

Probing the mammalian fossil record for patterns of competitive exclusion using computational randomization experiments

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1. The Hypothesis

Competitive exclusion

“complete competitors cannot coexist” (Hardin 1960)

competition-relatedness hypothesis of community assembly
(Darwin 1859)

more closely related species should compete more intensely
due to greater niche overlap, and consequently co-occur less
in space (Cahill et al. 2008)

Congeneric species

Congeneric species descend from a recent common ancestor
Hence, expect

- more similarity w.r.t. phenotype
- less niche divergence than species of different genera

Empirical support for competition-related segregation in extant communities is not univocal

Meta-analyses have found an excess of segregated species pairs relative to null expectations (Gotelli and McCabe 2002; Ulrich and Gotelli 2010), but interpretations are not settled yet

Little evidence in support of this excess resulting from intensified competition due to a recent common ancestry (Sfenthourakis et al. 2006)

Our goal


Look for **evidence** supporting or contradicting
the hypothesis of competitive exclusion
by contrasting **patterns of co-occurrence**
among **congeneric species** and species of different genera

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2. The Data

The NOW Database

<https://nowdatabase.org/>



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NOW

New and Old Worlds

Database of fossil mammals

- News
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- People
- Data Conventions
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- Acknowledgements

Database of fossil mammals

The NOW (New and Old Worlds) fossil mammal database contains information about Cenozoic land mammal taxa and localities. The emphasis of the database has been on the European Miocene and Pliocene but North American localities, covering the whole Cenozoic, were added to the public database in 2016. African localities are currently being added and updated, and the temporal scale is also becoming wider for both Eurasia and Africa, with Pleistocene and Paleogene localities being added into the database. The NOW database is maintained and coordinated by [Indre Zisabala](#) in collaboration with associate coordinators, a steering group and an international [advisory board](#).

NOW data

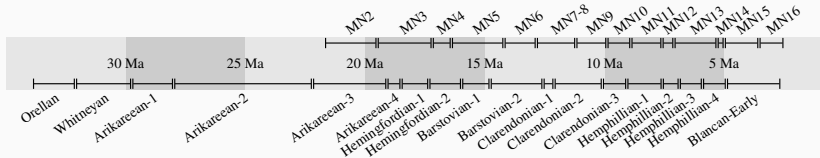
The nucleus of the database is a locality table and a species table, relationally linked by means of a locality-species correlation table (in essence, a table of localities and their faunal lists). Additions and updates are tied to references. The aim of the database is that each species (including higher taxa such as "Machirostomus indet. large sp." or "Rhinocerotidae indet.") is given certain attributes describing anatomy and inferred diet, locomotion and other properties. Similarly, the geographic location, age, stratigraphy, lithology, taphonomy and environmental interpretation of each locality is described to the extent that these are known. It is also worth noting that not all datasets that have been added to NOW are of equal quality, and users should be aware of this fact. Please also note that in the North American data spatially or temporally close localities have been fused to more inclusive spatiotemporal entities prior to entry, whereas in the Old World the localities are in most cases individual sites. This does not affect the analysis on continental or regional levels (see e.g. Jernvall & Fortelius 2002, 2004, available from [Publications](#)), but might affect locality-to-locality comparisons between North America and the Old World. Revision of the data by NOW advisory board members and all users is an ongoing process and an integral part of the NOW project.

NOW 25 years anniversary meeting is postponed to some time in 2022.

All welcome!

More info will follow.

Europe (in a wide sense), Miocene Mammalian Neogene zonation (MN)



American Land Mammal Ages (NALMA) North America, Oligocene and Neogene

Faunal groups

large herbivores *Artiodactyla*, *Hyracoidea* (absent from North America), *Perissodactyla*, *Primates* and *Proboscidea*.

large carnivorans *Carnivora*, *Creodonta* and *Tubulidentata* (absent from North America).

small mammals *Cimolesta* (absent from Europe), *Didelphimorphia*, *Eulipotyphla*, *Lagomorpha*, *Leptictida* (absent from Europe) and *Rodentia*.

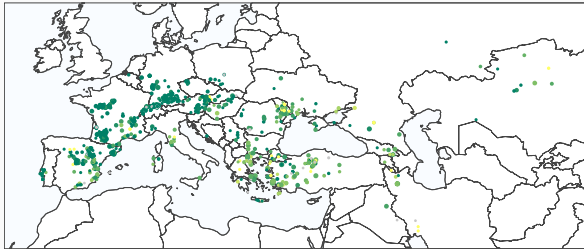
records with incomplete or uncertain taxonomic information

- (yet) unnamed species, annotated in NOW by “gen. sp.”
- species level affiliation uncertain, annotated by “indet.”

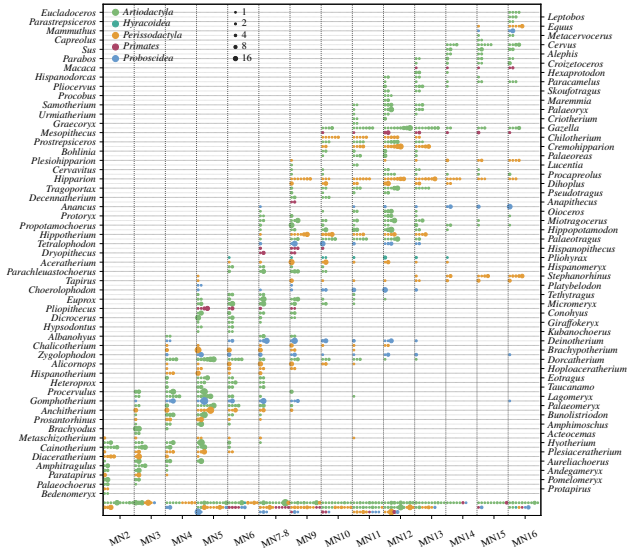
North America, large herbivores



Europe, large herbivores



Europe, large herbivores



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3. The Experiments

Statistics of species co-occurrences

Segregation of species pairs

s_i = number of localities where species i occurs

s_{ij} = number of localities where both species i and j occur

C-score (Stone and Roberts 1990)

$$C(s_{ij}, s_i, s_j) = (s_i - s_{ij}) \cdot (s_j - s_{ij}),$$

mid- P variant of Fisher's exact test

(Berry and Armitage 1995; Kallio et al. 2011)

$$p_F(s_{ij}, s_i, s_j, n) = \sum_{k=0}^{s_{ij}} P(X = k \mid n, s_i, s_j) - \frac{1}{2} P(X = s_{ij} \mid n, s_i, s_j)$$

$$\text{where } P(X = k \mid n, s_i, s_j) = \frac{\binom{s_i}{k} \binom{n-s_i}{s_j-k}}{\binom{n}{s_j}}$$

Distribution of species within genera

Among localities where genus g occurs, how many contain multiple distinct species of g ?

number of genera with co-occurring species

Random models

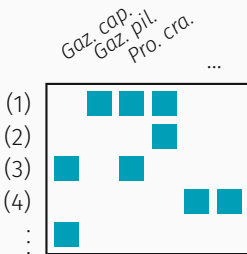
UG (Ulrich and Gotelli 2012)

proportional-proportional model (Gotelli 2000)

Curveball (Strona et al. (2014)

fixed-fixed model (Connor and Simberloff 1979)

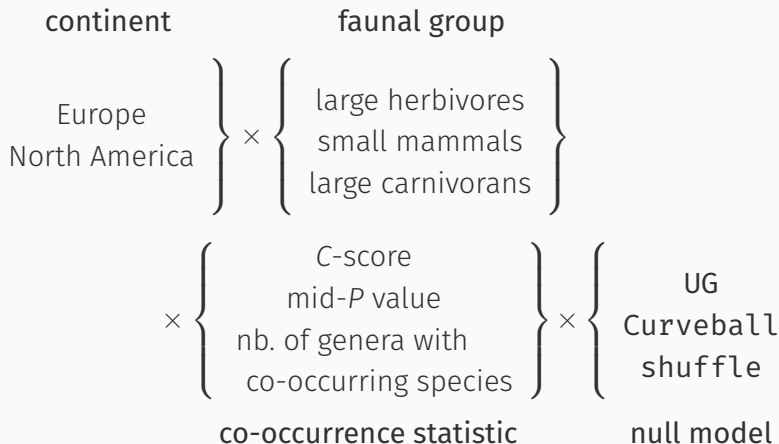
shuffle reassign taxonomic labels at random



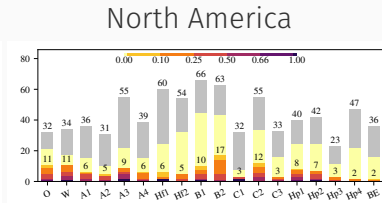
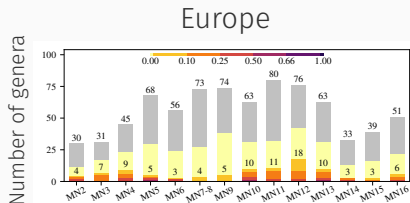
Three-steps computational experiment

1. computing co-occurrence statistics from original data
2. comparing values from original data to null models
3. examining trends in the environmental context

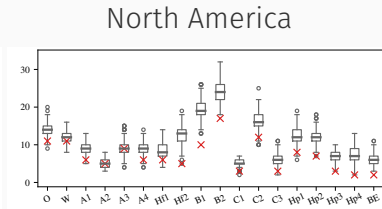
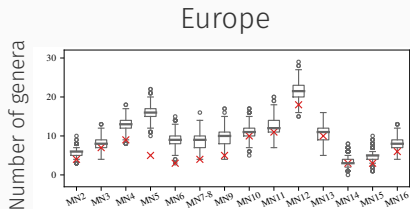
Fifty-four computational experiments



Results, large herbivores

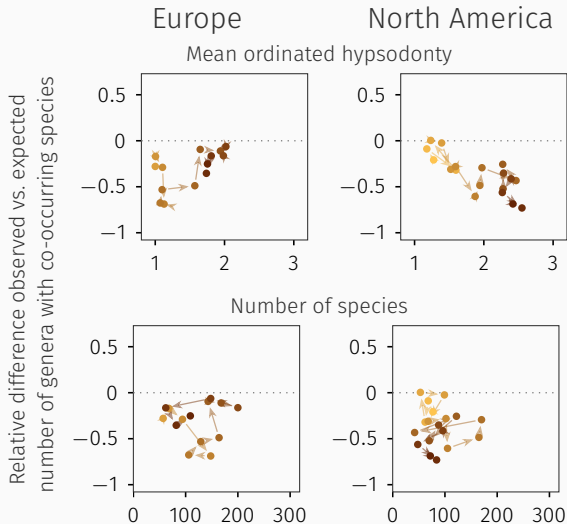


Counts of genera by fraction of multi-species occurrence localities



Nb. of genera with co-occurring species, org. data vs. 1000 **Curveball** null models

Results, large herbivores



Obs. vs. expected nb. of genera with co-occurring species against environmental context vars

For large herbivores

- under **mild** environmental conditions
similar level of segregation in Europe and North America
- when environmental conditions become **harsher**
segregation of congeneric species go in **opposite**
directions, decreasing in Europe and increasing in North
America

Overall, we find a **rather weak but consistent signal** over time and across continents that indeed, **congeneric species tend to be segregated in space**

Upcoming! NOW 25 years anniversary
Special volume in the *Vertebrate Paleobiology
and Paleoanthropology Series*



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