in Earth's history (24–26). This period of strong global climatic and tectonic changes coincides with a phase of massive faunal turnover (26–29). Faunal upheavals at the EOT—first referred to as the “Grande Coupure” (30)—have been recorded from Asia (31), Africa (32), and Western Europe where the extinction of ~50% of European placental mammals coincided with the arrival of crown mammalian clades from Asia (33–37). Most European species documented after the transition have no close relatives in the preceding fauna (38–40) as mammals evolved independently in an island system during the middle to late Eocene, after the spreading of epicontinental seas between Europe, North America, and Asia ~47 Mya (41–43). These geographic and temporal settings make the Eocene–Oligocene European mammals uniquely suited to address the role of abiotic and biotic forcings in the context of an extinction event.

Significance

The fossil and geological records provide unique insight into the history of species and how they responded to environmental changes over time. We analyzed an original, high-resolution dataset of fossil European ungulate mammals during the Eocene–Oligocene major faunal turnover (“Grande Coupure”) to establish diversity dynamics over 15 My and infer potential biotic and abiotic drivers. This transition involved the partial replacement of endemic by immigrant lineages (77% of species became extinct), and our results do not support a long-standing hypothesis of competitive exclusion. Instead, we show that environmental disruptions during a period of tectonic and global climatic changes were more likely the drivers of Grande Coupure faunal extinction and diversification.

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Artiodactyls were a major component of the endemic European mammal fauna during the Eocene (33, 44, 45). Previous studies indicated that they experienced a diversity drop during the EOT with preliminary evidence suggesting they were mostly replaced by crown artiodactyl taxa (ruminants, pigs, hippos) during the Oligocene (33, 36, 44). The strong and rapid global cooling at the EOT is often pinpointed as the causative driver of the Grande Coupure turnover (24, 31, 32, 46). Some previous authors offered an alternative argument that newcomers from Asia were the catalyst for the extinction of the endemic European mammals (43, 45–47). Land bridges due to local tectonics in the Alpine and Balkan regions (27) and eustatic sea level falls (28) allowed for the dispersal of new faunas toward western Europe during the early Oligocene (36, 43). The prevailing hypothesis is that endemic artiodactyls were supplanted, i.e., via competitive exclusion, by immigrant ruminants that possessed a more advanced dental morphology (selenodonty) and type of digestive physiology (rumination), advantageous in a general context of habitat opening (44, 45, 48). However, these conclusions relied on an incomplete sampling of fossil artiodactyl diversity, a lack of a fine-scale resolution on the underlying evolutionary processes, and the unknown or highly speculative paleoecology of endemic European artiodactyls, impeding testing of any link between their decline and its putative drivers. To our knowledge, there is no consensus regarding the proximal drivers of the mammalian turnover around the EOT at global scale (31, 32, 34, 43, 49). Their abundance on both sides of the transition makes the European artiodactyls a model group to study the underlying factors of their early diversity radiation, decline, and recovery over the Eocene–Oligocene interval.

Here, we assessed the main hypothesis that endemic European artiodactyls were supplanted by newcomers from Asia in the aftermath of the EOT, while considering the alternative hypothesis that environmental factors can explain their decline. We compiled, revised, and analyzed the fossil record of European artiodactyls (90 species, >2,100 occurrences) of the Quercy area (South-West France) spanning the middle Eocene–late Oligocene interval (42 to 25 Mya) (50). The Quercy area is famous for yielding an exceptional abundance of fossil material (Konzentrat-Lagerstätten) and documents regional faunal assemblages over a virtually continuous timescale (every million-year interval is represented; *SI Appendix*, Table S1). Each assemblage is associated with a Mammalian Paleogene (MP) biochronological reference level (50, 51) and is defined by a numerical age-adjusted by magnetostratigraphy (*SI Appendix*, *Extended Material and Methods*). Focusing on a small geographical region can limit the number of confounding effects inherent to the global scale such as contrasted climate conditions and averaging of biotic interactions (3). Relying on a Bayesian framework (analytical workflow shown in *SI Appendix*, Fig. S1), we estimated the regional diversification and diversity dynamics (i.e., changes in diversification rates and taxonomic richness through time, respectively) of endemic and immigrant artiodactyls, as well as for “all” European artiodactyls (endemics + immigrants). We used diversity dependence models to investigate whether and to what extent changes in diversity across multiple clades are correlated with changes of speciation and extinction rates to assess the effect of immigrants on endemic artiodactyl diversification. We further measured four continuous ecological traits (body mass and diet proxies) for 69 species to estimate the ecological spaces of endemic and immigrant artiodactyls through time. We then applied a multivariate birth–death (MBD) model to quantify the impact of environmental changes at the EOT on the diversification dynamics of endemic artiodactyls during and following the crisis. Our fine-scale analyses thus provide clues about the features of extinction victims and the modalities of

survival among endemic species in a context of climatic and tectonic changes and biotic interactions including immigrant clades. Our results allow significant progress in our understanding of the evolutionary and ecological processes driving the diversification and decline of mammalian clades across a major Cenozoic biological crisis.

Results and Discussion

Diversification Processes and Diversity Patterns of European Artiodactyls.

The Quercy fossil record of all European artiodactyls includes 2,196 occurrences for 90 species and 39 genera (*Dataset S1*), ranging from the middle Eocene to the late Oligocene. Considering the high temporal and taxonomic resolutions of the dataset, we inferred their diversification history using the birth–death model with constrained shifts (BDS) (52), at both the species and genus levels (*SI Appendix*, Fig. S1 and *Extended Material and Methods*). We estimated preservation rates averaging 13.83 occurrences/species/My (16.80 occurrences/genus/My), highlighting the excellent quality of the Quercy fossil record (*SI Appendix*, Table S2). To our knowledge, this is one of the highest rates obtained for terrestrial vertebrates [Caninae and Ursidae: 6.95 and 8.04, (7); Sparassodonta and Notoungulata: 1.21 and 1.14, (18); Rhinocerotidae: ~1–3 (6); Dinosaura: ~1.5–8.8, (11)], comparable high rates for species being obtained for the Cainotherioidea from Quercy [14.41; (45)] or for the “foreign ungulates” from South America [22.11, (18)]. High preservation rates allow for more accurate estimates of the macroevolutionary dynamics of European artiodactyls on both sides of the EOT. The dynamics of all European artiodactyls is characterized by high net diversification rates at the beginning of the middle Eocene, followed by a succession of ups and downs in net diversification rates until the mid-Oligocene (Fig. 1 A and C and *SI Appendix*, Figs. S2–S5). We found a major extinction peak coupled with a low speciation rate at the EOT, which precedes a strong speciation peak immediately after this event (Fig. 1 A and C and *SI Appendix*, Figs. S2–S5). The sensitivity analyses performed show remarkably similar estimated patterns of speciation and extinction rates, regardless of fossil sampling and preservation rates (*Datasets S1* and *S2* and *SI Appendix*, Figs. S4 and S5 and *Extended Material and Methods*). Variations in diversification rates obtained for the different taxonomic levels (genus and species) differ only at around 40 Mya, where an extinction peak is observed only for species-level data (Fig. 1 A and C and *SI Appendix*, Figs. S2 and S3).

Analyzing the diversity trajectories of endemic and immigrant artiodactyls confirms that the EOT marked a turnover in the contribution of these groups to the total artiodactyl diversity (Fig. 1E). The Eocene artiodactyl fauna underwent a strong diversification in the late Eocene with 22 species and 9 families (Fig. 1 B and E), which is equivalent to the extant ungulate diversity in equatorial-tropical regions (53, 54). However, the diversity of endemic artiodactyls dropped abruptly at the EOT with the extinction of 77% of species (62% of genera) in only 1 My, confirming the status of mass extinction for the EOT (25). This result refines previous lower extinction estimates (50%), reported at the European mammalian scale (34, 35), and contrasts with the hypothesis of several successive phases of minor extinctions bracketing the EOT rather than a single major extinction event at the transition (44).

Our results also indicate that only three of the nine endemic families (Dichobunidae, Anoplotheriidae, and Cainotheriidae) survived the transition and persisted during the Oligocene (Fig. 1B). Post-EOT artiodactyls are composed of immigrant taxa (Ruminantia, Suina, and Hippopotamoidea) that became established soon after

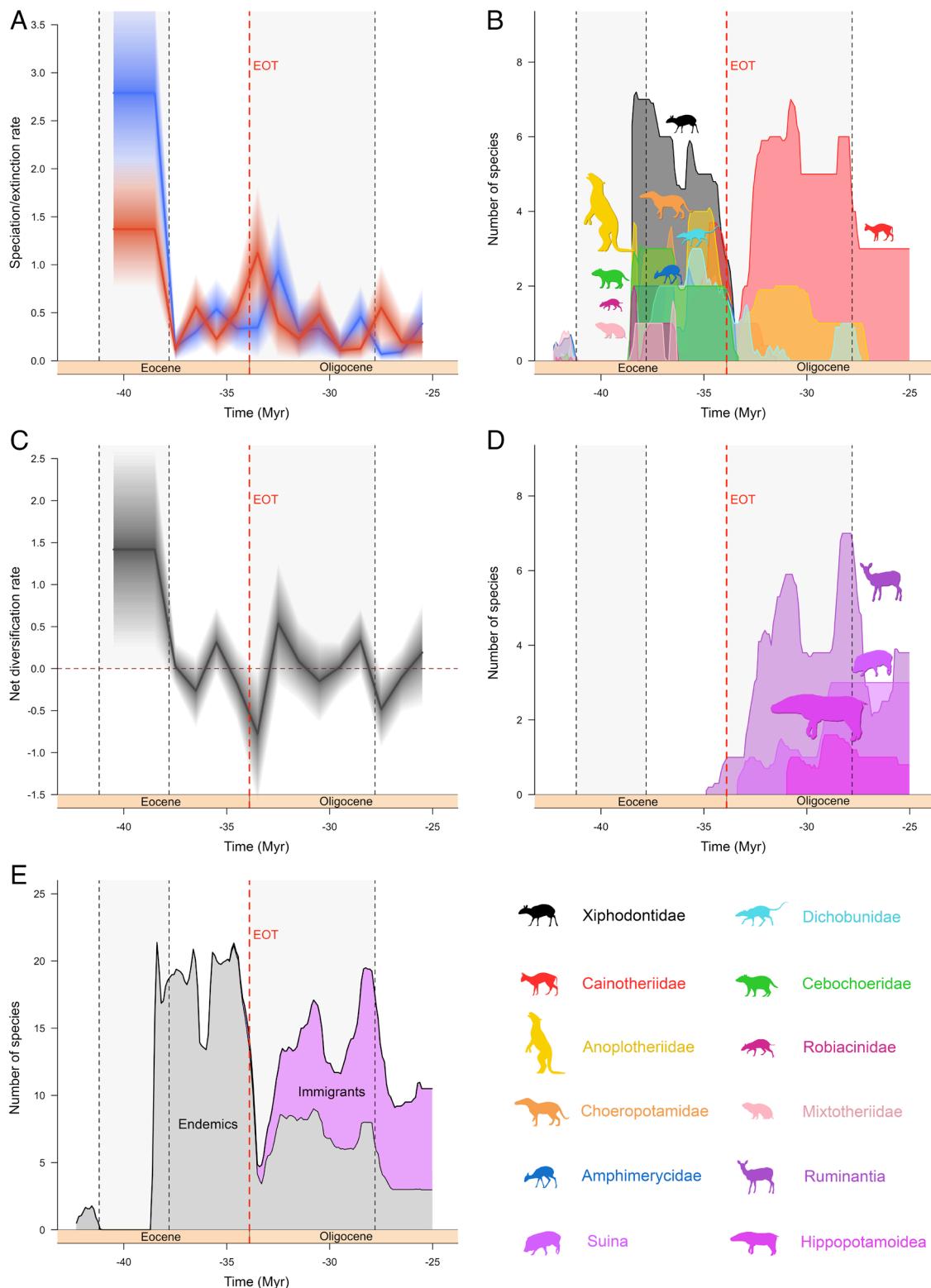


Fig. 1. Regional diversification and diversity dynamics of European artiodactyl species around the EOT crisis controlled by time-variable speciation and extinction. (A) the speciation (in blue) and extinction (in red) rates obtained under a birth-death model with constrained shifts (BDS) of 1 My. (B) the diversity trajectories between speciation and extinction rates (net diversification rate below zero indicating a decline in diversity). (C) the diversity trajectories of immigrant artiodactyl clades incorporating uncertainties around the age of the fossil occurrences. (E) the cumulated diversity curves of endemic and immigrant artiodactyls. In (A) and (C), solid lines indicate the mean posterior rates and the shaded areas show the 95% Credibility Interval (CI). All fossil occurrences (2,196) of European artiodactyls from 55 Quercy localities, spanning the middle Eocene-late Oligocene interval (42 to 25 Mya), are available in Dataset S1.

the EOT (Fig. 1 D and E). Together with the surviving endemic clades, these immigrant taxa constitute a “new European artiodactyl fauna” in the Oligocene. This fauna diversified rapidly after the

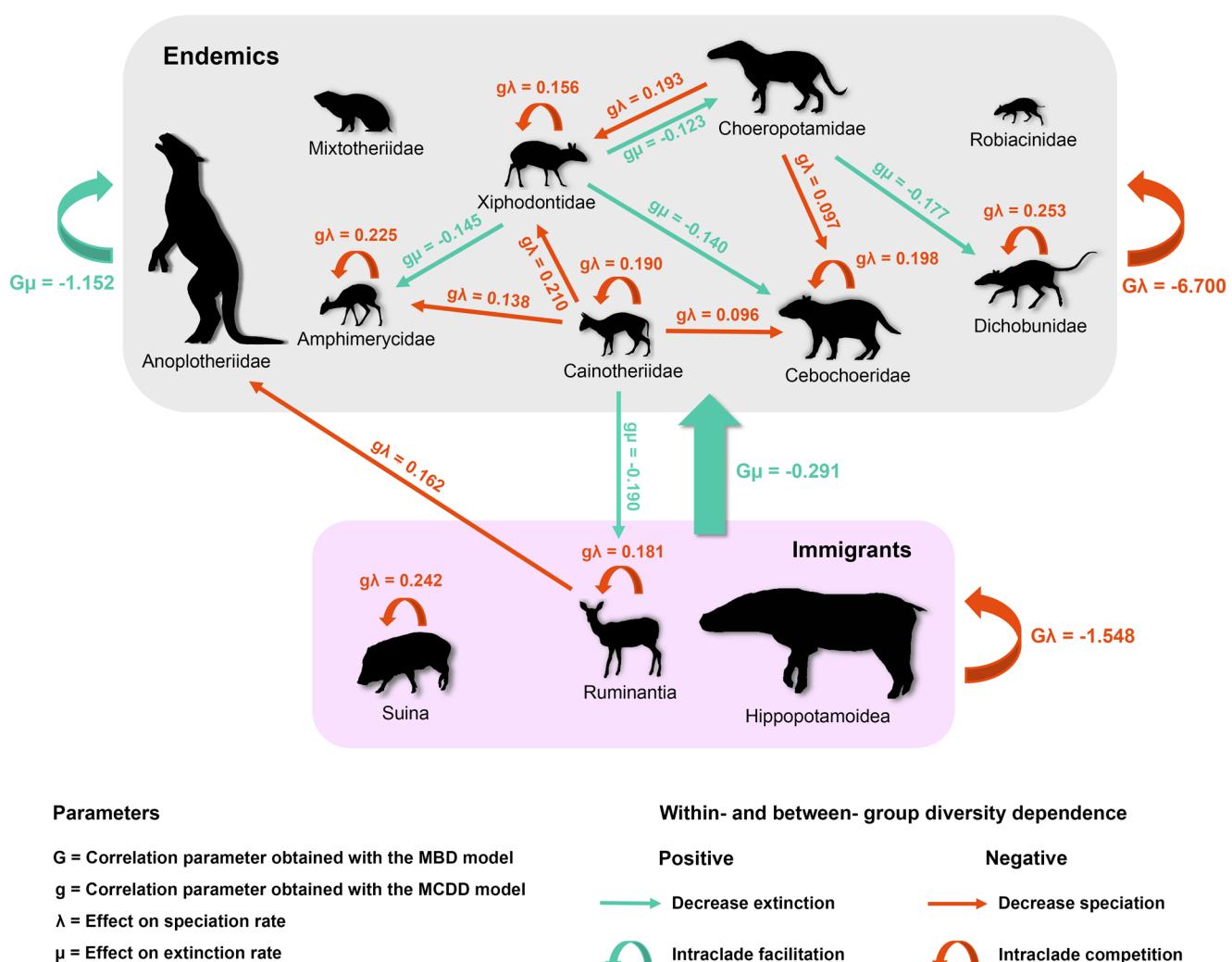
extinction event (Fig. 1 D and E), although it is difficult to distinguish between in situ speciation and multiple immigration events. The Oligocene fauna did not fully recover the pre-EOT diversity

level as it reached 19 species at the early-late Oligocene boundary (6 My after the EOT event), before declining significantly in the mid-Oligocene (50% of species became extinct, Fig. 1E). These results highlight a major turnover in the European artiodactyl fauna during and just after the transition and underline the importance of extinction events on the diversity decline, which is not necessarily accompanied by a decrease in speciation (4, 5).

Passive Replacement by Immigrants from Asia and Complex Interactions among European Artiodactyls. The extinction event at the EOT alone cannot explain the decline of endemic European artiodactyls, and environmental changes during the Oligocene and/or competition with other clades may also represent explanatory drivers. Here, we tested the hypothesis that endemic artiodactyl species have been supplanted by immigrant artiodactyl ones after the EOT. Active competition usually occurs between species with similar ecology (7–9) and manifests when increasing species diversity of one clade is correlated with reduced speciation and/or increased extinction rates of another clade. We explored the effect of diversity dependence (or clade interactions) on the diversification dynamics of European artiodactyls using the MBD and multiple-clade diversity dependence (MCDD) models

(7, 55) (Fig. 2 and *SI Appendix*, Fig. S1 and Tables S3–S6). The MCDD model evaluates the effects of diversity dependence within and between clades by estimating speciation and extinction rates for each clade, as well as interaction parameters that quantify the strength and sign of diversity dependence between clades. The MBD model, on the other hand, assesses the effects of external variables on the speciation and extinction rates of a given clade by estimating correlation parameters that quantify the strength and sign of the dependence. The MCDD model thus allows testing past ecological interactions between clades, while the MBD model allows studying several factors (biotic and abiotic) simultaneously while estimating intraclade diversity dependence.

The MBD results show that within-clade diversity dependence played a significant role in the diversification of endemic and immigrant artiodactyls. We found a negative correlation between species richness and their speciation for both entities ($G\lambda_{\text{endemics_endemics}} = -6.7$, $G\lambda_{\text{immigrants_immigrants}} = -1.548$; Fig. 2 and *SI Appendix*, Tables S4 and S5), suggesting that their speciation rates decreased as they diversified over time. A negative relationship between speciation rates of a clade and its taxonomic richness can be explained by ecological constraints caused by the competition for resources or by the limited availability of ecological niches



(10, 56, 57). The MBD results also show a negative correlation between extinction rates of endemic artiodactyls and their own diversity ($\text{Gu}_{\text{endemics_endemics}} = -1.152$; Fig. 2 and *SI Appendix, Table S4*), implying a decrease in extinction rates as diversity increased. This favorable relationship can be explained by the central role of herbivorous species in the trophic network and environmental structuring (vegetation, environmental condition) (58–60); the high diversity of endemic species during the Eocene would therefore have facilitated their survival. Furthermore, our results indicate a significant correlation between endemic artiodactyl diversification and immigrant artiodactyl diversity. Interestingly, the immigrant diversity is negatively correlated with extinction rates of endemic species over time ($\text{Gu}_{\text{endemics_immigrants}} = -0.279$; Fig. 2 and *SI Appendix, Table S4*), suggesting that the arrival of immigrants is not the factor responsible for the marked endemic artiodactyl decline during and after the transition. This result is in line with BDS results (Fig. 1) where the major increase in immigrant diversity largely follows the diversity drop of endemic clades during the crisis. Our results suggest a passive or opportunistic replacement of endemic artiodactyl species by immigrant ones after the EOT in Western Europe, rather than an active competition. Immigrant species would then have reduced the selective pressure (e.g., predation) on surviving endemic species, a mechanism already proposed for large herbivorous groups (11, 59).

Clade interaction analyses (MCDD) highlight complex interactions between European artiodactyl groups over time (Fig. 2 and *SI Appendix, Table S6*). Within-clade diversity dependence has significantly impacted speciation of endemic families and immigrant suborders ($\text{g}\lambda_{\text{Caino_Caino}} = 0.190$, $\text{g}\lambda_{\text{Amphi_Amphi}} = 0.225$, $\text{g}\lambda_{\text{Cebo_Cebo}} = 0.198$, $\text{g}\lambda_{\text{Dicho_Dicho}} = 0.253$, $\text{g}\lambda_{\text{Xipho_Xipho}} = 0.156$, $\text{g}\lambda_{\text{Rumi_Rumi}} = 0.181$, $\text{g}\lambda_{\text{Suina_Suina}} = 0.242$; Fig. 2 and *SI Appendix, Table S6*). These clades experienced episodes of strong radiation during the Eocene and/or the Oligocene, which subsequently limited their specific diversity (Fig. 1 B and D). The high within-clade diversity dependence also suggests an important partitioning of the ecological niches occupied by European artiodactyls, especially during the Eocene. Endemic species exhibited a high diversity of ecological and morphological specializations (45, 61–63) (*SI Appendix, Figs. S6–S8*), but the relative morphological homogeneity observed within families probably partly constrained their ecological distribution and favored the process of within-clade diversity dependence (see below) (9–11). The MCDD results also show the significant impact of between-clade diversity dependence on European artiodactyl clades (Fig. 2 and *SI Appendix, Table S6*). We found that the endemic families Xiphodontidae and Choeropotamidae played a key role in the persistence of other families during the Eocene. The increase in xiphodontid diversity is correlated with reduced extinction rates of Amphimerycidae, Cebichoeridae, and Choeropotamidae ($\text{gu}_{\text{Amphi_Xipho}} = -0.145$, $\text{gu}_{\text{Cebo_Xipho}} = -0.140$, $\text{gu}_{\text{Choero_Xipho}} = -0.123$), while the diversity increase of choeropotamids is correlated with reduced extinction rates of Dichobunidae ($\text{gu}_{\text{Dicho_Choero}} = -0.177$) (Fig. 2 and *SI Appendix, Table S6*). The negative correlation between the diversity of one clade and extinction rates of another (facilitation) has been observed in other vertebrate groups (9, 11, 18). As mentioned above, facilitation could be linked to a decrease in predatory pressures or to more favorable environmental structuring induced by herbivorous species (11, 58, 59). These results suggest that the EOT crisis disrupted this balance with a significant drop in xiphodontids and choeropotamids diversity that precipitated the decline of other European endemic families. Interestingly, we found that the diversity of Choeropotamidae and Cainotheriidae was negatively correlated with speciation rates of Amphimerycidae, Cebichoeridae, and Xiphodontidae ($\text{g}\lambda_{\text{Amphi_Caino}} = 0.138$; $\text{g}\lambda_{\text{Cebo_Choero}} = 0.097$, $\text{g}\lambda_{\text{Cebo_Caino}} = 0.096$; $\text{g}\lambda_{\text{Xipho_Choero}} = 0.193$, $\text{g}\lambda_{\text{Xipho_Caino}} = 0.210$; Fig. 2 and

SI Appendix, Table S6). This result can be explained by relatively close ecological niches between these families, which is highlighted by the distribution of mandibular and dental traits measured in this study (see below; *SI Appendix, Fig. S7*). Finally, our results indicate that endemic artiodactyl species positively affected the diversification of immigrant artiodactyls during the Oligocene, with the Cainotheriidae diversity correlating negatively with extinction rates of the Ruminantia ($\text{gu}_{\text{Rumi_Caino}} = -0.190$; Fig. 2 and *SI Appendix, Table S6*). This suggests that Cainotheriidae could have played an important role in the establishment and evolutionary success of Ruminantia in Western Europe with a strong impact in the structure of Oligocene ecosystems, as indicated by the high diversity and abundance of Cainotheriidae remains in the Quercy fossil record (Dataset S1) (45, 63).

Niche Replacement and Innovative Traits of Endemic Species through the EOT.

Assessing the link between interspecific biotic interactions and macroevolutionary dynamics is particularly challenging (12, 64). Evidence of interaction between clades may be generated by specific evolutionary responses to the same underlying factors (9, 10). The inclusion of traits retracing the ecology of species is a relevant way to assess the soundness of correlations, the former also playing an important role in clades' diversification (10, 65, 66). To assess the MBD/MCDD results and test potential correlation between trait evolution and diversification of European artiodactyls, we compiled and measured four mandibular and dental traits for 69 species: third lower premolar (P/3) median width (LP3); mandibular corpus width at the third lower molar (M/3; LCM3); mandibular corpus height at the M/3 (HCM3); and lower molar row length (LMRL) (*SI Appendix, Fig. S6*). The first three traits, once normalized to body size, are considered as proxies for diet in ungulates (63, 67, 68), whereas LMRL corresponds to a proxy for body mass (69). Our results first show that trait evolution over time supports clear partitioning of ecological niches occupied by European artiodactyls, especially during the Eocene, which would have enhanced the process of intraclade diversity dependence highlighted by the MCDD analysis. We retrieved a partitioning for the four continuous traits studied (*SI Appendix, Figs. S7 and S8*), the latter indicating very similar morphological distributions between clades over the Eocene–Oligocene period. The morphological clusterings arising from a principal component analysis (PCA) also show that the morphological diversity of endemic European artiodactyls reduced abruptly after the transition and that the ecological niches left vacant were largely filled by immigrant artiodactyl species (Fig. 3 and *SI Appendix, Fig. S9*). The morphological range of extinct endemic species is mostly replaced by the immigrant ones, the latter overlapping only slightly with the former throughout the mid-Oligocene (Fig. 3 and *SI Appendix, Fig. S9*). These results illustrate the passive replacement of the endemic species by the immigrant ones suggested by the BDS and MBD/MCDD analyses. The drastic reduction of the endemic artiodactyl ecological space after the EOT (Fig. 3 and *SI Appendix, Fig. S9*) further underlines the global character of the extinction during the crisis. Finally, the Covar model (6) results indicate that none of the four traits tested is significantly correlated with speciation, extinction, or preservation rates of European artiodactyls over time (*SI Appendix, Tables S7–S9*). This could be related to the large morphological and ecological disparity of European artiodactyl species, especially among endemic artiodactyl species (Fig. 3 and *SI Appendix, Figs. S7–S9*).

Interestingly, species surviving the transition display a particularly derived morphology and/or ecology. For instance, *Diplobune minor* (Anoplotheriidae) exhibits morphological characteristics of

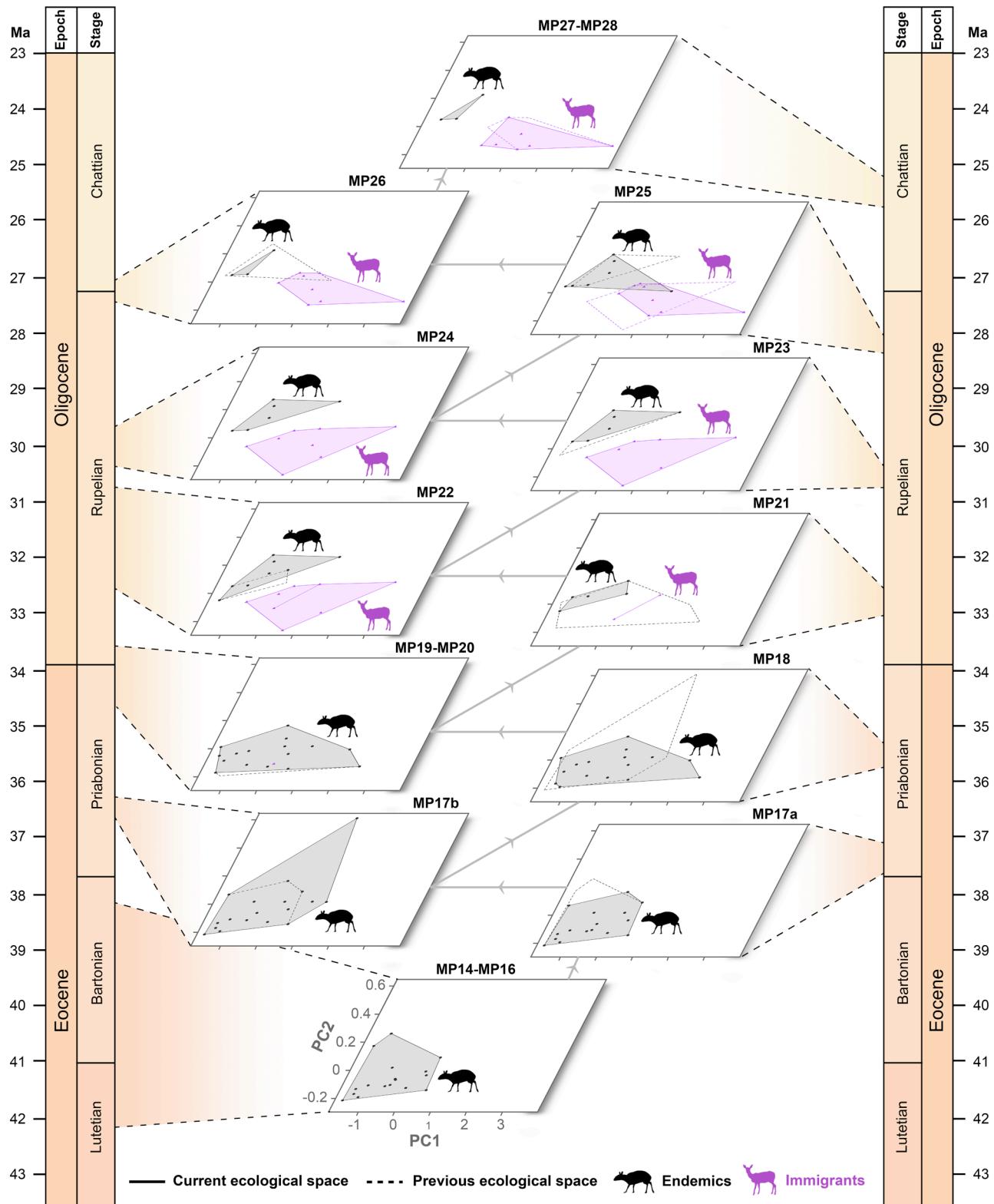


Fig. 3. Ecological space shifts of European artiodactyl over time by MP reference levels. PC1 (97.48%) and PC2 (1.42%) axes are illustrated. Ecological spaces were obtained by a PCA of the four (log-transformed) traits studied: LMRL, mandibular corpus width at the third lower molar (M/3; LCM3), mandibular corpus height at the M/3 (HCM3), third lower premolar (P/3) median width (LP3). Solid lines represent the ecological space at a given MP; dotted lines represent the previous one. The compilation of mandibular and dental trait measurements is available in Datasets S3 and S4.

arboreal animals (62); species of Cainotheriidae (selenodonts) and Dichobunidae (bunoseleodonts) have distinctive dental patterns with an additional large distal cusp on the upper molars [protocone and hypocone, respectively; *SI Appendix*, Fig. S10; (63)]; whereas *Tapirus hyracinus* (Choeropotamidae) has a bilophodont dental

morphology convergent with present-day Tapiridae (*SI Appendix*, Fig. S10). These “key” or “innovative” traits (70) may have enabled the survival of these species during and after the crisis. Hunter and Jernvall (65) notably highlighted the key role of the hypocone in mammalian evolution, and other works (45, 63, 71) underlined

the importance of the “*Cainotherium* plan” in the evolution of Cainotheriidae. The acquisition of an additional large cusp enables increased chewing surface and improved food decomposition efficiency (65). This feature may have been selectively advantageous during the degradation of environmental conditions and concurrent spreading of more abrasive vegetation in Europe around the EOT (44, 63, 72–75).

Eocene Tropical Conditions and Oligocene Seasonality Drove the Diversification of Endemic European Artiodactyls. Two macroevolutionary models have been proposed to explain the evolution of clade diversity over time (19): i) the Red Queen model (76), in which diversity changes are induced by biotic factors such as competition or life-trait evolution; and ii) the Court Jester model (77), where changes are driven by physical factors such as climate change. These two models are not mutually exclusive and can prevail at different levels and timescales (19). Our results already highlighted that the major environmental disturbances at the EOT (28, 29, 72, 78) coincided with the strong extinction of endemic artiodactyl that led to the Grande Coupure and that immigrant species and ecological traits considered here were not the drivers of the decline of endemic species in the aftermath of the transition. We here propose that the longevity and extinction probability of species, as well as long-term abiotic changes, may be relevant explanatory factors for the dynamics of European artiodactyls and for the decline of endemic species.

Van Valen’s law of constant extinction states that the probability of extinction is independent of the taxon age (76), but recent studies on various clades have shown a significant relationship between these two parameters (11, 79). We tested for the effect of taxon age over extinction probability using an age-dependent extinction (ADE) model (79). In line with BDS, species-level ADE analyses highlight two distinct evolutionary histories: we found higher extinction probability for young species in the Eocene, whereas the Oligocene fauna shows no effect of taxon age on extinction probability (*SI Appendix, Table S10*). Estimates of species longevity corroborate these results, with the median longevity of Eocene species being much lower (1.5 My) than that of Oligocene species (3.2 My). These pre- and post-EOT species longevity estimates are relatively low in comparison with other analyses on artiodactyls (i.e., 5.6 My in ref. 80; 4.4 My in ref. 81). The limited geographic range (~1,800 km²) of the study area and the short time range considered (below 10 My for each fauna) can explain these results (10, 45, 82). Furthermore, the observed differences in species longevity and extinction probability between Eocene and Oligocene faunas mirror different climatic regimes characterizing both periods. The Eocene fauna of western Europe evolved in an insular context for nearly 10 to 15 My (41–43) under tropical/subtropical (warm and humid) conditions with closed environments, whereas the Oligocene fauna evolved in a more open environment under temperate (colder and drier) and seasonal climate (72, 73, 83). The more favorable and stable environment of Eocene tropical regions could have fostered higher speciation rates, but newly emerged species would compete directly with established ones. Changing Oligocene conditions resulting in higher extinction rates could have led to similar selective pressure on young and old species. In addition, the environmental upheavals at the transition, removing 77% of the Quercy species, freed up ecological niches and allowed new Oligocene species to establish with a lower extinction risk.

The EOT marks a period of significant decrease in temperature, sea level, and precipitation (26, 28, 29, 72), and a concurrent increase in seasonality in Europe during the Oligocene (72, 75, 78).

We investigated the impact of these environmental factors over the diversification of European artiodactyl species using the MBD model (55). At the scale of all European artiodactyls, results show that five abiotic factors are significantly correlated with speciation rates over time (Fig. 4 and *SI Appendix, Table S3*). Changes in continental fragmentation, atmospheric CO₂, and mean annual precipitation correlate positively with variations in speciation rate ($G\lambda_{\text{fragmentation}} = 27.107$, $G\lambda_{\text{CO}_2} = 1.823E-3$, $G\lambda_{\text{precipitation}} = 2.131E-3$), whereas fluctuations in organic carbon and seasonality correlate negatively with speciation ($G\lambda_{\text{organic_carbon}} = -0.263$, $G\lambda_{\text{seasonality}} = -0.097$) (Fig. 4 and *SI Appendix, Table S3*). These results suggest that strong speciation events of all European artiodactyls occurred in humid and closed environments with low seasonality. These conditions are found in tropical/subtropical regions of the Eocene (72–74) and are typically associated with periods of radiation in mammals (14). Furthermore, the correlation between continental fragmentation and speciation rates is a common feature in vertebrate evolutionary patterns (17, 18, 45, 84), and it is generally assumed that geographic range fragmentation fosters species richness over time by promoting allopatric speciation (17, 21). Europe experienced important tectonic events during the Eocene–Oligocene period. These include an active phase of the Alpine orogeny (27, 43) that led to a decrease in continental fragmentation around the EOT (85), and the onset of the split of the Corso-Sardinian compartment in the mid-Oligocene (86), which coincides here with a strong speciation event. Finally, our results indicate a single significant positive correlation between extinction rates of all European artiodactyls and atmospheric CO₂ ($G\mu_{\text{CO}_2} = 1.105E-3$). This climatic factor is considered as an important driver of diversity over time and its impact has already been documented in invertebrates or mammals (15, 18).

Since the scaling effect and biotic interactions can significantly influence the results of correlations with environmental drivers (55), we tested for correlations between rates and abiotic factors for the endemic and immigrant artiodactyl groups separately. Our results show that the abiotic correlations for the all European artiodactyls are mainly driven by the diversity dynamics of endemic artiodactyls, while no correlates were found for immigrant ones (Fig. 4 and *SI Appendix, Tables S4 and S5*). These results underline the marked sensitivity of endemic species to environmental changes and highlight the higher robustness of immigrant species living in temperate regions with higher climatic instability (90–92). However, the lack of correlation between abiotic parameters and rates of immigrant artiodactyls may also be explained by their smaller dataset and shorter time interval analyzed. We recovered a positive correlation between variations in speciation rate of endemic artiodactyls and atmospheric CO₂ and mean annual precipitation ($G\lambda_{\text{CO}_2} = 8.242E-3$, $G\lambda_{\text{precipitation}} = 7.366E-3$) and a negative correlation between speciation and organic carbon and seasonality ($G\lambda_{\text{organic_carbon}} = -0.215$, $G\lambda_{\text{seasonality}} = -0.325$) (Fig. 4 and *SI Appendix, Table S4*). Although broadly similar to those obtained for all European artiodactyls, these results differ in the lack of significant correlation with continental fragmentation. Further differences are found in the correlates with the extinction rates of endemic artiodactyls, as a positive correlation with seasonality is found for this group ($G\mu_{\text{seasonality}} = 0.122$). The onset of marked seasons at the transition likely had a deep impact on local vegetation structure (72, 73, 75, 83), and it is expected that it significantly affected the diversity of endemic mammals in Western Europe.

In this paper, we provide insights into the evolutionary and ecological processes of the diversification and decline of endemic European artiodactyls around the EOT crisis. We show that the radiation of endemic artiodactyls was mainly related to favorable

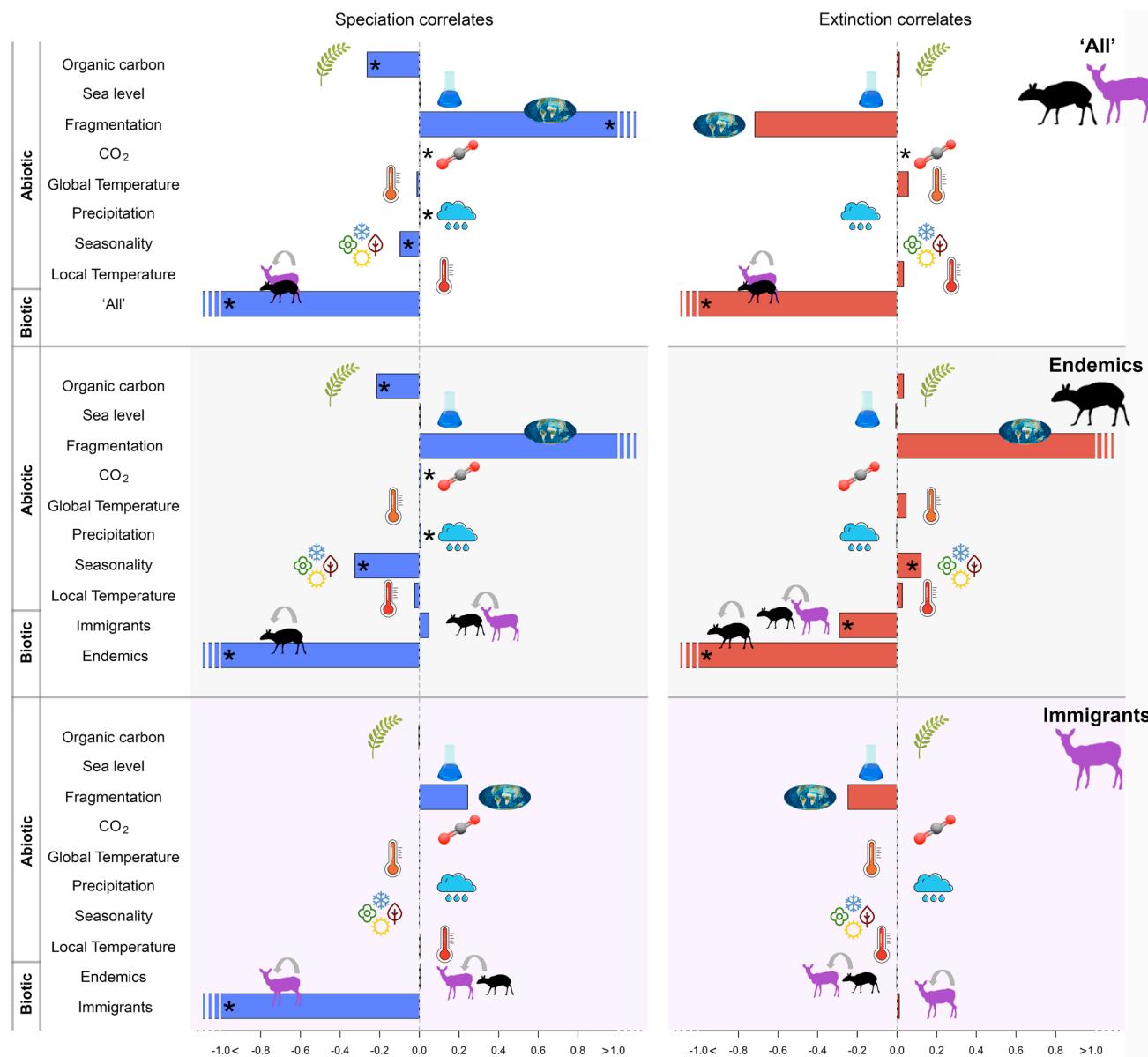


Fig. 4. Bayesian inferences of correlation parameters between speciation (blue) and extinction (red) rates of European artiodactyl species (all, endemic, and immigrant) and abiotic and biotic factors across the Eocene–Oligocene interval. The factors are as follows: local abiotic factors including the mean annual local temperature, seasonality, and mean annual precipitation (72); global abiotic factors including the organic carbon (87), sea level (28), continental fragmentation (85), atmospheric CO₂ (88), and sea surface global temperature [(29, modified by the equation in ref. 89)]. Biotic factors including the diversity over time of endemic and immigrant artiodactyls and the within-clade diversity dependence. The asterisk (*) indicates a significant correlation parameter for a given variable [$|P(G > 0) > 0.8$ and $\omega > 0.5$]. In blue, the speciation correlates, and in red, the extinction correlates. The hatched lines correspond to a value of the correlation parameter superior to 1 or inferior to -1.

tropical conditions of the Eocene, combined with biotic controls on speciation and clade-related diversity dependence and that the major environmental changes at the transition, coupled with increased seasonality during the Oligocene, were probably the main drivers of their decline in Western Europe. Our results do not support the widely-held hypothesis of active competition between endemic and immigrant artiodactyls but rather indicate that the massive arrival of immigrant species during the Grande Coupure actually appears to have reduced the extinction rates of endemic ones. However, between-clade competition with other mammal groups may also help to explain the decline in endemic European artiodactyls during the Oligocene. The arrival of a wide range of competitors from Asia, such as new taxa of rodents, carnivores, and perissodactyls may have exerted selective pressure on the diversity of surviving endemic species by sharing similar diets

or by creating new predator–prey interactions. Future studies reviewing and compiling the fossil occurrences of these mammal groups in western Europe would provide a relevant test for their role in the decline of endemic artiodactyls after the EOT.

Material and Methods

Fossil Dataset and Diversity Dynamics Estimation. We compiled all fossil occurrences (2,196) of European artiodactyls at the specific (93) and generic (39) levels from 55 Quercy localities (**Dataset S1**), spanning the middle Eocene–late Oligocene interval (42 to 25 Mya). This work follows the compilation performed by ref. 45 for the Cainotherioidea. Species occurrences for each locality result from the direct systematic revision and determination of the fossil material (dental, mandibular, and cranial). Each locality is associated with both a European MP reference level (50, 51) and an adjusted numerical age (93) (**Dataset S1** and

SI Appendix, Table S1). All studied fossil specimens are curated in the collections of the University of Montpellier (UM).

We analyzed the *Dataset S1* with PyRate (52) under a birth-death model with constrained shifts (BDS) to estimate the preservation process (q), the times of speciation (T_s) and extinction (T_e) of each species, the speciation (λ) and extinction (μ) rates, and their variations through time (*SI Appendix, Fig. S1*). We ran the BDS model for 10 million Markov chain Monte Carlo (MCMC) generations with λ and μ estimated in time bins of 1 My and sampled every 10,000 generations to approximate the posterior distribution of all parameters. The analysis was performed with preservation rates q estimated every 2 My and varying between taxa according to a Gamma model. We replicated the analysis 10 times by randomizing fossil ages under a uniform law and we combined the posterior estimates obtained across all replicates to generate rates-through-time plots (speciation, extinction and net diversification) and past diversity dynamics using T_s and T_e of all species. We performed the BDS analysis for the all European artiodactyl dataset at the species and genus levels. We also performed sensitivity analyses to test the robustness of the estimated diversification rates from PyRate (*Datasets S1 and S2 and SI Appendix, Figs. S4 and S5 and Extended Material and Methods*). For endemic and immigrant artiodactyl datasets and subsequent analyses (*Dataset S1*), we used the estimated T_s and T_e of corresponding taxa, which avoids remodeling the heterogeneity of preservation and reestimating T_s and T_e .

Trait Measurements, Trait Evolution, and Trait-Dependent Diversification. We compiled and measured four mandibular and dental traits for 69 species (1,119 specimens): LP3, LCM3, and HCM3, as proxies for diet (63, 67, 68); and LMRL, as proxy for body mass (69). For each species, a trait value corresponds to the species' arithmetic mean and depends on the number of specimens available for each species. Measurements were taken in millimeters using a Nikon 10 measurescope (binocular microscope with measuring device) and a digital caliper or were taken directly from the literature (615 specimens measurements derived from the compilation of ref. 45, *Dataset S3*).

The distribution of trait values and ecological spaces over time were performed using R 4.1.3 software (94). They are based on the *Dataset S4* combining the fossil species from *Dataset S1*, their lifespan (T_e and T_s from PyRate), and the mean trait value (*Dataset S3*). All ecological spaces derive from a global PCA of the log-transformed traits (to linearize any allometry) and represent the species' morphological repartition at given MP reference level(s). For the trait distributions over time (*SI Appendix, Figs. S6–S8*) and the Covar birth-death model (see below), diet traits were standardized by LMRL to reduce the effect of size on the data distribution.

We used the Covar birth-death model (6) with similar settings as in the BDS model to test for the influence of these four mandibulo-dental traits on the diversification dynamics of European artiodactyls on the Eocene-Oligocene interval. Under this model, changes in λ , μ , and q rates are correlated with changes in continuous (log-transformed) traits through estimated correlation parameters ($\alpha\lambda$, $\alpha\mu$, and αq), with $\alpha > 0$ indicating positive correlation between the trait value and a birth-death rate and conversely with $\alpha < 0$. The correlation is considered significant when the 95% Credibility Interval (CI) does not overlap with 0. We performed the analyses for the all European artiodactyl dataset and for endemic and immigrant artiodactyl datasets.

MCDD Model. We used the MCDD model (7) to estimate the influence of clade interactions over the diversification dynamics of European artiodactyls across the Eocene-Oligocene interval. The MCDD model assesses diversity dependence effects within and between clades, and estimates baseline speciation and extinction rates for each clade, along with interaction parameters that quantify the strength of diversity dependence between each clade pairs. We ran 20 million MCMC iterations and sampled every 20,000 generations under an exponential model and repeated the analyses on the 10 replicates of the T_s - T_e dataset. For each of the artiodactyl clades considered (endemic and immigrant families and suborders), we computed median and 95% CI of the baseline speciation and extinction rates (λ_i and μ_i), the within-clade diversity dependence parameters $g\lambda_i$ and $g\mu_i$, and the between-clade diversity dependence parameters $g\lambda_{ij}$ and $g\mu_{ij}$. We used the median of the diversity dependence parameters (e.g., $g\lambda_{ij}$) as a measure of intensity of competition (if positive) or positive interaction (if negative) between each pair of groups and considered the correlation significant

when the 95% CI does not overlap with 0 (7). Groupings of European endemic families are based on previous systematics works (47, 63, 95).

Selection of Abiotic Variables and Multivariate Birth-Death Model. We quantified the effect of environmental variables on diversification rates on the Eocene-Oligocene interval with the MBD model (55). In this model, λ and μ can vary through correlations with time-continuous variables over time, and the strength and sign of the correlations are estimated for each variable. We selected eight abiotic variables that have been shown to impact past vertebrate diversification (*SI Appendix, Extended Material and Methods*): three regional variables at the European scale (i.e., seasonality and mean annual temperature and precipitation) and five global variables (i.e., sea surface temperature, sea level, continental fragmentation, atmospheric CO₂, and organic carbon), for which regional-scale data were not available. We aim to highlight the importance of regional proxies, as climate and flora variations across the EOT appear to be heterogeneous at the global scale (75, 78). In particular, the insular setting of western Europe, surrounded to the south by the warm Tethys Sea, may have tempered the impact of global cooling during the Oligocene (27). We obtained regional seasonality, mean annual temperature, and precipitation from the paleoclimate reconstructions of ref. 72 and calculated the seasonality making the difference between warm mean temperatures and cold mean temperatures over time. At global scale, we obtained the sea-surface temperature curve from ref. 29 based on oxygen isotope ratios from benthic foraminiferal shells ($\delta^{18}\text{O}$) and modified by the equation of ref. 89 and the atmospheric CO₂ curve in ref. 88 by the most likely LOESS fit from p.p.m. data obtained from different carbonate sources. We retrieved the global sea level change trends over time from $\delta^{18}\text{O}$ data indirectly recorded in foraminiferal chemistry in 28 and the continental fragmentation index from paleogeographic reconstructions in ref. 85. Finally, we obtained the organic carbon data in ref. 87 from marine sediment cores.

The MBD model jointly estimates the baseline speciation (λ_0) and extinction (μ_0) rates and all correlation parameters ($G\lambda$ and $G\mu$) using a horseshoe prior to control for over-parameterization and for the potential effects of multiple testing (55). We ran the MBD model using 10 million MCMC iterations and sampling every 1,000 generations to approximate the posterior distribution of all parameters (λ_0 , μ_0 , $G\lambda$, and $G\mu$) and the shrinkage weights (ω) of each correlation parameter, under an exponential model. We summarized the results of the MBD analyses (10 replicates of the T_s - T_e dataset) by calculating the median and 95% CI of all parameters and considered the effect of a variable significant when more than 80% of the posterior distribution of the correlation parameter does not overlap with 0 and the median of ω is greater than 0.5 (*SI Appendix*). We performed MBD analyses for the all European artiodactyl dataset and for the endemic and immigrant artiodactyl datasets. We also incorporated the diversity dependence factors and tested the within-clade diversity dependence for the all European artiodactyl dataset, and the within- and between-clade diversity dependence for the endemic and immigrant artiodactyl datasets.

ADE Model. We estimated the longevity of each taxon and the probability for a taxon to become extinct as a function of its age (extinction probability) by fitting the ADE model (79). We ran PyRate for 10 million MCMC generations and sampled every 10,000 generations under an exponential model. We performed analyses with the fossil occurrence data (*Dataset S1*) and preservation rates estimated every 2 My and varying between taxa according to a Gamma model. We replicated the analyses on 10 randomized datasets and combined the posterior estimates across all replicates. We focused on the shape (Φ) of the Weibull distribution knowing that $\Phi < 1$ indicates that the extinction rate is higher for young species and decreases with species age, and $\Phi > 1$ indicates that the extinction rate increases with species age, while $\Phi = 1$ indicates no effect of age on extinction (79). We considered the correlation significant when the 95% CI does not overlap with 1. We performed independent ADE analyses for genera and species before and after the EOT (*SI Appendix, Fig. S11*), in order to test for ADE in faunas on both sides of the EOT.

Data, Materials, and Software Availability. Datasets have been deposited in figshare: Datasets_AEA_Weppe et al_Drivers of the artiodactyl turnover in insular western Europe at the Eocene-Oligocene Transition (<https://figshare.com/s/c8867118995628a4d894>). Previously published data were used for this work: This work follows the compilation (*Dataset S1*) performed by Weppe et al. (45).

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