PALEONTOLOGY

Punctuated ecological equilibrium in mammal communities over evolutionary time scales

Fernando Blanco[1]*, Joaquín Calatayud[2], David M. Martín-Perea[3,4,5], M. Soledad Domingo[6], Iris Menéndez[4,7], Johannes Müller[1], Manuel Hernández Fernández[4,7], Juan L. Cantalapiedra[8]

The study of deep-time ecological dynamics has the ability to inform conservation decisions by anticipating the behavior of ecosystems millions of years into the future. Using network analysis and an exceptional fossil dataset spanning the past 21 million years, we show that mammalian ecological assemblages undergo long periods of functional stasis, notwithstanding high taxonomic volatility due to dispersal, speciation, and extinction. Higher functional richness and diversity promoted the persistence of functional faunas despite species extinction risk being indistinguishable among these different faunas. These findings, and the large mismatch between functional and taxonomic successions, indicate that although safeguarding functional diversity may or may not minimize species losses, it would certainly enhance the persistence of ecosystem functioning in the face of future disturbances.

In the context of the current biodiversity crisis, conservation efforts can be directed to safeguarding interactions and processes within ecosystems (ecosystem functioning), including those that are—and will be—beneficial to people (ecosystem services) (*1*, *2*). This notion departs from taxon-based approaches and rather focuses on phenotypic features of species, with an emphasis on functional traits—those traits that condense multiple aspects of a species' ecological role (*3*). The conviction is that conserving a higher phenotypic diversity should help to stabilize ecosystems in the face of disturbances (the "insurance effect") (*4*), increasing the persistence of ecosystem functioning and ensuring yet-unknown future benefits to humanity (*5*). Even so, current conservation decisions will have consequences on the evolutionary future of life that we cannot fully understand by investigating ongoing habitat perturbations (*6*, *7*).

Only by looking into the past can we ask fundamental questions regarding the persistence of ecosystem functioning over evolutionary time and guide long-term future conservation actions (*1*). How long does ecosystem functional structure typically endure, and how much of this functioning is tied to the wax and wane of taxonomic faunas over millions of years? Ecological assessments of faunas have a long tradition in paleobiology (*8*–*10*). However, to answer such questions, rather than conducting a functional assessment of chronofaunas (taxonomy-defined temporal faunas), we need to assess the duration of FFs (functional faunas) independently from taxonomy (*1*), exclusively on the basis of functional coherence of communities. If temporal associations of ecosystems with similar functional structures (that is, similar FFs) are found to weather the succession of taxonomic faunas, this would further endorse prioritizing the conservation of ecosystem functioning.

We turned to the fossil record, adopting a taxon-free perspective that enabled us to evaluate ecological dynamics over evolutionary time (*1*). Investigating deep-time patterns in ecological assembly at the community level demands a high-resolution fossil record (*11*). Our study draws on a new dataset of the exceptional and well-resolved fossil record of large Iberian mammals spanning the past 21 million years (Myr), including 167 fossil and two extant communities with an average resolution of around 0.1 Myr and an estimated 0.8 probability that a 1-Myr-duration taxon is sampled (supplementary materials and data file S1) (*12*, *13*). Our dataset contains a total of 396 mammalian species, for which we compiled information on three fundamental functional traits: body size, diet, and locomotion (table S1 and data file S1). Species were assigned to functional entities (FEs), which are distinct combinations of these three traits (*14*). We used a community detection algorithm (CDA), borrowed from network theory, to reveal both the functional and taxonomic structure of mammalian communities (supplementary materials). Network-based CDA identifies clusters of communities with similar functional or taxonomic structures (modules) defined by the presence of functional entities or taxa (species), respectively. Shifts in past ecological community structure were assessed by the emergence of new associations of functional entities over time and compared with shifts in taxonomic structure (presence of taxa). Our CDA ignores the age of communities, and it is only later that we evaluated the tempo of module succession by plotting the sites within each module against their age (Fig. 1 and supplementary materials).

We used several analysis configurations. We first selected localities with representatives of the orders Proboscidea, Carnivora, Perissodactyla, and Artiodactyla because these were frequent constituents of Neogene-Quaternary ecosystems (Fig. 1A). Second, we selected only exceptional localities (*11*): those sites whose richness values were above the 75th percentile of sites with similar age (figs. S1 to S3). Last, we analyzed the data aggregated into 0.5-Myr temporal bins, which reflect regional trends (an extended methodological explanation is provided in the supplementary materials) (figs. S1 to S3). The results from the first configuration are shown in Fig. 1.

A common pattern emerges from all approaches: Ecosystem functional composition shows longer persistence than taxonomic composition (Fig. 1). Both functional and taxonomic faunas follow a virtually irreversible temporal succession, but taxonomic modules are replaced every 0.9 Myr on average, whereas functional modules have a mean span of 2.8 Myr. A randomization analysis indicates that such organization reflects a genuine ecological signal (P = 0.01) (fig. S4) and does not simply arise because FEs are an aggregation of taxa. Furthermore, taxonomic modules at the generic level [a taxonomic aggregation of taxa (*15*)] show a labile pattern similar to the species-level network (figs. S2 and S3). Sensitivity analyses show that our approach is robust toward reasonable error in functional categorizations (supplementary materials and fig. S5), stochasticity inherent to the detection of modules, and the choice of community detection algorithms (supplementary materials and tables S2 and S3).

We identified three periods with marked functional stability corresponding with three long-lasting and robust modules: earlier Middle Miocene (FF1), later Middle Miocene to earlier Late Miocene (FF2), and later Late Miocene to present (FF3), with durations of 2.58, 4.66, and 9.37 Myr, respectively (summing 80% of the analyzed interval) (Fig. 1). An exploration of the transitional intervals between FFs demonstrates that ecological reassembly was fast, lacking communities with intermediate functional configurations (Fig. 1A, fig. S6, and supplementary materials). Altogether, our procedure reveals gradual changes in taxonomic assembly that contrast with the punctuated

[1]Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, an der Humboldt- Universität zu Berlin, Invalidenstrasse 43, 10115 Berlin, Germany. [2]Departamento de Biología, Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Calle Tulipán s/n, 28933 Móstoles, Spain. [3]Museo Nacional de Ciencias Naturales–Consejo Superior de Investigaciones Científicas (CSIC), Calle José Gutiérrez Abascal 2, 28006 Madrid, Spain. [4]Departamento de Geodinámica, Estratigrafía y Paleontología, Universidad Complutense de Madrid, C/ José Antonio Nováis 12, 28040 Madrid, Spain. [5]Instituto de Evolución Humana en África IDEA, Calle Covarrubias 26, 28010 Madrid, Spain. [6]Departamento de Didáctica de las Ciencias Experimentales, Ciencias Sociales y Matemáticas, Universidad Complutense de Madrid (UCM), C/Rector Royo Villanova s/n, 28040 Madrid, Spain. [7]Departamento de Cambio Medioambiental, Instituto de Geociencias (UCM, CSIC), C/ Severo Ochoa 7, 28040 Madrid, Spain. [8]Departamento de Ciencias de la Vida, GloCEE Global Change Ecology and Evolution Research Group, Universidad de Alcalá, Plaza de San Diego s/n, 28801 Alcalá de Henares, Spain.
*Corresponding author. Email: fblancosegovia@gmail.com, fernando.blanco@mfn.berlin

stasis shown by the functional faunas, revealing an emergent property of ecosystem functioning observable only over broad time scales (Fig. 1).

The contrasting timing of change in ecosystem functioning compared with taxonomic turnover became even more evident when we examined the regional diversification and dispersal patterns through time (Fig. 1C, fig. S7, and supplementary materials). Overall, species-level volatility in Iberian Neogene-Quaternary faunas has been severe (average speciation and immigration rate = 1.40 Myr^{-1}; average regional extinction rate = 1.17 Myr^{-1}), ensuring a continuous replacement of the Iberian species pool over the past 21 Myr, as captured through network analysis (Fig. 1B). Nevertheless, only major faunal events were able to push the system toward a new state, around 14 and 9 Myr ago (Ma), triggering fast reassembly of ecological guilds into new functional faunas.

The onset of the FF2 around 14 Ma seems related to profound reconfiguration of biogeographic and climatic settings. There is

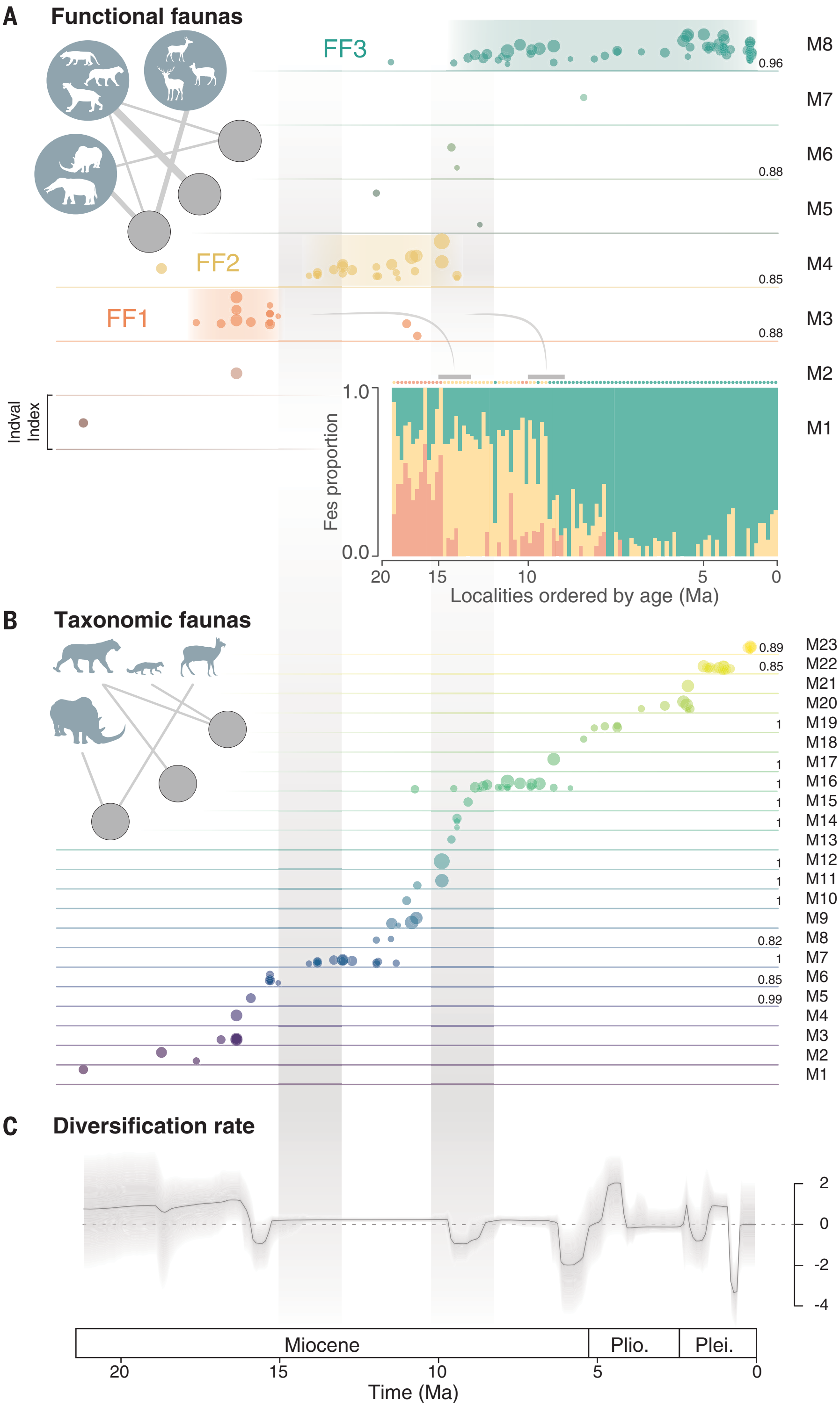

Fig. 1. Temporal trends of Iberian mammal communities over the past 21 Myr. (**A** and **B**) Localities colored by modules (M) are plotted against time. Dots indicate communities (localities), and each dot's size is proportional to the species richness of that community. (A) Modules derived from the functional network analysis show the succession of FFs. The height of the points reflects relevance within the module (IndVal index) (supplementary materials). Numbers above the module lines indicate the module robustness as the probability of being found in different runs of the community detection algorithm (only values above 0.8 are shown) (supplementary materials). (A) Color-shaded areas indicate the three long-lasting FFs. Vertical gray bars indicate the transitions between FF1 to FF2 and FF2 to FF3. (Inset) The proportion of functional entities belonging to the three main FFs in each locality (dots). (B) Modules based on species composition represent the taxonomic succession. (**C**) Changes in taxonomic composition are represented by the net diversification rate over time. Shaded regions indicate the 95% confidence interval. Plio., Pliocene; Plei., Pleistocene. [Silhouettes are from PhyloPic (www.phylopic.org).]

evidence of a higher resemblance of Iberian taxonomic faunas with Eurasian faunas by this age (*16*). Regional isotopic data depict a sustained trend toward a prevalence of more forested, less arid habitats in the Iberian Peninsula (*16*), which is consistent with the observed enrichment of communities with browsing herbivores of all sizes (fig. S8). The FF2-FF3 transition (around 9 Ma) seems triggered by an intensification of hydric seasonality and the associated spread of grassland habitats (*16*). In fact, this second major reassembly pulse replaced the browser-rich faunas of the later Middle Miocene and earlier Late Miocene with ecosystems that packed a broad variety of mixed-feeders (feed both through browsing and on grass) (fig. S8) (*17*).

The context of both functional transitions suggests an important role of abiotic changes (climate and climate-driven biogeographic context) on the system shifts. However, a trait-dependent extinction model (*18*) did not find an overall effect of particular traits or their combinations (FEs) on extinction across different time bins. The influence of such abiotic factors was not expressed through trait-mediated local extirpation. Instead, these analyses show that during functional transitions, characteristic species (those species with at least 60% of their occurrences in localities of one of the three FFs) of the outgoing functional fauna showed significantly higher extinction risk than that of the incoming fauna (Fig. 2A and fig. S9). Thus, the extinction of species during severe ecological shifts seems to be determined by their attachment to a collapsing functional system rather than their particular functional traits (*19*).

Altogether, these findings portray a system in which species gains and losses are governed by their restriction to functional scaffolds defined by ecological interactions. These interactions should limit the inclusion of new functional strategies into established ecosystems (*20*), constraining both the evolution (*21*) and the immigration of species belonging to other FEs (*22*). Major disturbances forced the system into new ecological states, rendering the disassembly of the prevailing functional fauna and the assembly of a new functional scaffold (Fig. 1).

Not all major faunal events caused a reorganization of ecosystem functioning. During the past 8 Myr, the most recent functional fauna (FF3) survived three severe extinction events (Fig. 1C): the Messinian salinity crisis (6 to 5 Ma), the beginning of the Plio-Pleistocene glaciations (~2.5 Ma), and the Early-Middle Pleistocene transition (~0.8 Ma) (fig. S7). Thus, FF3 is not only the most enduring but also the most resistant functional fauna of the studied time interval. Overall, the Neogene-Quaternary Iberian functional systems have increased in duration and persistence.

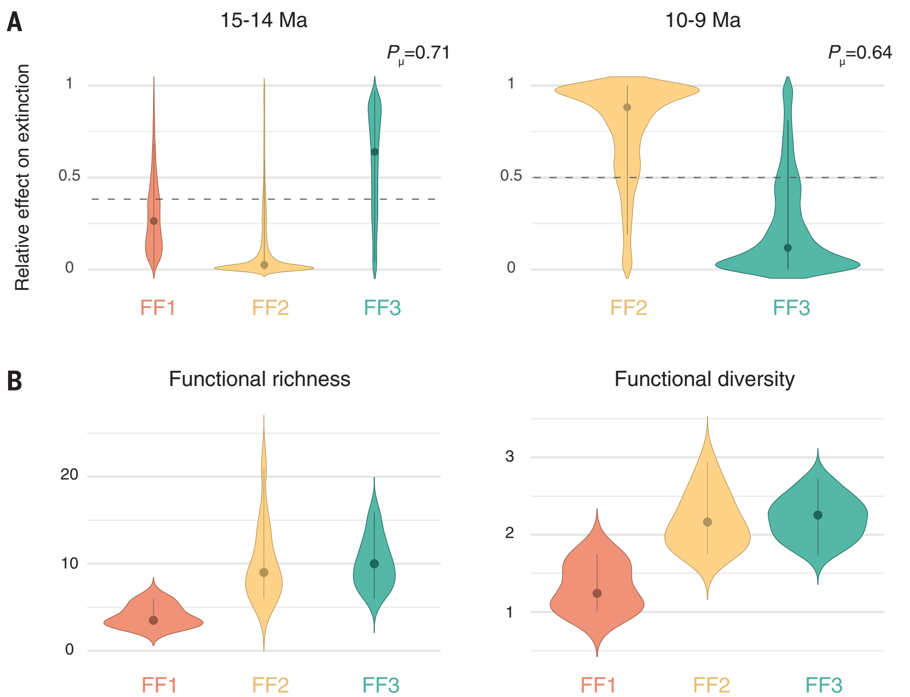

Fig. 2. Differential extinction risk during functional transitions and functional richness and diversity among the three main functional faunas. (**A**) Violin plots indicate the differential extinction risk of species associated with the FFs during the two major transitions (15 to 14 Ma and 10 to 9 Ma). P_μ is the probability of the trait affecting extinction risk. The horizontal dashed lines indicate the expected effect if the trait had no effect. (**B**) Functional richness and functional diversity of the FFs (supplementary materials). Colors are as in Fig. 1.

Why do functional faunas increase in persistence during the analysis interval? The above-mentioned trait-dependent extinction model shows no evidence of lower extinction risk in species associated with more persistent FFs, suggesting that persistence of each functional fauna draws from emergent properties of the system and not from the persistence of the constituent species. Linear models show that communities in successive functional faunas increased their functional diversity (F_{div}, as the Shannon index) (tables S4 to S6), which is mostly driven by an increase in functional richness (F_{ric}) (tables S7 to S9) rather than by functional evenness (tables S10 to S12). FF2 and FF3 show increases in F_{ric} and F_{div} with respect to FF1 (Fig. 2B and tables S4 to S9). A higher F_{ric} associated with more persistent functional faunas agrees with the idea that biodiversity enhances ecosystem resilience (*4*, *23*). Differential persistence in FF2 and FF3 may be further explained by environmental conditions that operated during their onset. Whereas FF2 originated during milder climatic conditions, the inception of FF3 took place during an episode of increased aridity in the region (*24*). Such conditions brought an entourage of arid-adapted immigrants from Eurasia and Africa (*16*, *25*). Their ecological assemblage, forged by strong abiotic forces from FF3's inception, would have coped with the milder conditions of the latest Iberian Miocene first (*16*) and, subsequently, with the increasing seasonality and glacial regimes in Pliocene and Pleistocene times.

Our analyses of the fossil record set out key differences in the mode that taxonomic and functional assemblages wax and wane over evolutionary time scales. The marked decoupling between taxonomic and ecological turnover further demonstrates the value of functional and trait-based procedures when assessing the magnitude and consequences of environmental disturbances in paleobiological studies. Moreover, because the collapse of FFs seems to be the main force pulling species out of the system, investigation of preterit turnover episodes should look beyond trait selection in extinction events and also account for the integration of species into particular FFs during ecological dismantling.

Our study provides a deep-time dimension to the functional perspective in conservation (*2*): Actions carried out to ensure ecosystem functioning will tend to endure longer than actions oriented toward protecting taxonomic structure. We found that higher F_{div} enhances the persistence of ecosystem functioning, yielding a long-term version of the temporal insurance (*4*, *23*). However, the vague connection between taxonomic and ecological assembly yields a cautionary reading. Because species in high-F_{div} faunas do not show lower extinction risk, betting on higher-F_{div} systems would not necessarily minimize species loss in the long term. If the past is useful to illuminate the future, our paleobiological perspective further emphasizes the gap between conservation policies that minimize extinctions and those that target ecosystem functioning and its benefits to people (*26*).

REFERENCES AND NOTES

1. A. D. Barnosky *et al*., *Science* **355**, eaah4787 (2017).
2. C. M. Tucker *et al*., *Biol. Rev. Camb. Philos. Soc.* **94**, 1740–1760 (2019).
3. F. Mazel *et al*., *Nat. Commun.* **9**, 2888 (2018).
4. M. Loreau, C. de Mazancourt, *Ecol. Lett.* **16** (suppl. 1), 106–115 (2013).
5. S. Díaz *et al*., *Science* **359**, 270–272 (2018).
6. F. Aubree *et al*., *Ecol. Lett.* **23**, 1263–1275 (2020).
7. J. L. Cantalapiedra *et al*., *Proc. Biol. Sci.* **286**, 20182896 (2019).
8. R. K. Bambach, J. B. Bennington, *Evolutionary Paleobiology* (Univ. of Chicago Press, 1996), pp. 123–160.
9. B. Figueirido, P. Palmqvist, J. A. Pérez-Claros, C. M. Janis, *Proc. Natl. Acad. Sci. U.S.A.* **116**, 12698–12703 (2019).
10. J. A. Dunne, C. C. Labandeira, R. J. Williams, *Proc. Biol. Sci.* **281**, 20133280 (2014).
11. R. A. Close *et al*., *Nat. Ecol. Evol.* **3**, 590–597 (2019).
12. F. Blanco *et al.*, R. Scripts Blanco *et al*. 2021. Figshare (2021); doi:10.6084/m9.figshare.13516253.
13. F. Blanco *et al.*, Occurence data Blanco *et al*. 2021. Figshare (2021); doi:10.6084/m9.figshare.13332755.
14. D. Mouillot *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **111**, 13757–13762 (2014).
15. G. G. Simpson, *The Major Features of Evolution* (Columbia Univ. Press, 1953).
16. J. L. Cantalapiedra, M. S. Domingo, L. Domingo, *Sci. Rep.* **8**, 13413 (2018).
17. M. S. Domingo, C. Badgley, B. Azanza, D. DeMiguel, M. T. Alberdi, *Paleobiology* **40**, 197–221 (2014).
18. C. Pimiento *et al*., *Proc. Biol. Sci.* **287**, 20201162 (2020).
19. P. D. Roopnarine, K. D. Angielczyk, *Biol. Lett.* **8**, 147–150 (2012).
20. G. E. Hutchinson, *Am. Nat.* **93**, 145–159 (1959).
21. P. J. Morris, L. C. Ivany, K. M. Schopf, C. E. Brett, *Proc. Natl. Acad. Sci. U.S.A.* **92**, 11269–11273 (1995).
22. T. A. Kennedy *et al*., *Nature* **417**, 636–638 (2002).
23. S. Yachi, M. Loreau, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 1463–1468 (1999).
24. L. Domingo *et al*., *PLOS ONE* **8**, e63739 (2013).
25. M. Fortelius *et al*., *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **238**, 219–227 (2006).
26. A. Purvis, *Nat. Ecol. Evol.* **4**, 768–769 (2020).

ACKNOWLEDGMENTS

We thank J. Morales, M. Ríos, O. Sanisidro, and A. Valenciano for their insights on functional traits; D. Silvestro for technical assistance; and N. Baird, F. Bibi, M. Fabbri, P. Medina-García, I. A. Lazagabaster, G. Navalón, M. A. Rodríguez, and two anonymous reviewers for their valuable comments and advice. We acknowledge the effort of all the people working in Iberian fossil sites over the decades that made this study possible. **Funding:** F.B. was funded by Deutsche Forschungsgemeinschaft (LO 2368/1-1). D.M.M.-P. was funded by an FPI predoctoral grant BES-2016-079560 from the Spanish Government associated with project CGL2015-6833-P and PGC2018-094122-B-100. I.M. was funded by a predoctoral grant from the Complutense University of Madrid (CT27/16-CT28/16). J.L.C. was funded by the Talent Attraction Program of the Madrid Government and the Universidad de Alcalá (2017-T1/AMB5298). D.M.M.-P., I.M., M.H.F., and M.S.D. acknowledge the project PGC2018-094955-A-I00 granted by the Spanish Ministerio de Ciencia, Innovación y Universidades. **Author contributions:** F.B., J.L.C., and J.M. conceptualized the research. F.B., D.M.M.-P., I.M., M.S.D., and M.H.F. gathered the data. F.B., J.C., and J.L.C. designed and performed the analysis. F.B., J.C., and J.L.C. wrote the paper with input from all authors. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** All data and code are available at (*12*, *13*).

SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/372/6539/300/suppl/DC1
Materials and Methods
Figs. S1 to S10
Tables S1 to S12
References (*27*–*52*)
Data File S1

25 June 2020; accepted 23 February 2021
10.1126/science.abd5110

Science

Punctuated ecological equilibrium in mammal communities over evolutionary time scales

Fernando Blanco, Joaquín Calatayud, David M. Martín-Perea, M. Soledad Domingo, Iris Menéndez, Johannes Müller, Manuel Hernández Fernández and Juan L. Cantalapiedra

Science **372** (6539), 300-303.
DOI: 10.1126/science.abd5110

Paleontology for conservation
Human activities are leading to broad species and system declines. Prevention of such declines has led us to focus on either protection for species or protection for ecosystem function. Looking at past patterns of species and system change can help to inform our understanding of the long-term impacts of these strategies. Blanco *et al.* studied mammals from the last 21 million years on the Iberian Peninsula, finding long periods of functional stasis, even in the face of taxonomic variability (see the Perspective by Roopnarine and Banker). Functional ecosystems were more resistant to ecosystem collapse.
Science, this issue p. 300; see also p. 237

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.