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

Patterns of co-occurrence

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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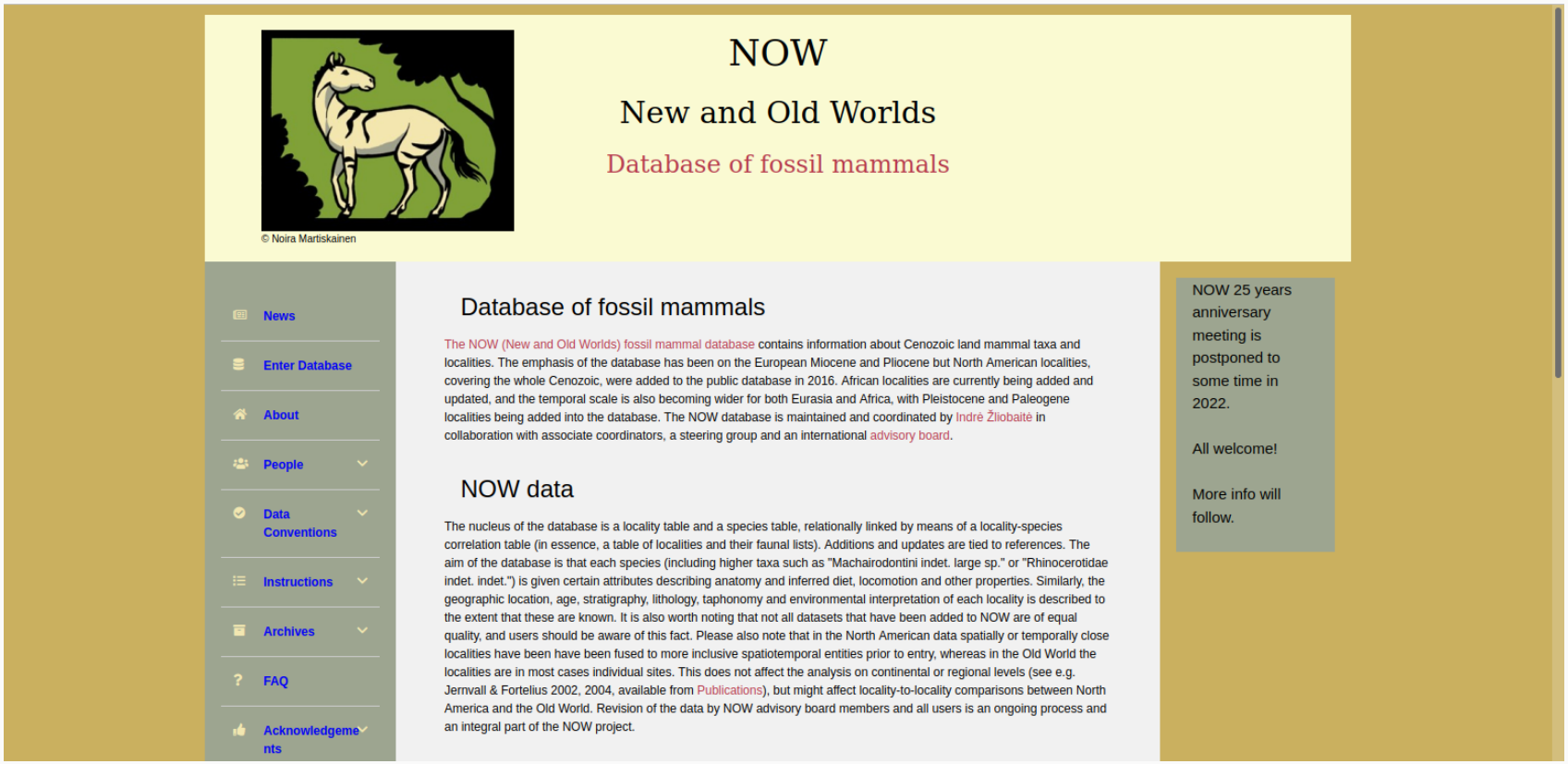
2. The Data

The NOW Database

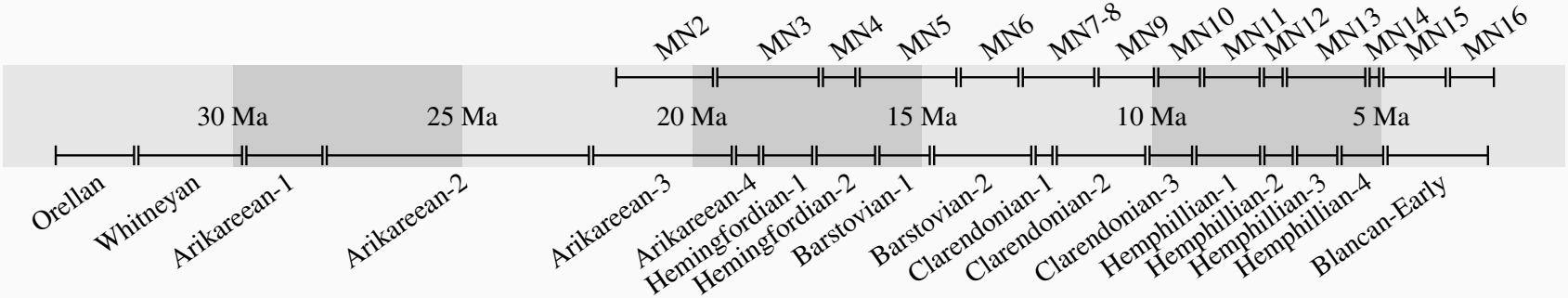
https://nowdatabase.org/



Continents and time units

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).

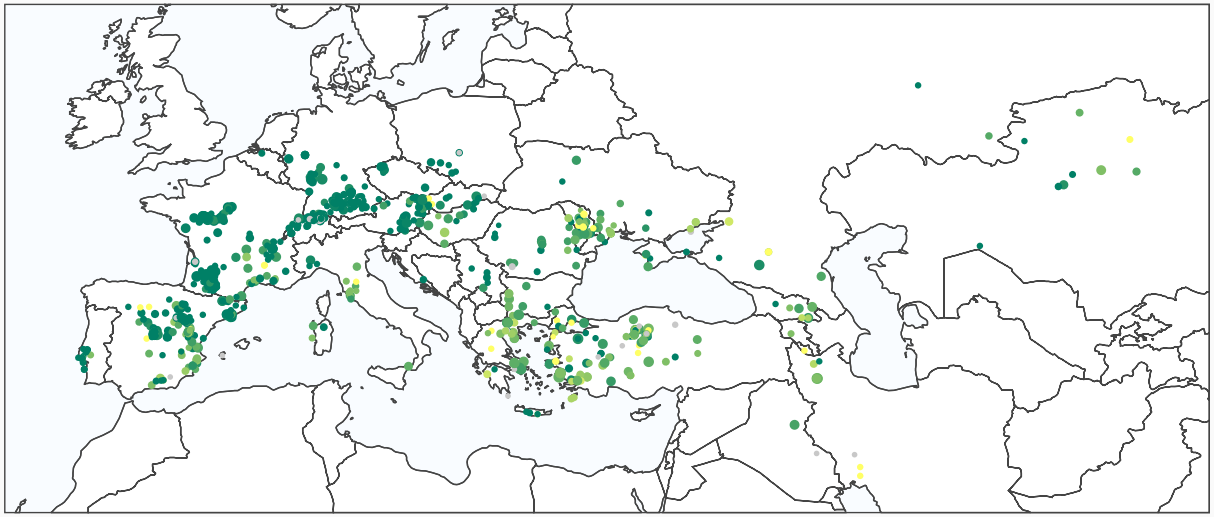
small mammals *Cimolesta* (absent from Europe), *Didelphimorphia*, *Eulipotyphla*, *Lagomorpha*, *Leptictida* (absent from Europe) and *Rodentia*.

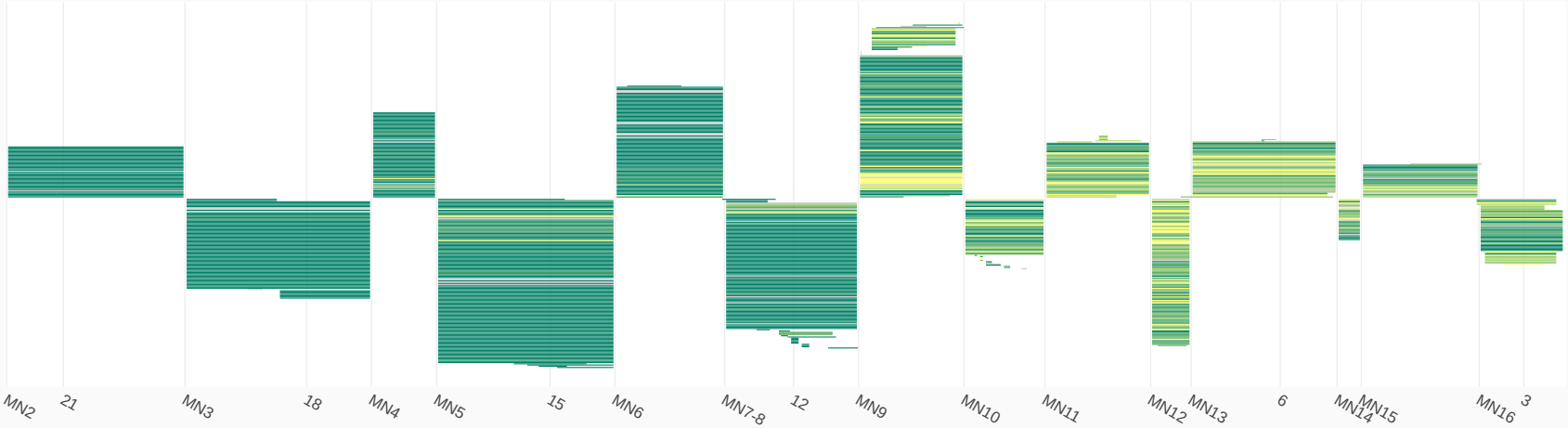
records with incomplete or uncertain taxonomic information

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

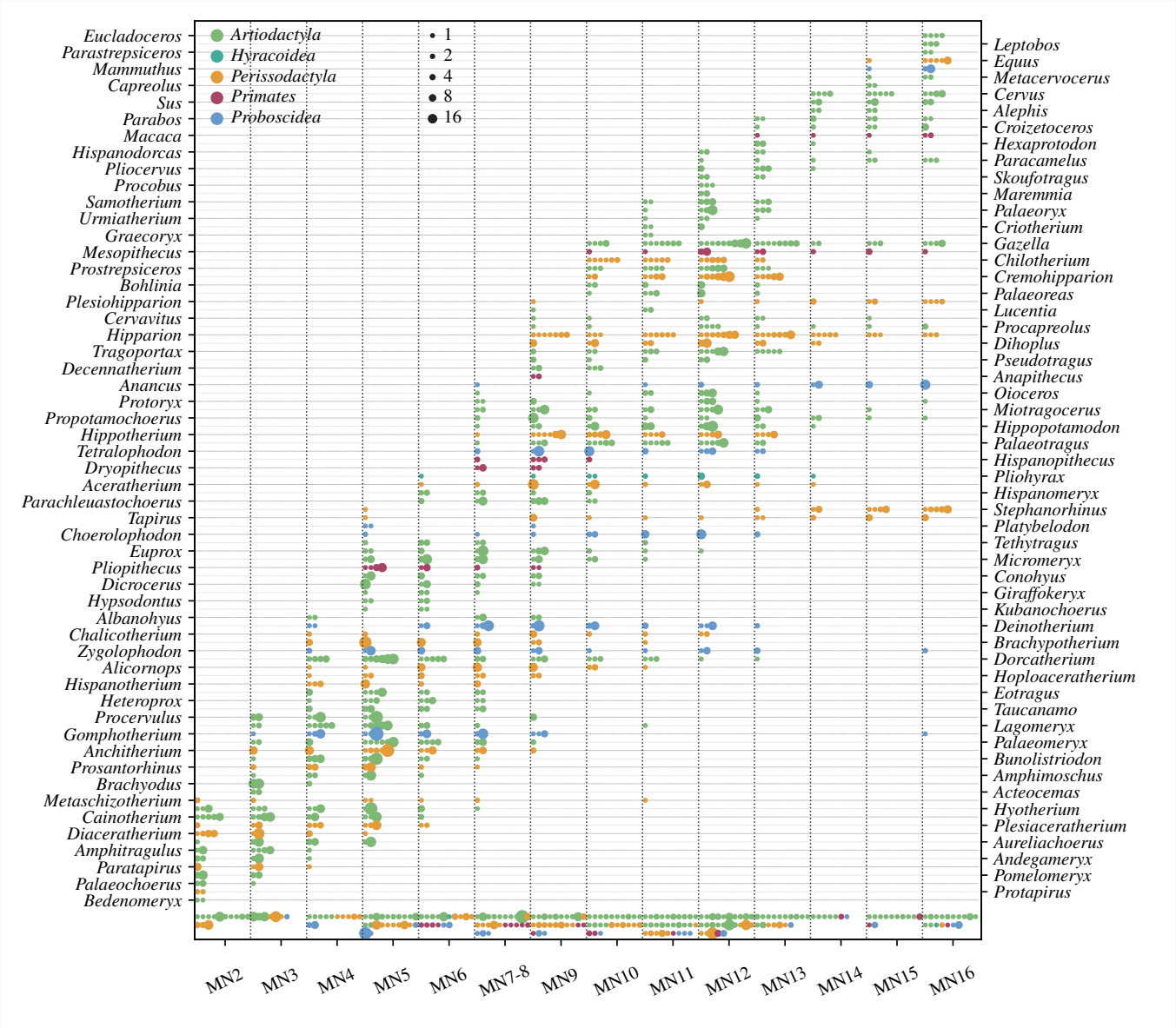
North America, large herbivores

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)

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

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

Statistics of species co-occurrences

Distribution of species within genera

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

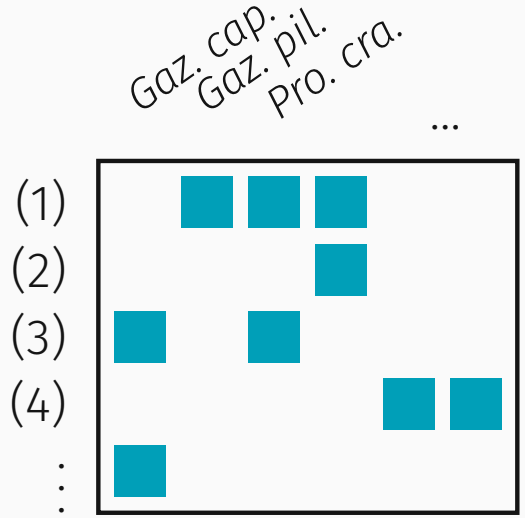
number of genera with co-occurring species

Random models

UG (Ulrich and Gotelli 2012)
proportional–proportional model (Gotelli 2000)

Curveball (Strona et al. (2014)
fixed–fixed model (Connor and Simberloff 1979)

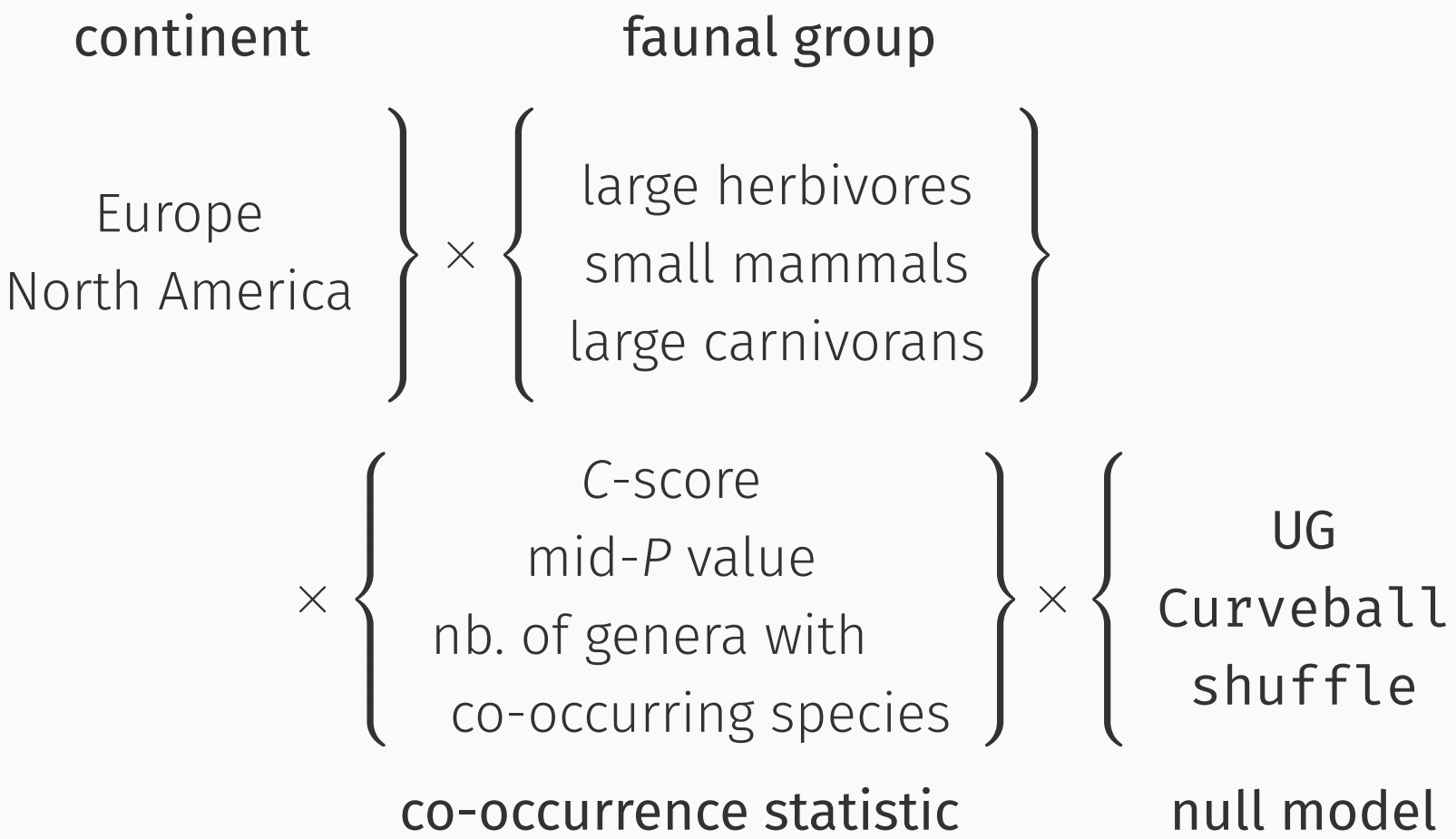
shuffle reassign taxonomic labels at random



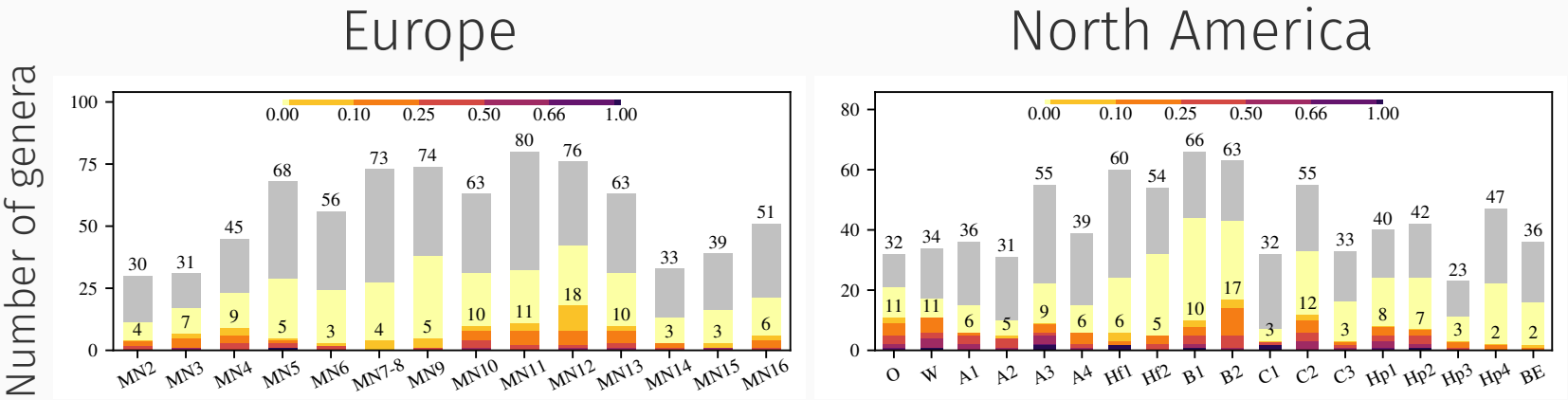
Three-steps computational experiment

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

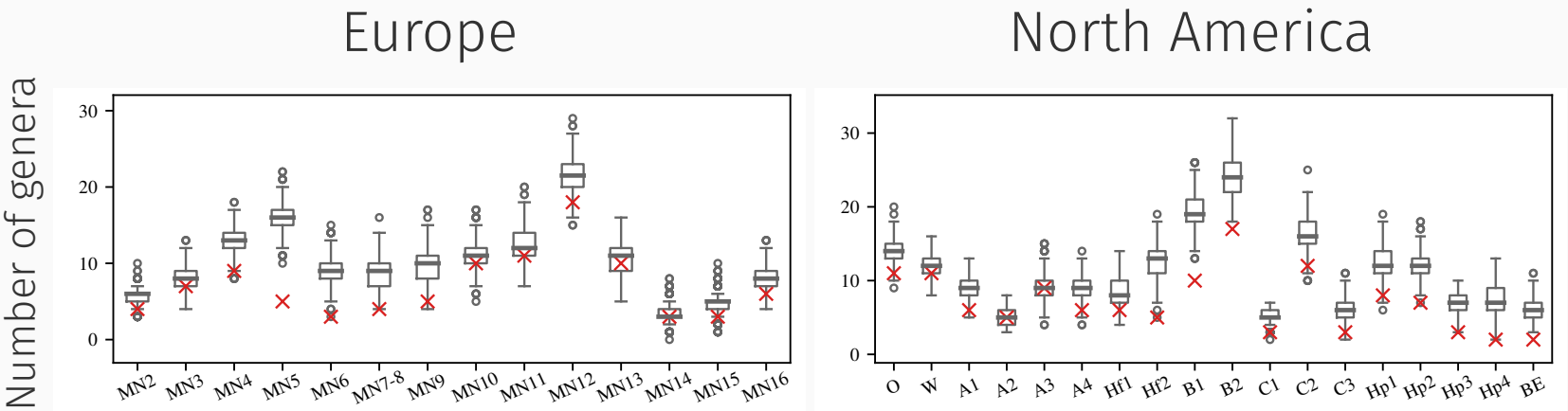
Fifty-four computational experiments



Results, large herbivores

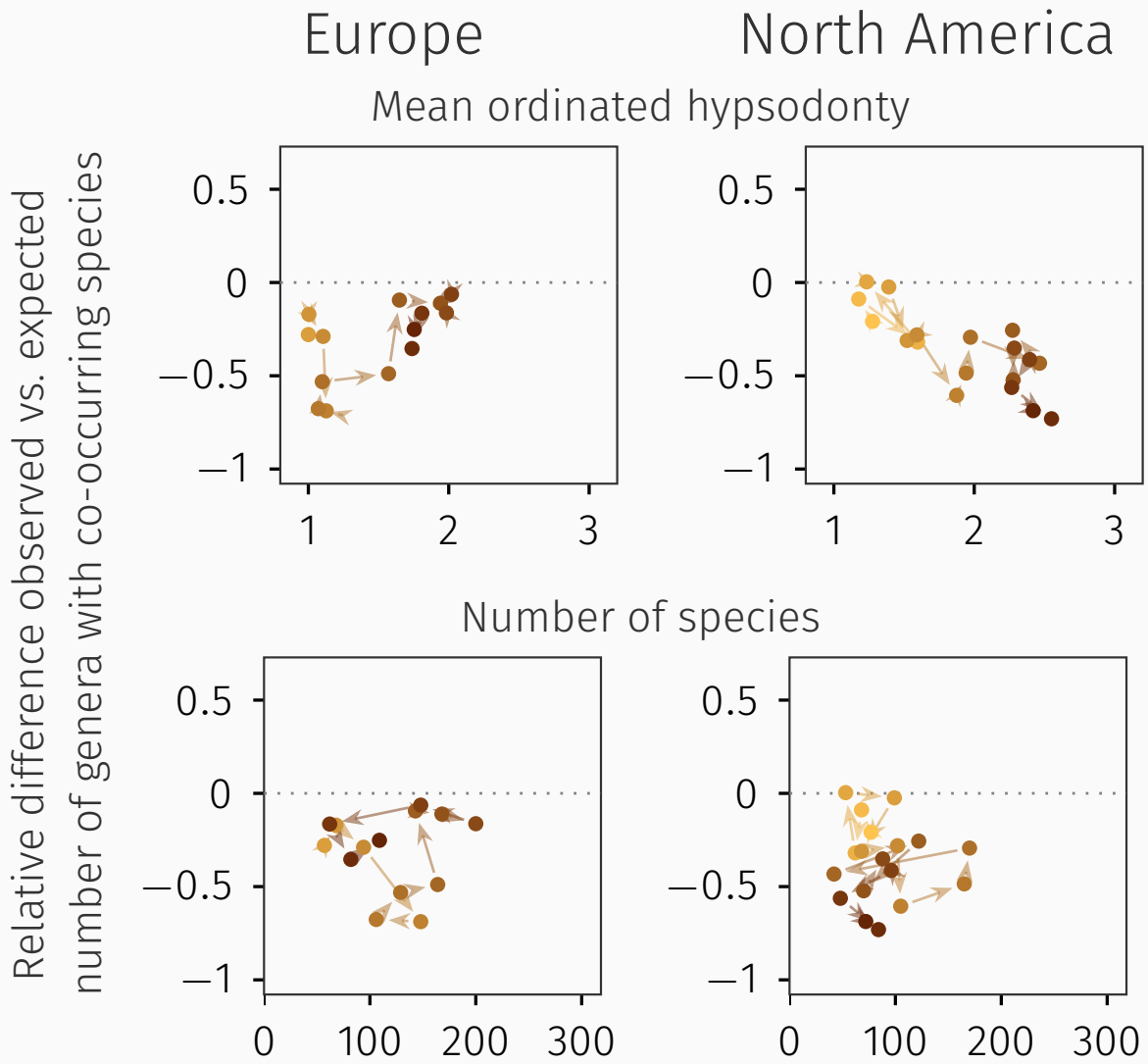


Counts of genera by fraction of multi-species occurrence localities



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

Results

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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