Format Cetaceans Data

Contents

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This notebook aims at exploring the Cetacean occurrence dataset from the PaleoBiology DataBase (PBDB), looking for potential biases invalidating to our model assumptions and how to mitigate them. Subsampling this dataset will allow (1) to reduce the computational burden of our analysis and (2) to compensate for the biases mentioned above.

Load occurrence dataset

Load the list of occurrences with morphological information

These are the specimens that are already included in the tree thanks to their morphological characters, and must therefore be removed from the occurrence dataset.

Combine these taxa with extant taxa to get all the species included in the tree.

Idem at the generic level for the genus analysis.

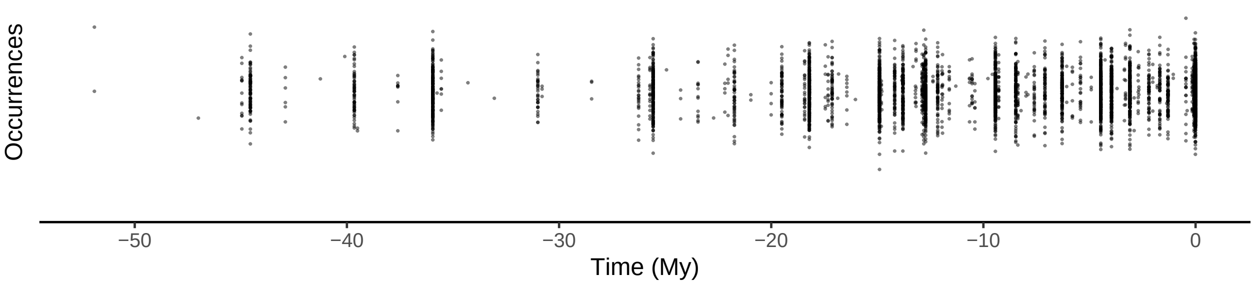
Remove those occurrences from our initial dataset to avoid redundancy.

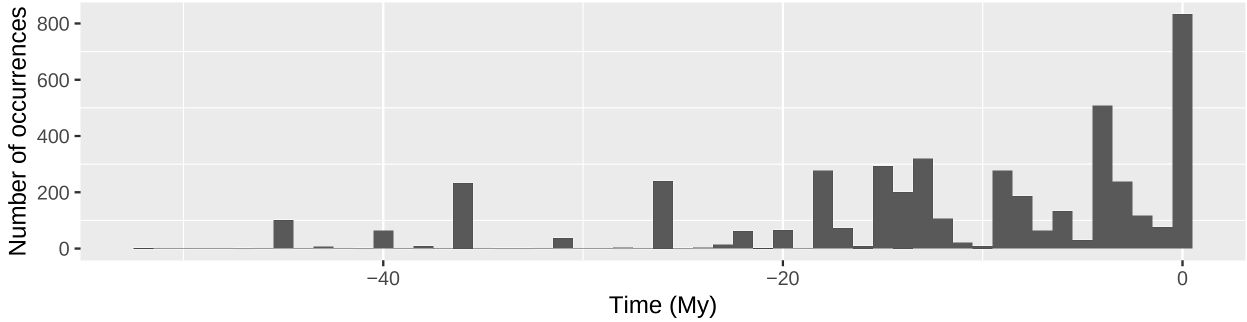
Explore the dataset

Repartition through time

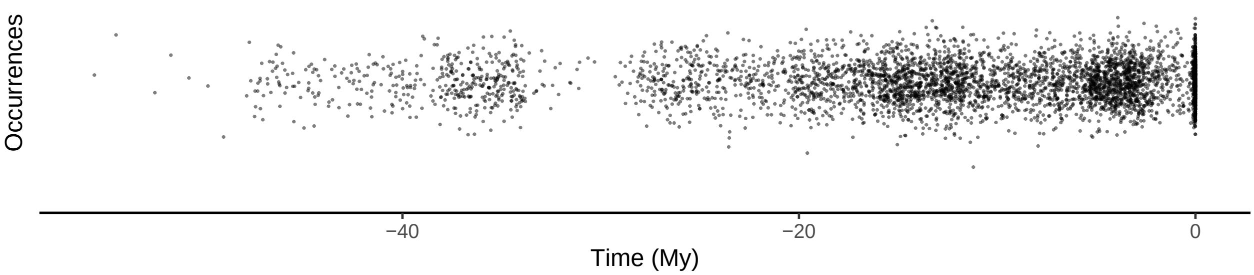
Full fossil record

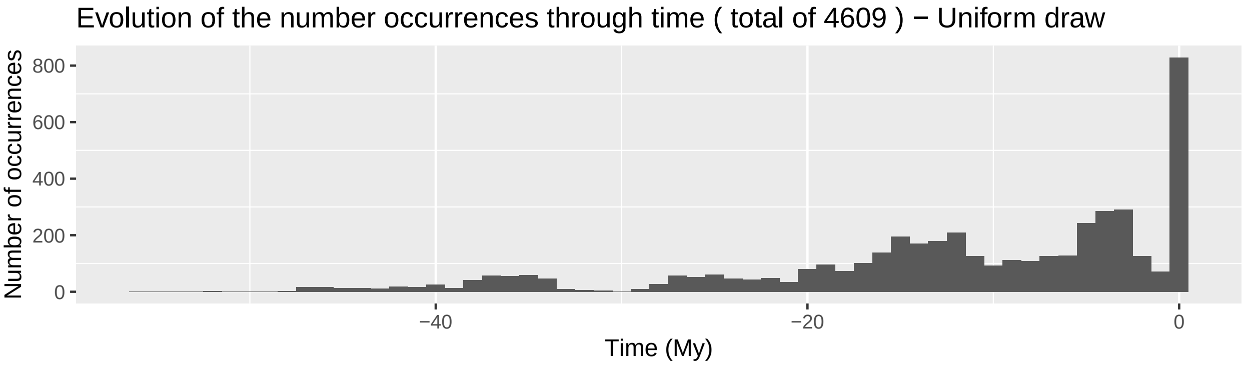
First, use the stratigraphic range's midpoint as the occurrence fixed age.


Repartition of 4609 recorded occurrences through time − Midpoint


Evolution of the number occurrences through time (total of 4609) − Midpoint

→ Numerous occurrences seem to have the same age interval so in order to avoid clusters let's draw them uniformly in their stratigraphic range rather than taking the midpoint.

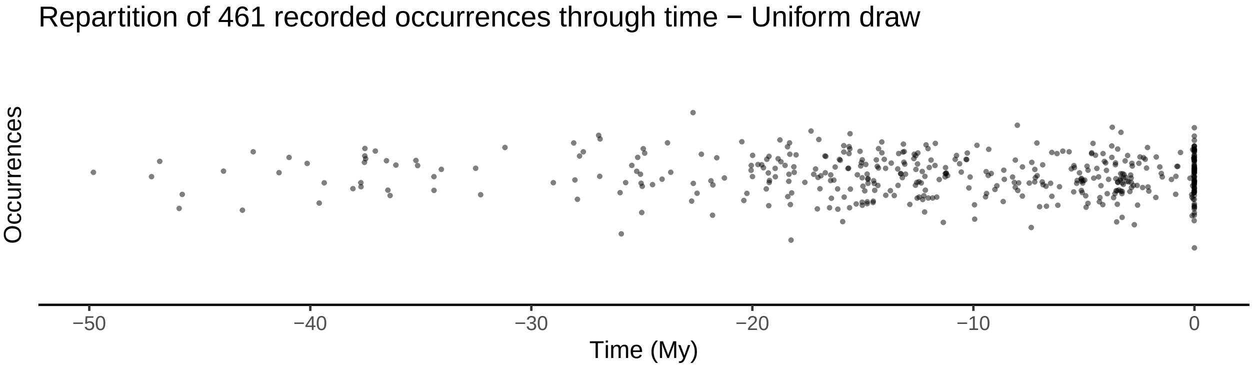

Repartition of 4609 recorded occurrences through time − Uniform draw

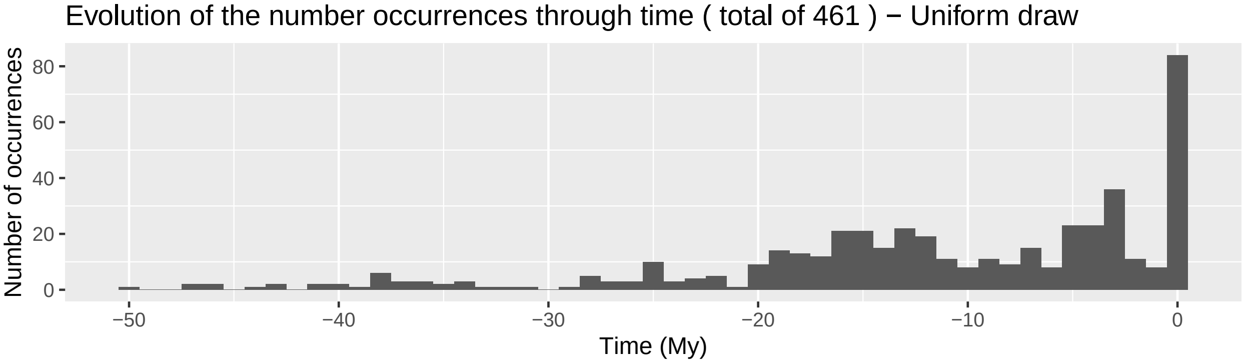


→ The repartition seems much smoother now.

Subsampling

These occurrences are too numerous for a faster preliminary analysis, let's randomly subsample a fraction of them.

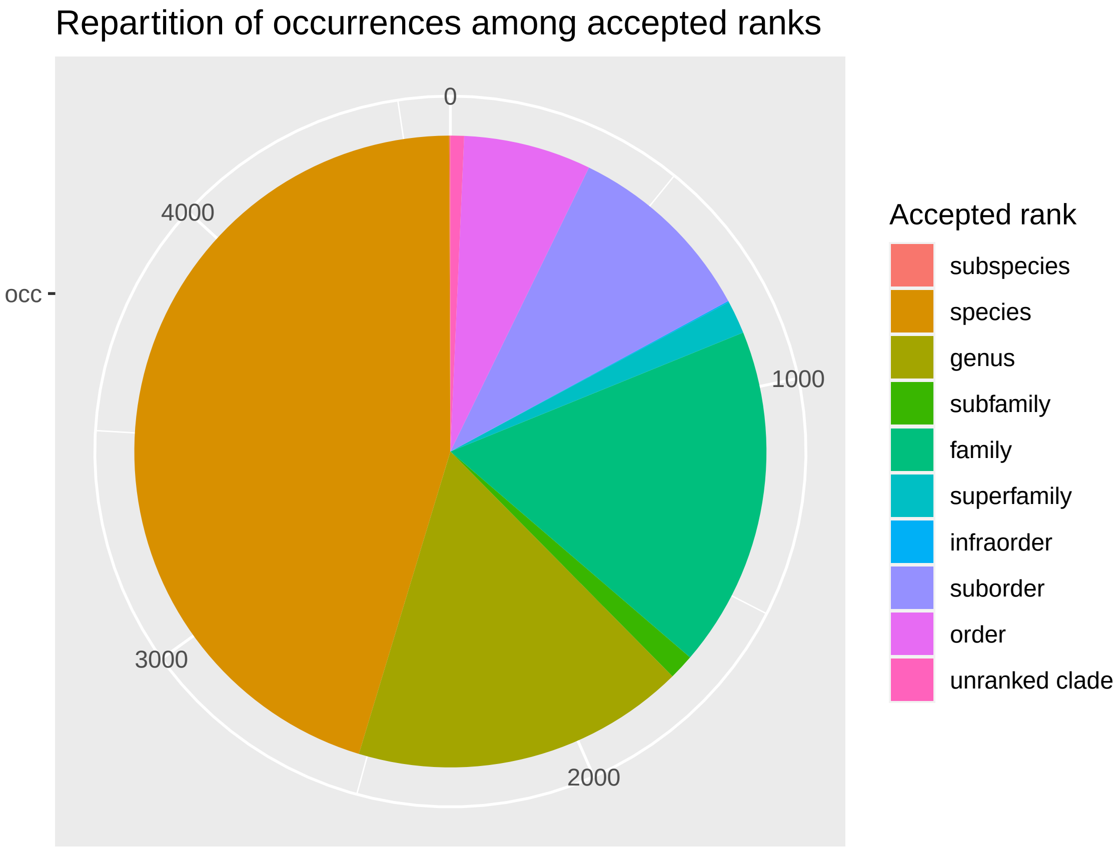




→ The distribution looks similar, with some noise due to higher variance with smaller sample.

Repartition among accepted ranks

Pie chart

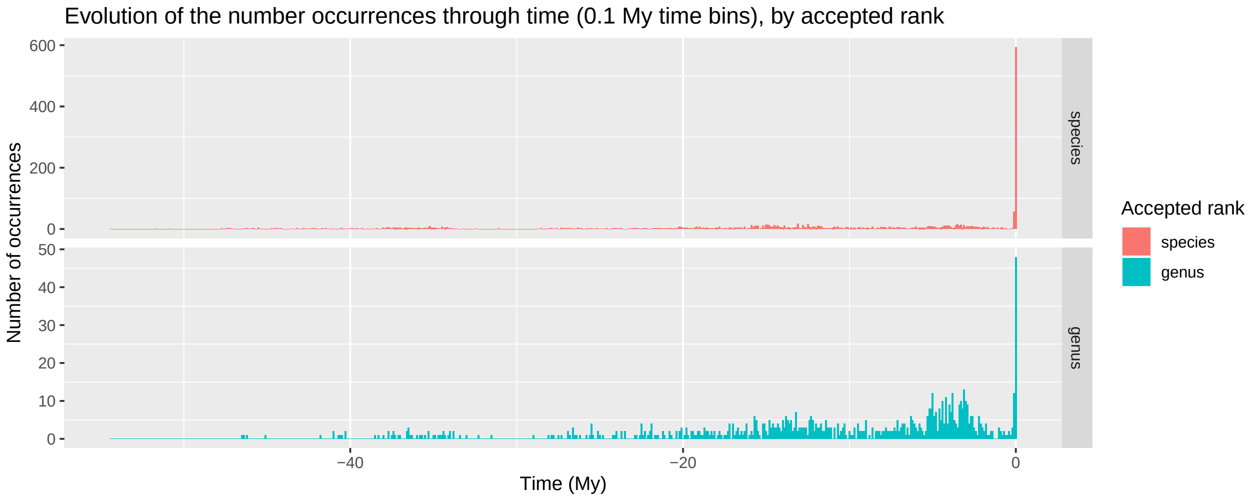


→ Half of the occurrences are identified at the level of the secies and 1/3 at the genus or family.

Some clades are unranked :

```
##
##   Chaeomysticeti          Neoceti Panphyseteroidea       Pelagiceti
##                26                2                1                1
##  Platanidelphidi       Squaloceti
##                 1                1
```

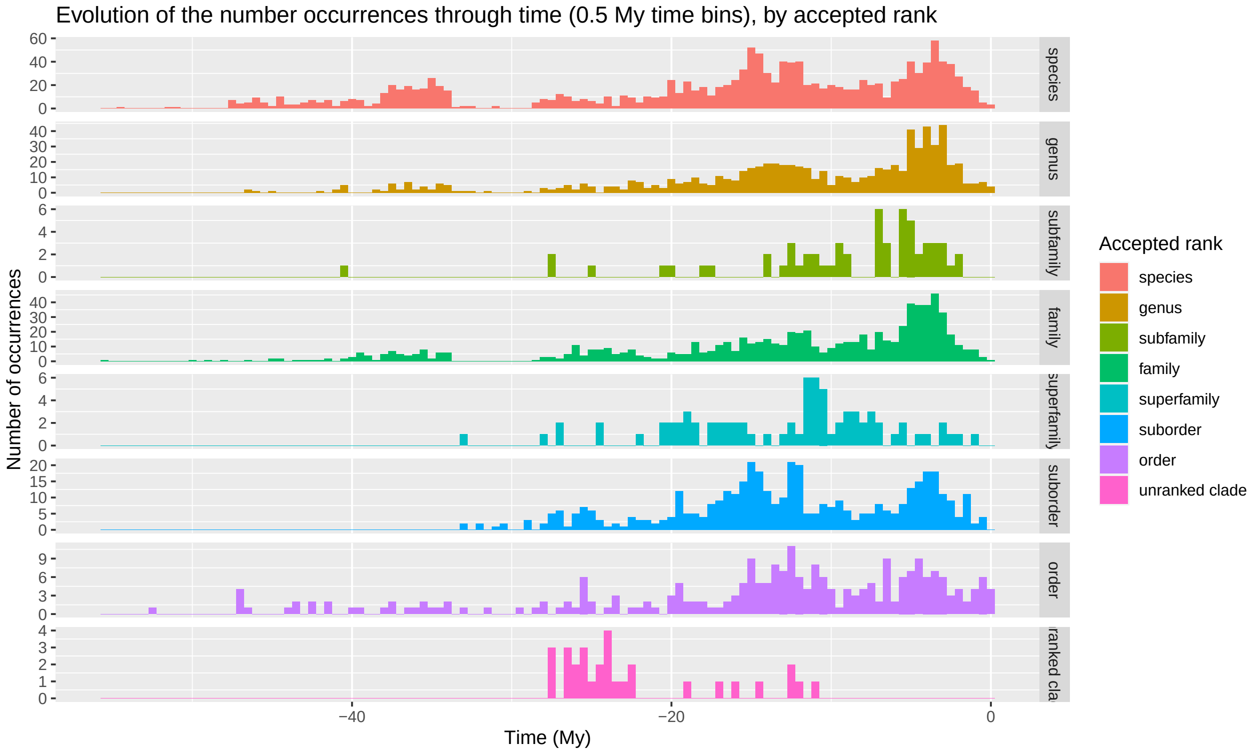
Time repartition by rank



→ Apparent huge cluster of occurrences in recent times, with very precise dating = Artefact due to the “Pull of the Recent” effect ?

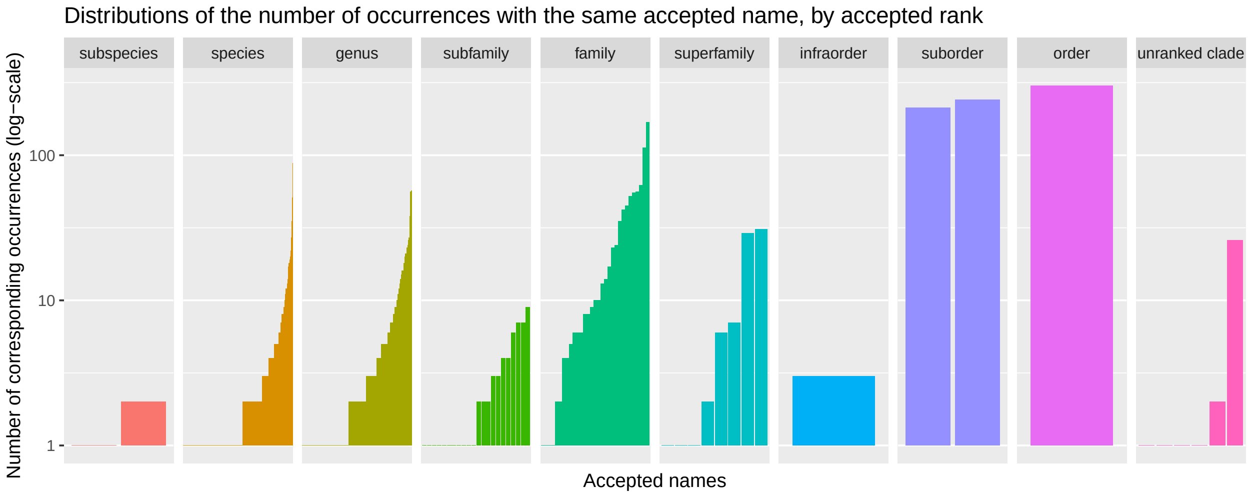
⟹ We decided to **remove all Late Pleistocene and Holocene occurrences** (thus setting the ω-sampling to 0) in order to avoid this bias.

```
##                          cetacea_pbdb Cetacea_occ removed
## Number of occurrences            4609        3804     805
```



→ We observe similar trends at each rank, with peaks at ~15My and ~5My.

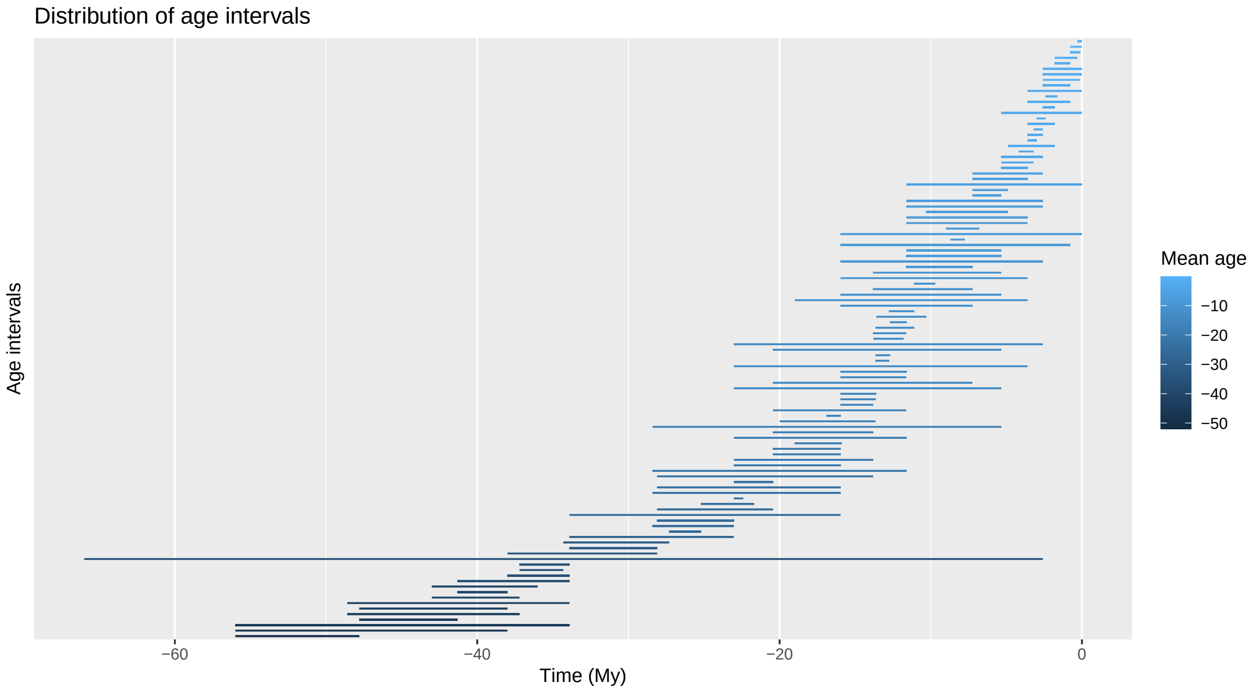
Redundancy of occurrences with the same accepted name



→ ~Half of species/genera/subfamilies have only one specimen by accepted name, but it could go up to ~50 within the same species and ~200 occurrences within the same suborder. **In our model all species are upposed to have the same abundance (identical sampling rates among branches), so those huge differences will have to be mitigated.** See later for a quantification of this discrepancy.

⟹ Our goal now will be to correct this abundance bias.

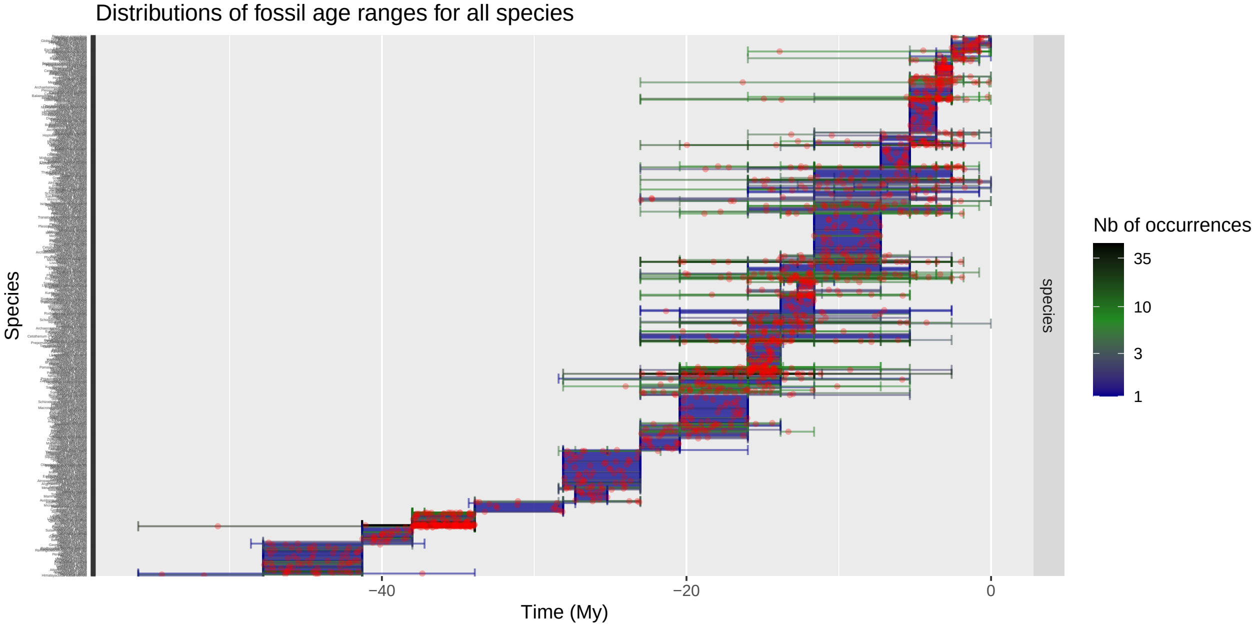
Time intervals = stratigraphic age uncertainty (minimum and maximum ages)

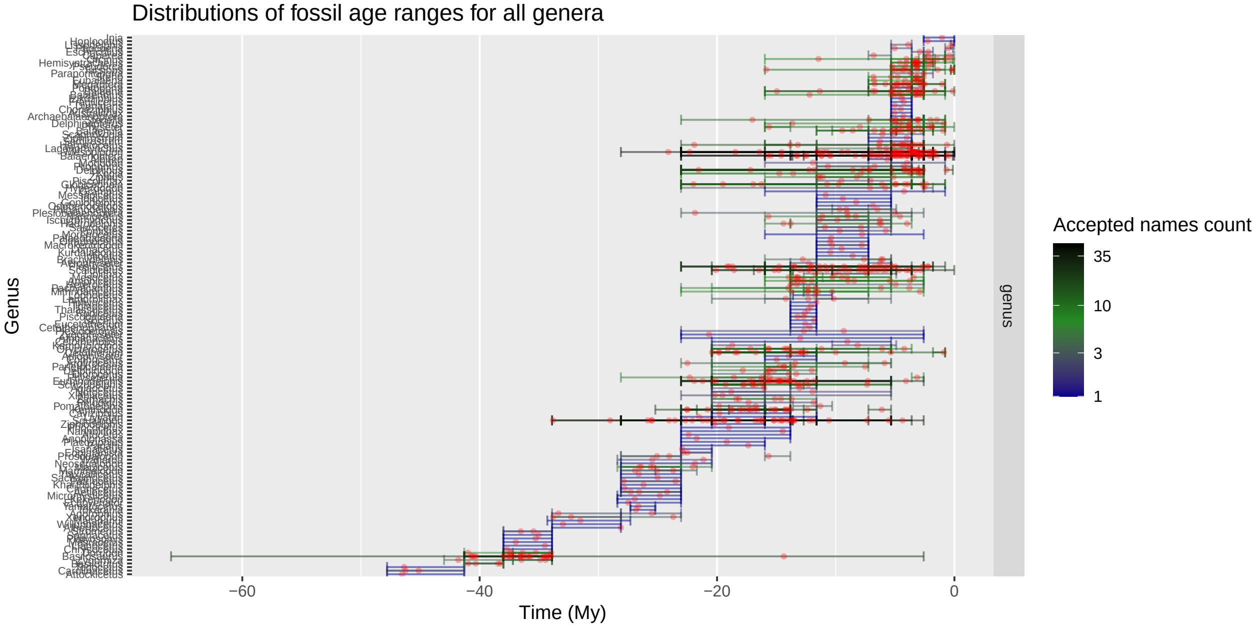


Time ranges = duration of the time intervals (maximum age - minimum age)

Count occurrences by accepted name

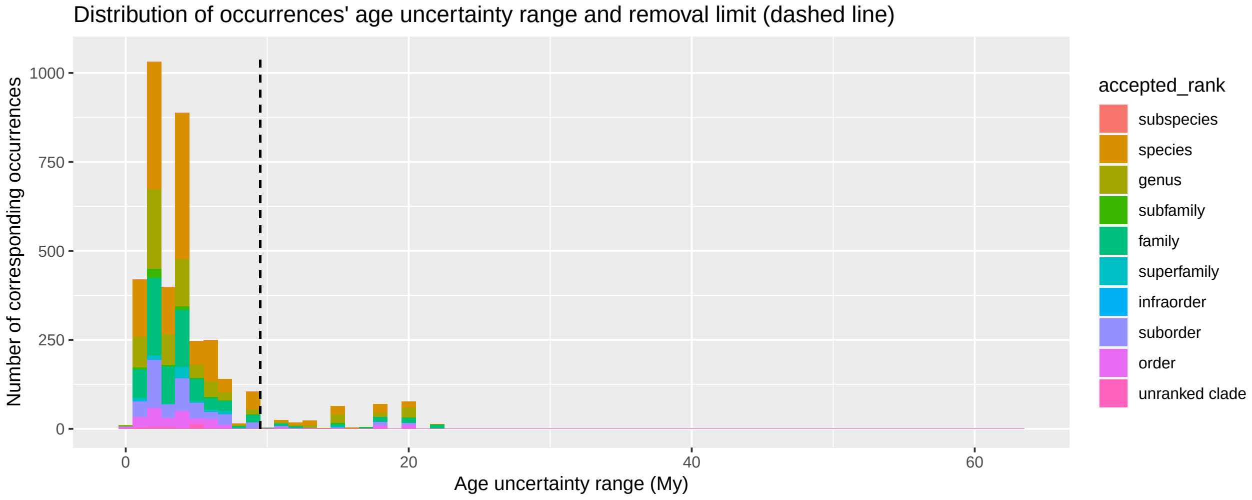
Count the number of occurrences with the same accepted name


Distributions of fossil age ranges for all species


Distributions of fossil age ranges for all genera

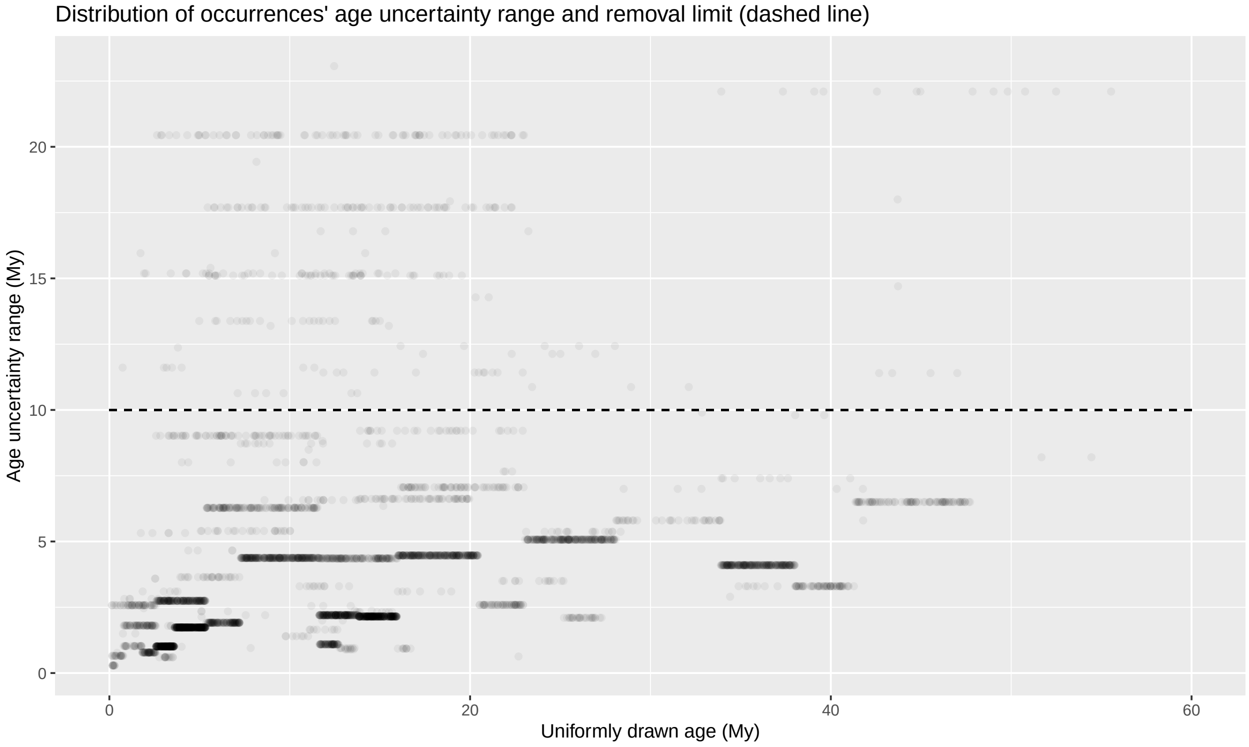
→ Some occurrences have too much age uncertainty (unrelated to species longevity in extreme cases like the one spanning 60My), they risk to artificially increase species durations.

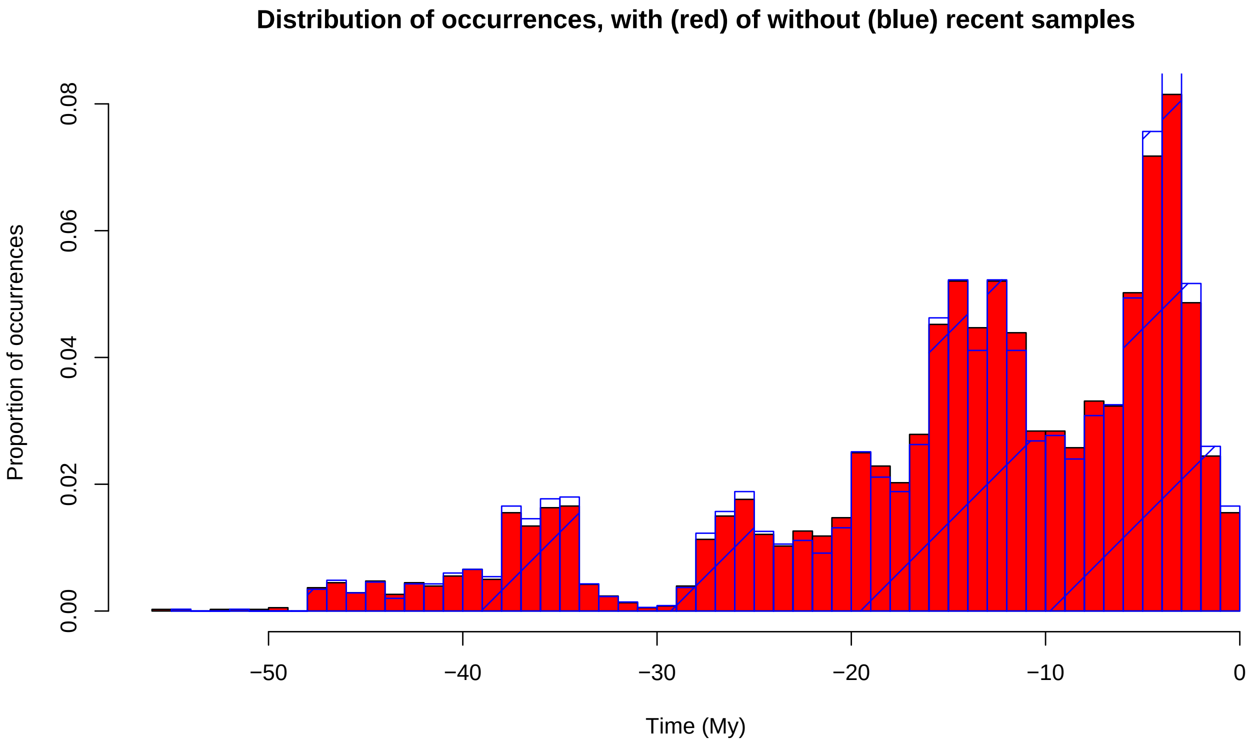
Remove occurrences with highly uncertain dating (range > 10My)


Distribution of occurrences' age uncertainty range and removal limit (dashed line)

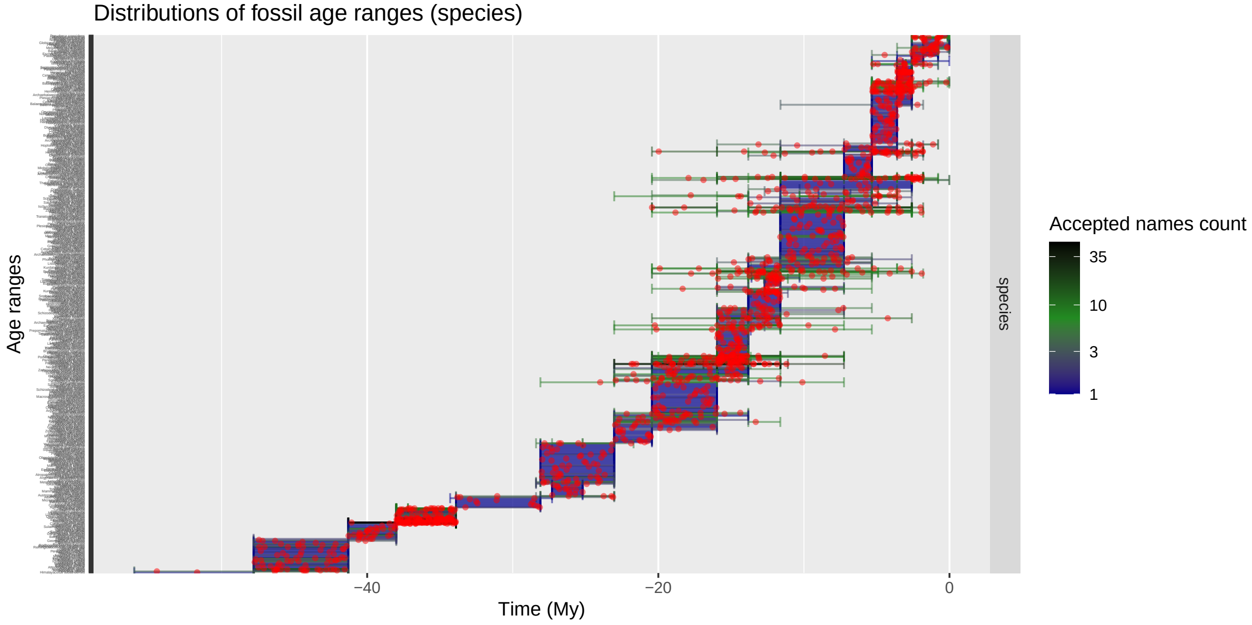
Most of occurrences show less than 10 My age uncertainty, let's keep only these ones.

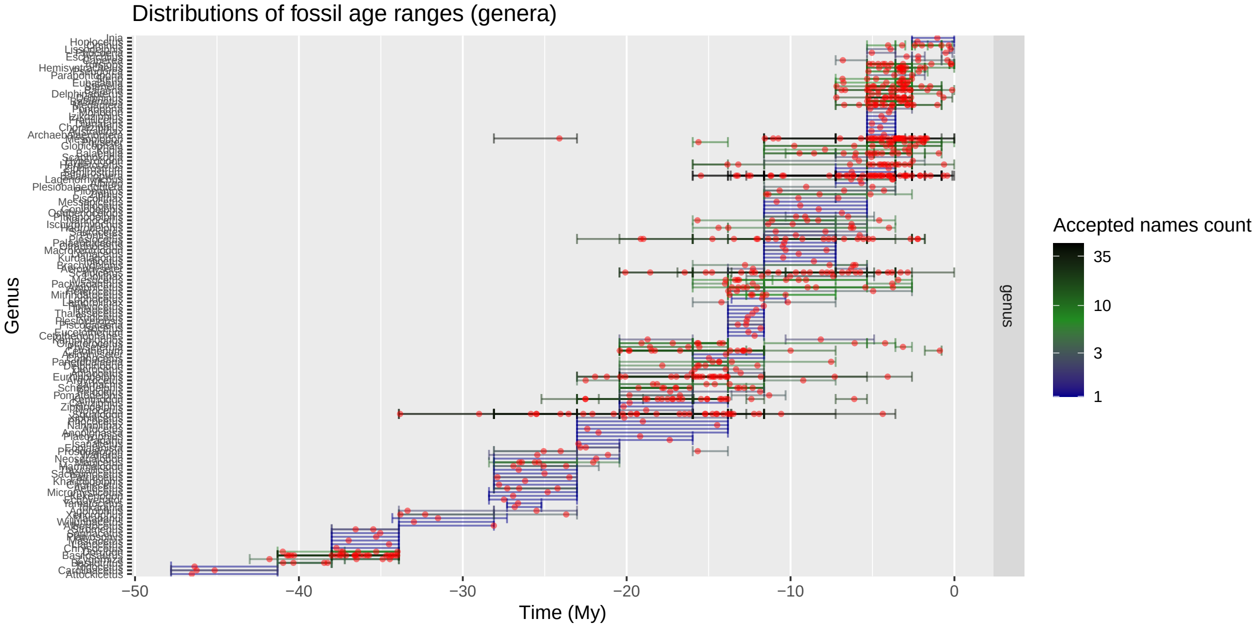
```
##                         all_ranges smaller_10My removed
## Number of occurrences         3804         3503     301
```


Distribution of occurrences' age uncertainty range and removal limit (dashed line)



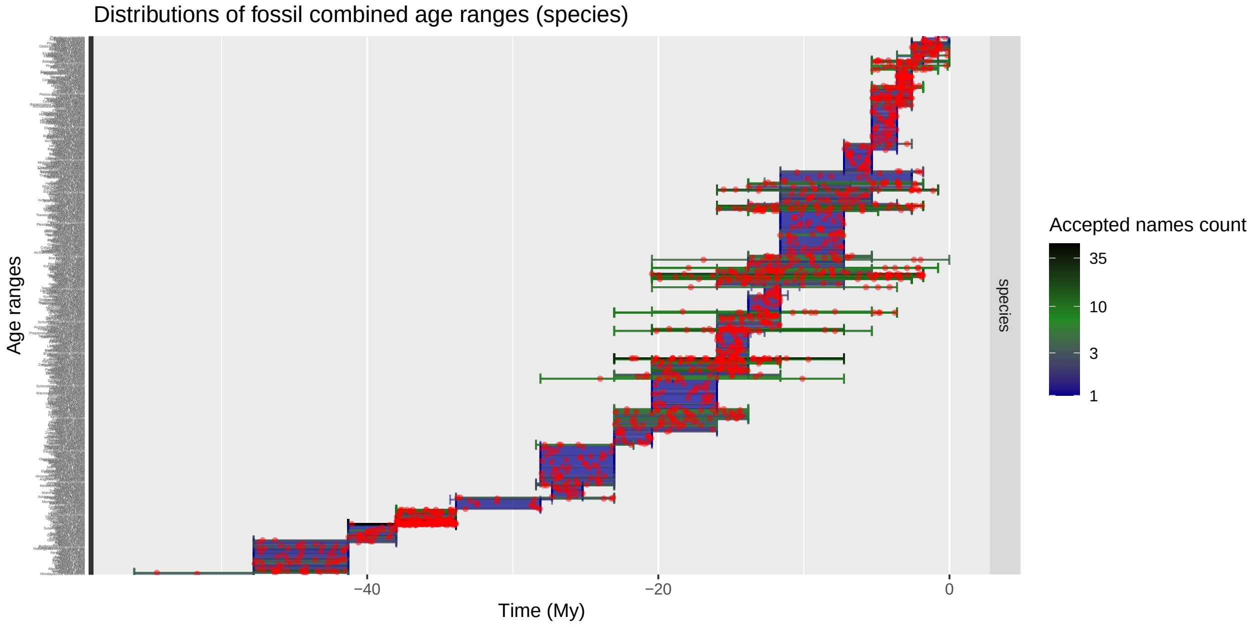
→ The removal of highly uncertain occurrences seems to be only a little biased, even if uncertainty globally increases with age.

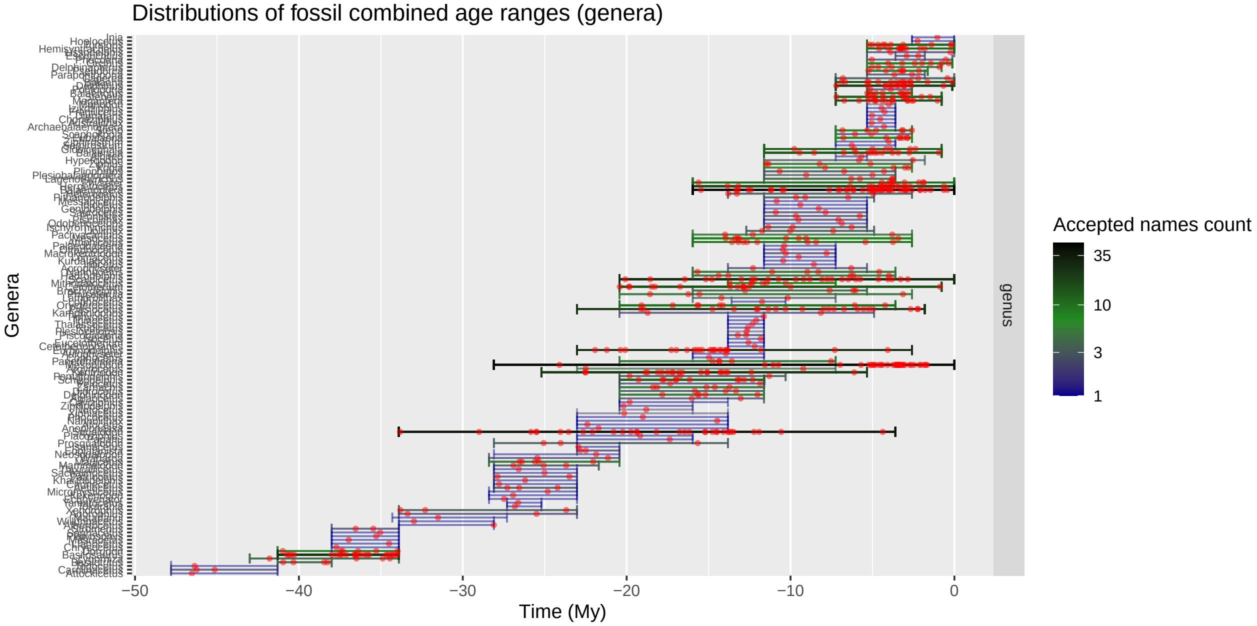




→ Some species (or other ranks) have several occurrences with several time ranges, **let's combine them into a unique range covering all the others**.

Combined time ranges = unique time range for occurrences with the same name (without the biggest ones)

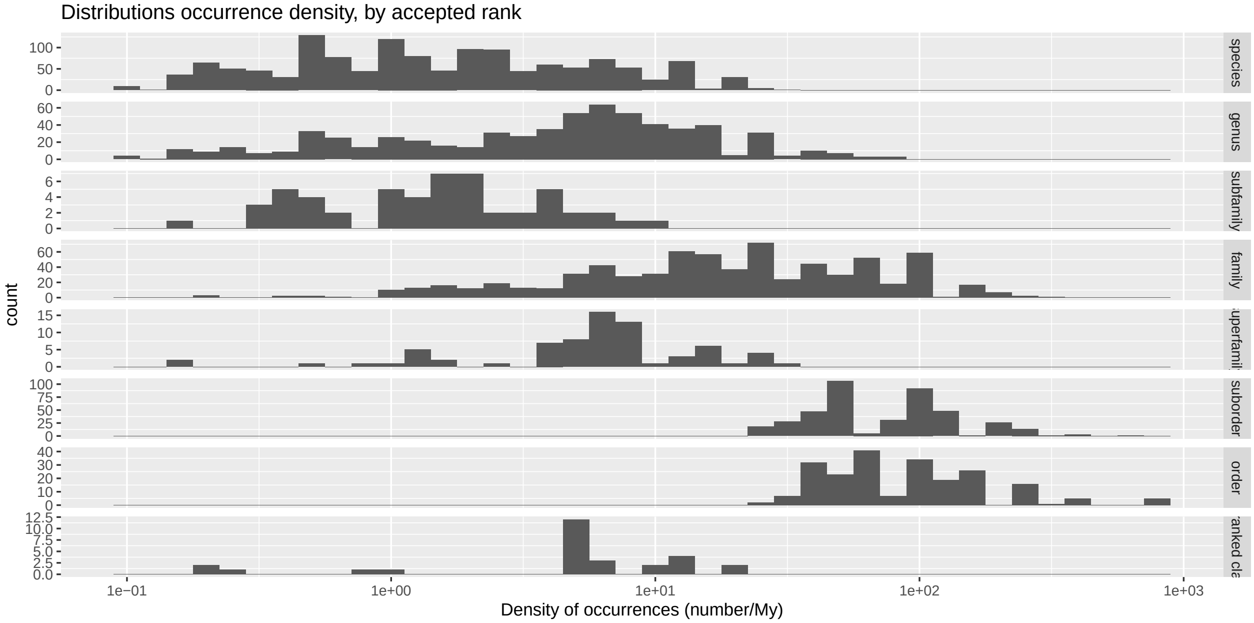




Occurrence density = number of occurrences by unit of time, in the stratigraphic interval of a taxon

Density distributions

Plot the density of occurrences for each taxonomic rank, and highlight the role

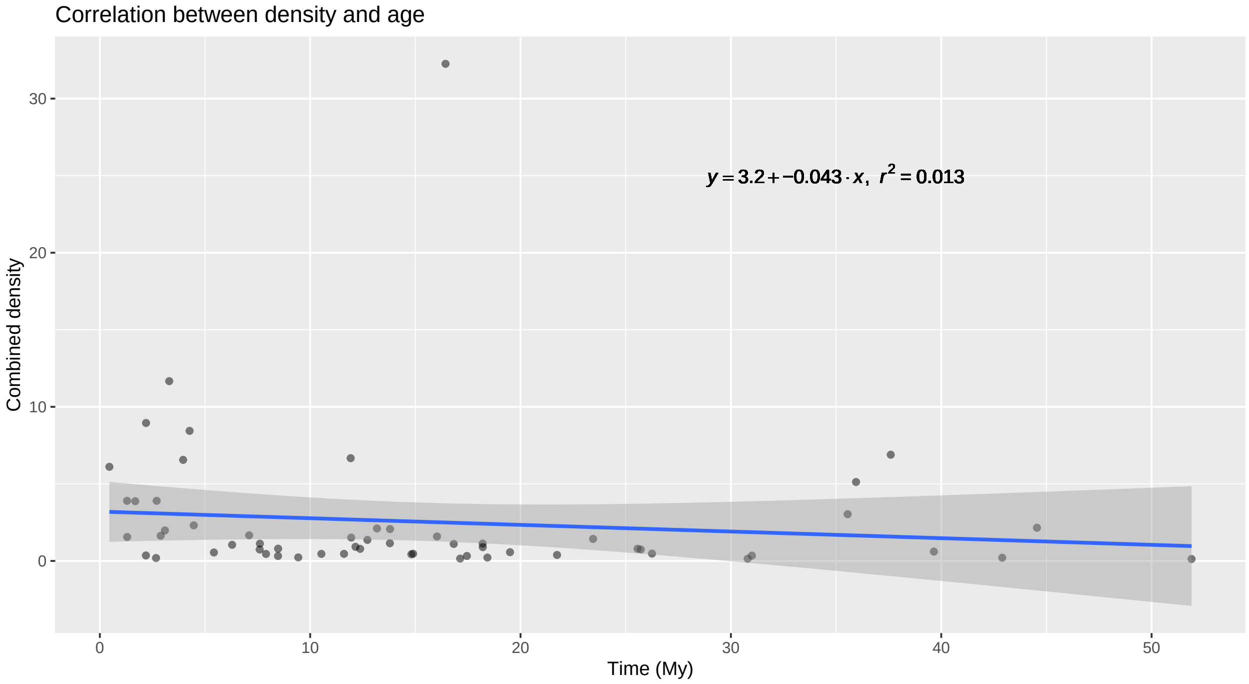


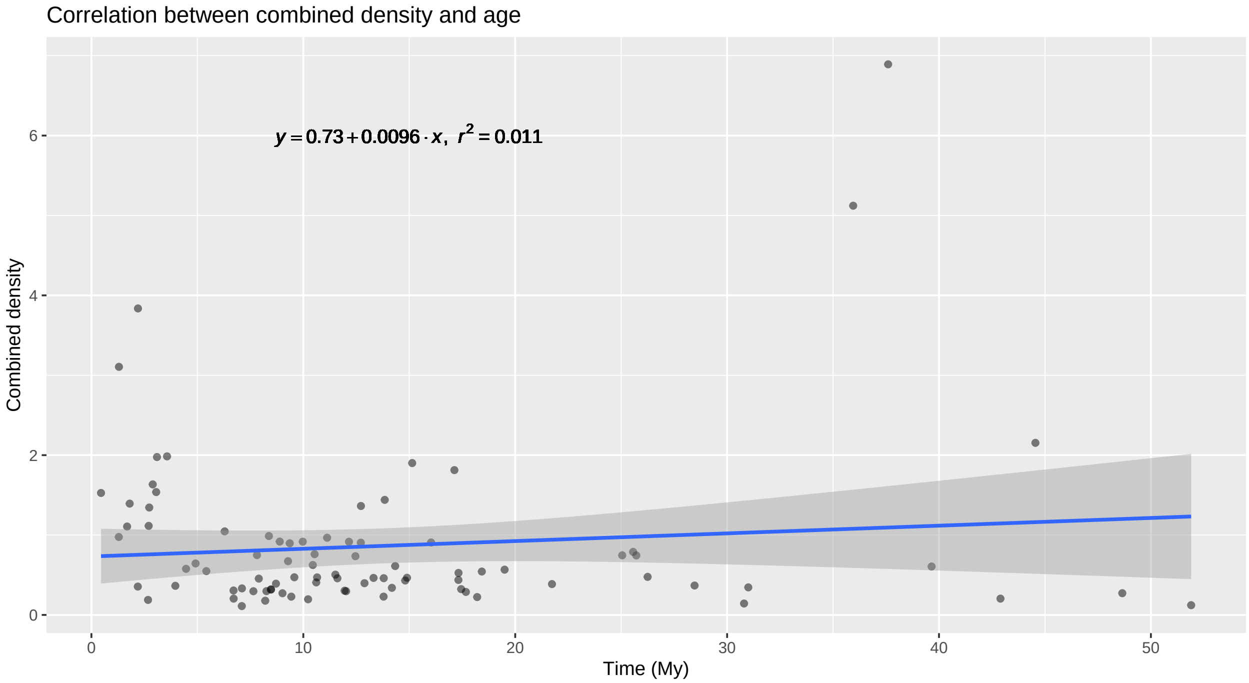
→ Density logically increases with taxa ranks, but the distributions for species and genera dramatically spread over two orders of magnitude.

Correlation between time range and age

If we want to correct species abundance differences based on the density of occurrences in the age interval, those factors should not depend on time in order to avoid penalizing periods with higher densities.

Let's compare the occurrence densites computed with the initial time ranges and the *combined densities* computed with the combined ranges.





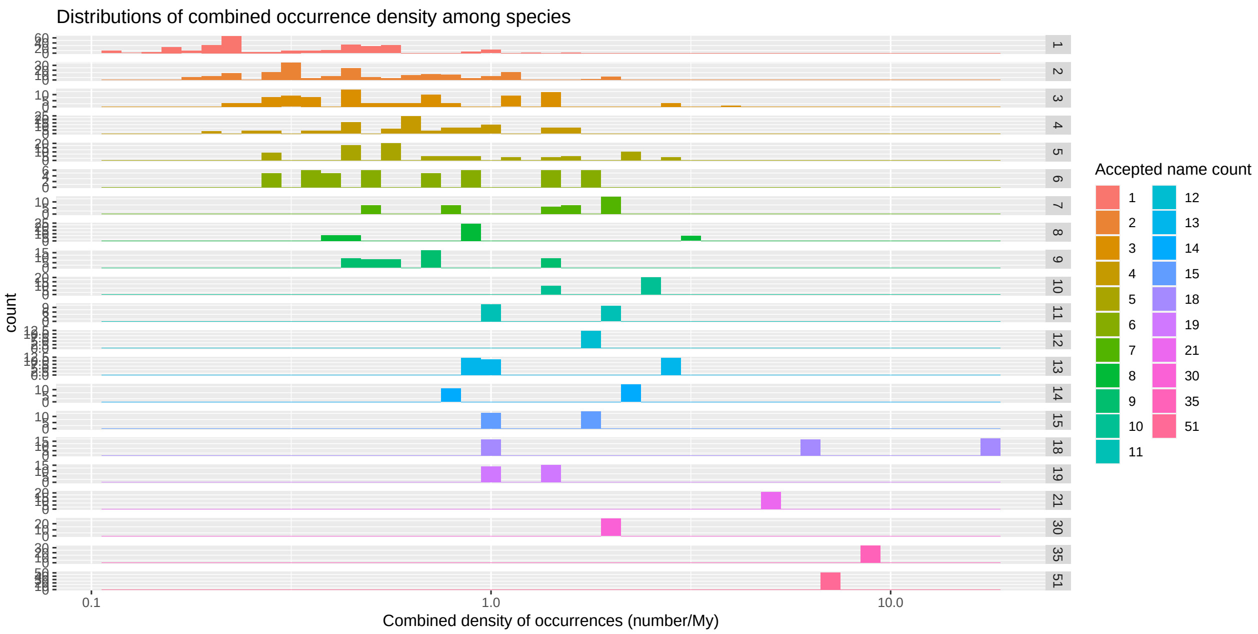
→ The density based on combined ranges seems less time-dependant than the density based on initial time ranges. We will therefore use the combined density for our corrections.

Subsampling occurrences by homogenizing the combined occurrence density

Subsampling by homogenization = reducing the discrepancy between high and low occurrence densities among taxa by subsampling preferencially the densest ones.

Compare densities by accepted name count (species only)

Let's focus now on the occurrences accepted at the species level because they are the one for which we can correct the abundance bias by subsampling the most concentrated combined intervals.



→ Their is a huge span of densities driven by the number of occurrences for the same species that we can reduce by subsampling the most concentrated intervals.

Impact of correcting subsampling on density distributions (species only)

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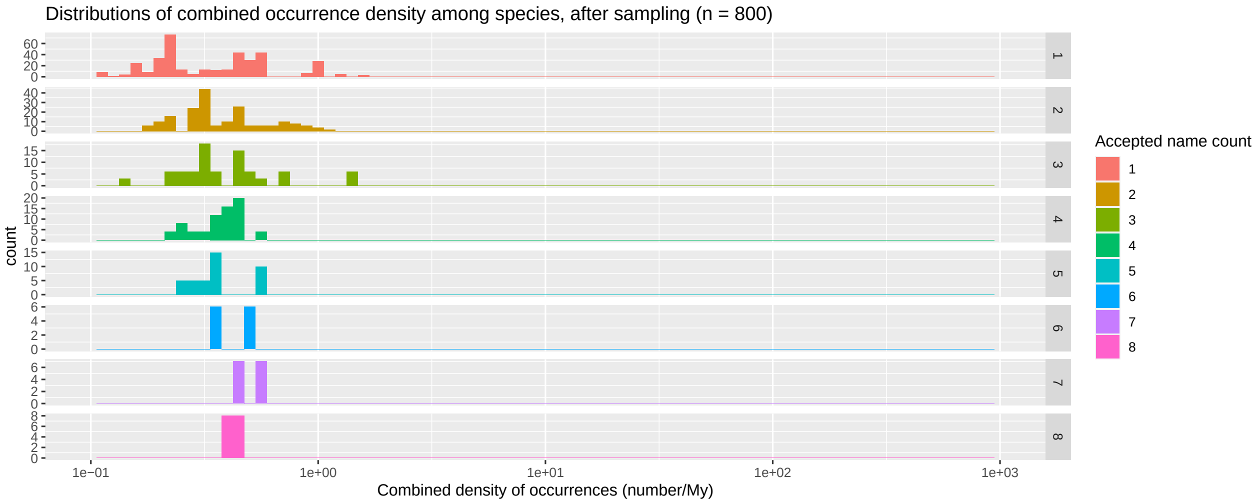
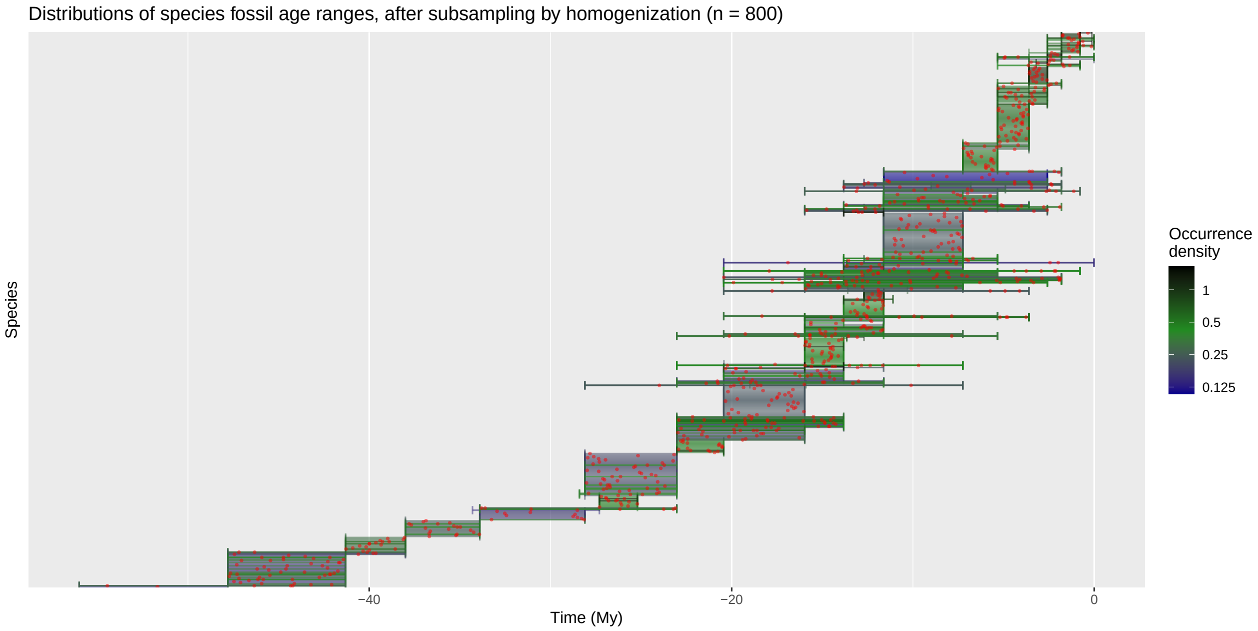
```



→ Subsampling by homogenization successfully reduces the density span from 2 to 1 order of magnitude.

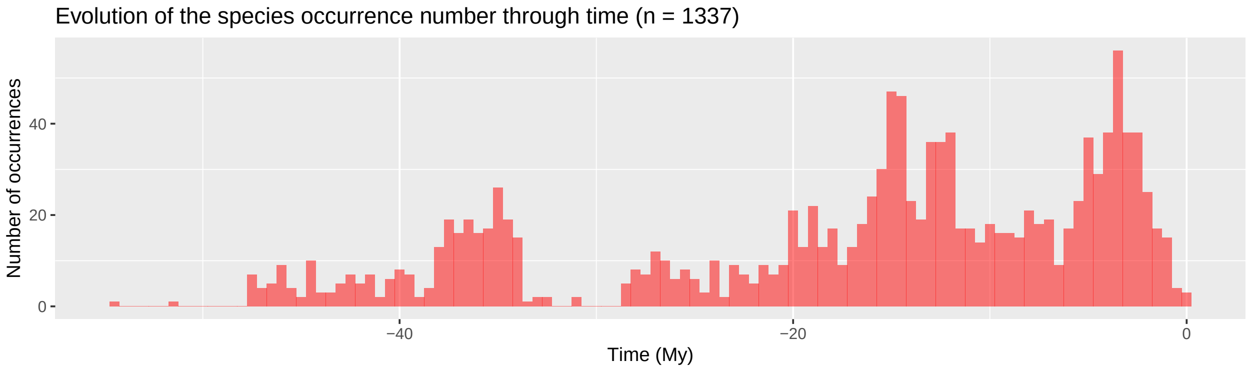
Impact of subsampling on occurrences repartition (species only)

See what our distributions look like after subsampling :

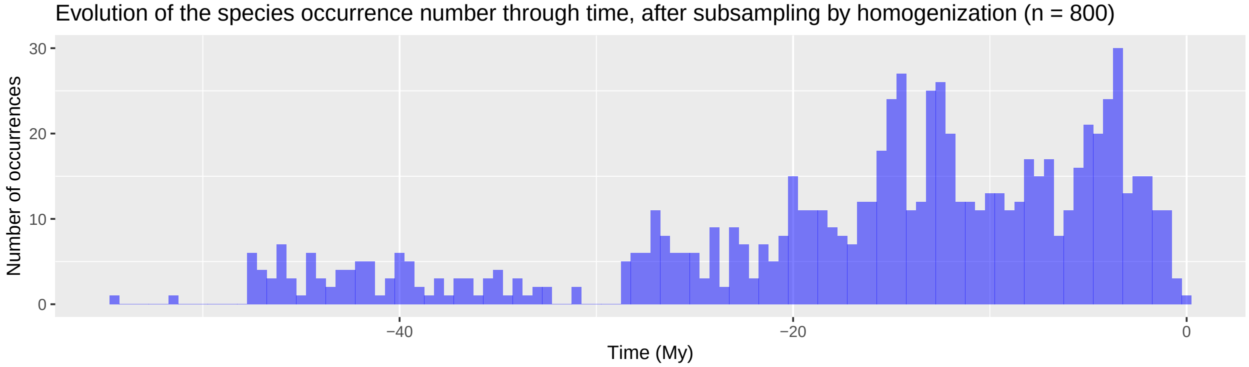


Distributions of species fossil age ranges, after subsampling by homogenization (n = 800)

→ Some highly dense cluster became much more similar to the others.

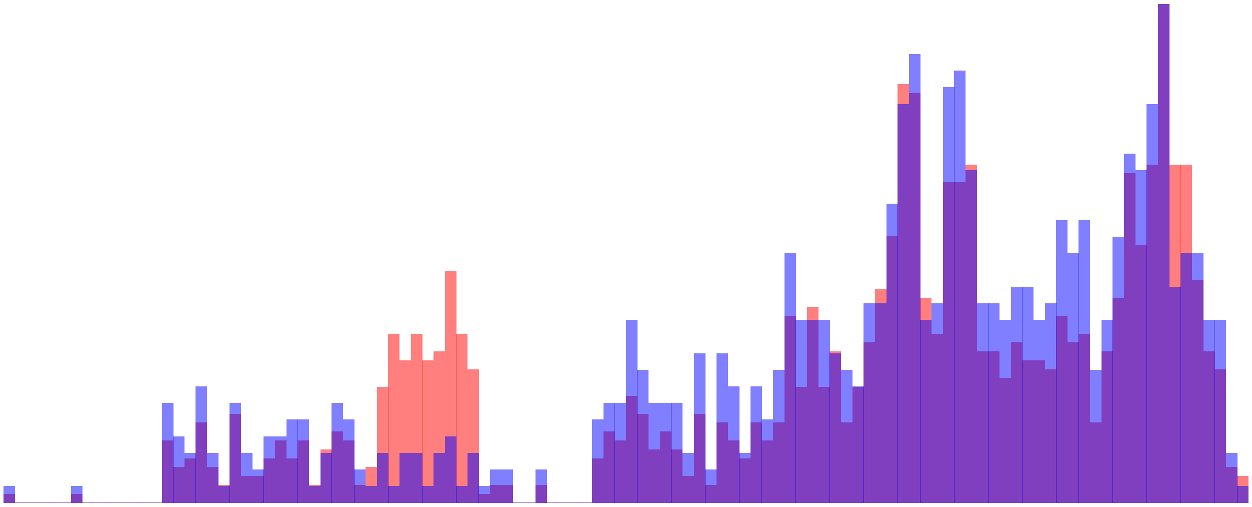


Evolution of the species occurrence number through time (n = 1337)



Evolution of the species occurrence number through time, after subsampling by homogenization (n = 800)

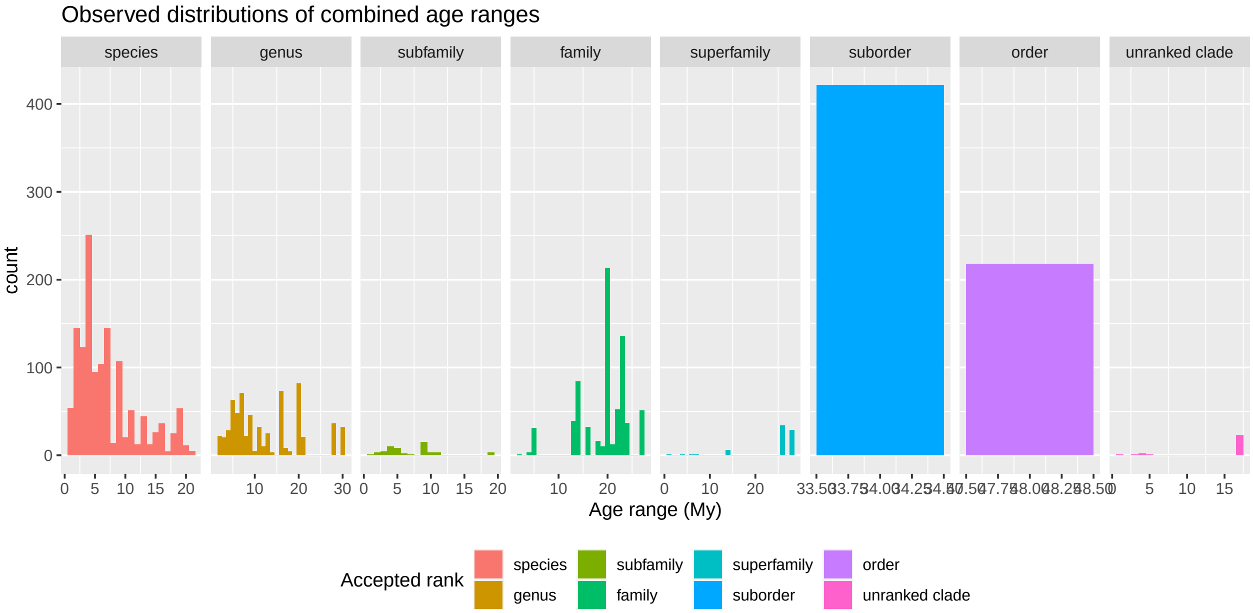
If we superpose these 2 plots :

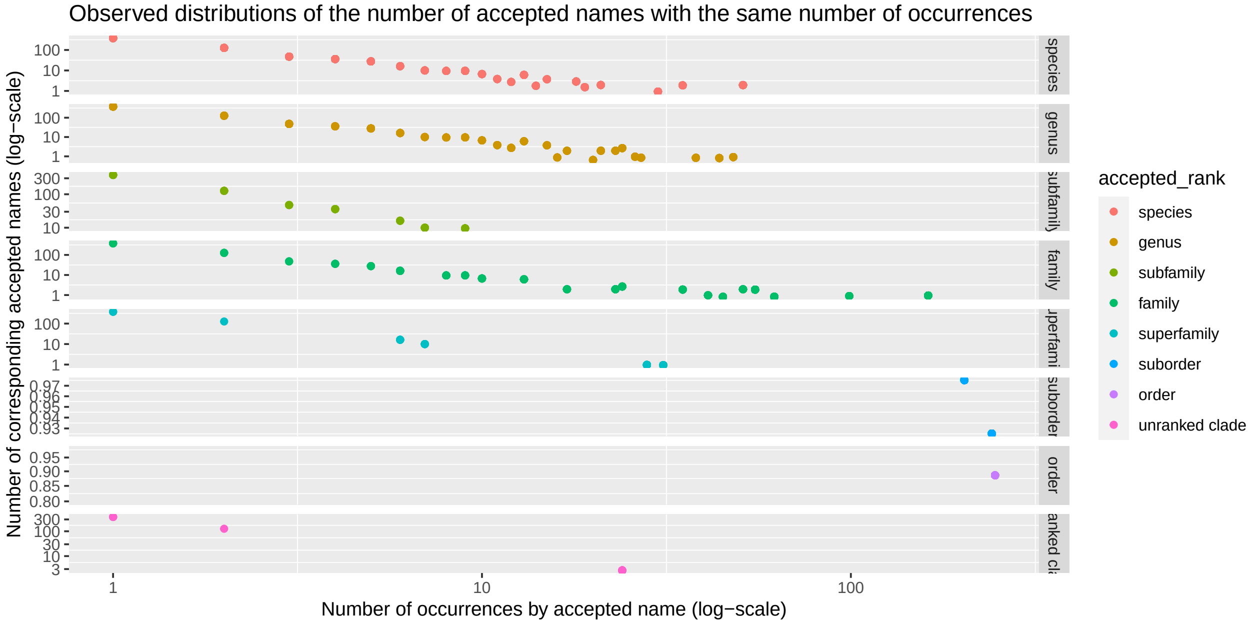


→ We get the new species occurrence repartition after subsampling, that could be used for doing inference with the occurrence birth-death model.

Compare with a Poisson sampling process

In order to check if the data fit our assumptions of constant-fossilisation-rate Poisson sampling we compare the observed occurrences distributions with the expected ones. Specifically, we will look at the number of taxa represented by 1, 2, 3, … occurrences and the one that we would expect for a given distribution of combined age ranges (seen here as a proxy for species duration).





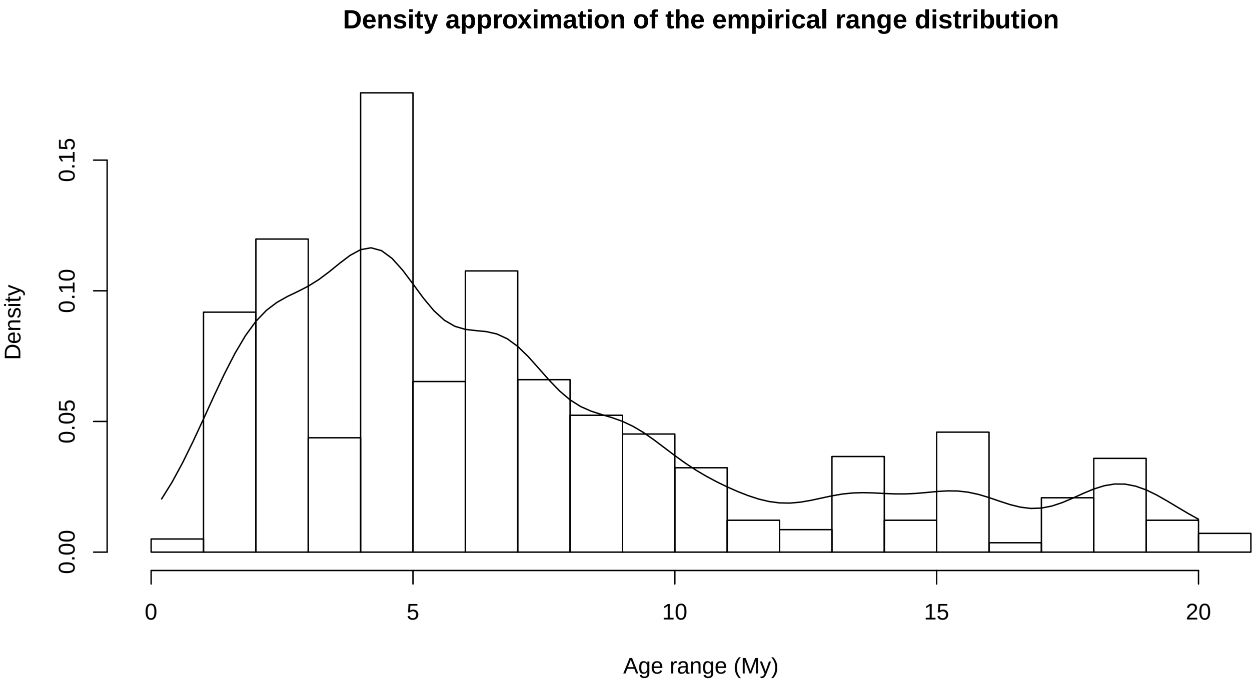
In a Poisson process with occurrence sampling rate ω and for a given time interval of length t, the probability of observing $N_t = k$ occurrences is given by the Poisson distribution of mean of parameter $\omega \times t$:

$$\mathbb{P}(N_t = k) = e^{-\omega t}\frac{(\omega t)^k}{k!}$$

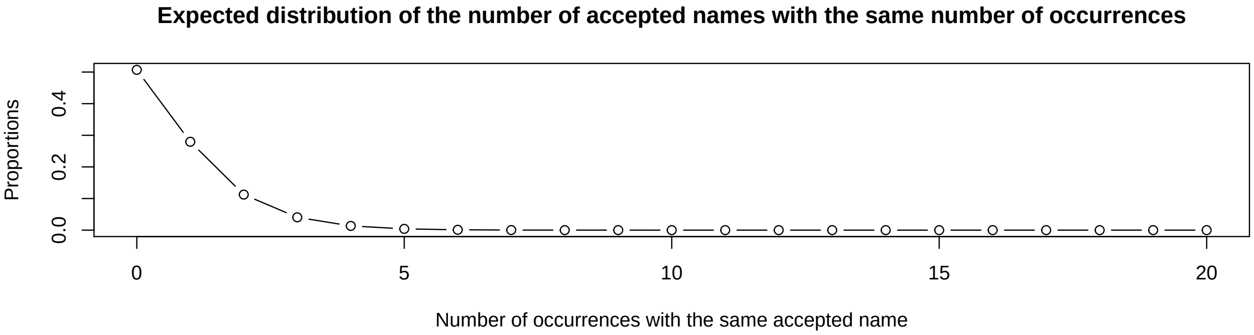
So in order to have the absolute probability of observing $N_0 = n$ occurrences we have to integrate over the full distribution of age ranges t, called $f(t)$:

$$\mathbb{P}(N_0 = n) = \int_t P(N_t = n)f(t)dt = \int_t e^{-\omega t}\frac{(\omega t)^n}{n!}f(t)dt$$

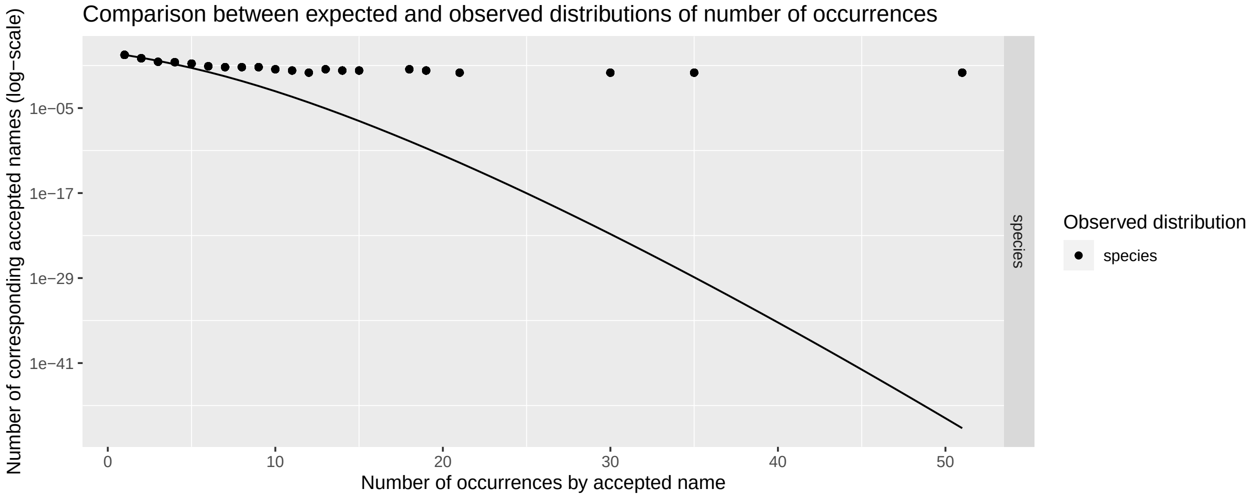
First, approximate this distribution :

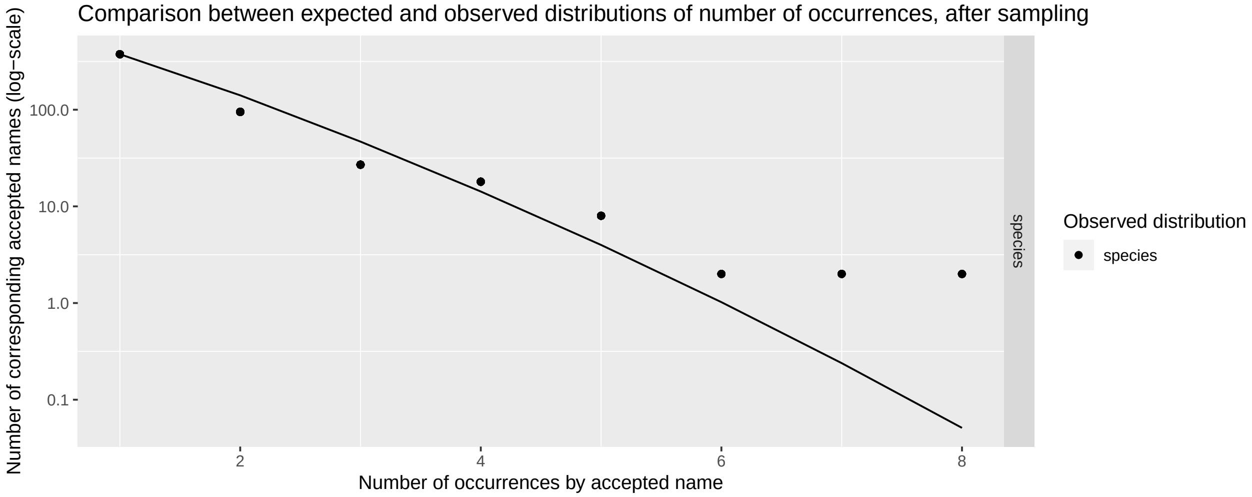


Then integrate and plot the expected distribution for a given omega :



Finally, try to find an ω value that approximately fits the first points (the least affected by oversampling biases) and check if the other points follow the expected curve :





⟹ Initial observations really do not fit the expectations, **species with more than 5 occurrences must remain very rare** ! But our subsampling seems to correct most of this bias.

However, this method requires to make several arbitrary choices that may introduce new biases so we will instead subsample at other levels (palaeontological collection, geological formation). In each case only one occurrence will be sampled for the similarly identified, a process we will refer to as **aggregating** these occurrences according to the chosen factor.

Subsampling occurrences by aggregating similarly identified occurrences in each collection

Subsampling by aggregation = aggregate all the occurrences of a given taxon according to a given criterium (collection, geological formation, country, geological plate).

Aggregate similarly identified occurrences in each collection

In order to reduce the abundance bias, we may keep only one occurrence for each collection :

```
##                                       Cetacea_occ Cetacea_occ_aggreg removed
## Number of occurrences                        3804               3556     248
## Number of occurrences (species only)         1436               1363      73
```

→ Not enough occurrences are removed to make a sufficient difference. If we look at the collection with the highest number of occurrences :

```
##
##         Aprixokogia kelloggi                      Balaena
##                            1                            2
##   Balaenoptera acutorostrata              Balaenopteridae
##                            2                            2
##                    Balaenula      Bohaskaia monodontoides
##                            2                            1
##               Cetotheriinae               Delphinapterus
##                            1                            3
##                 Delphinidae                    Delphinus
##                            2                            2
##                 Globicephala          Gricetoides aurorae
##                            2                            1
##                Herpetocetinae       Herpetocetus sendaicus 
##                             1                            1 
## Herpetocetus transatlanticus              Kogia breviceps 
##                             1                            1 
##                     Kogiidae                     Kogiinae 
##                             1                            2 
##          Kogiopsis floridana               Lagenorhynchus 
##                             1                            2 
##     Lagenorhynchus harmatuki                    Megaptera 
##                             1                            2 
##      Mesoplodon longirostris                      Monodon 
##                             2                            1 
##     Ninoziphius platyrostris                Orycterocetus 
##                             3                            1 
##       Physeter macrocephalus                Physeteridae 
##                             1                            1 
##                 Physeterinae          Physeterula dubusi 
##                             2                            1 
##                  Plesiocetus        Pliopontos littoralis 
##                             1                            1 
##                   Pontoporia                Pontoporiidae 
##                             1                            2 
##                    Pseudorca                 Scaldicetus 
##                             2                            1 
##                      Stenella                Stenella rayi 
##                             2                            1 
##                     Tursiops          Ziphius cavirostris 
##                             2                            2 
```

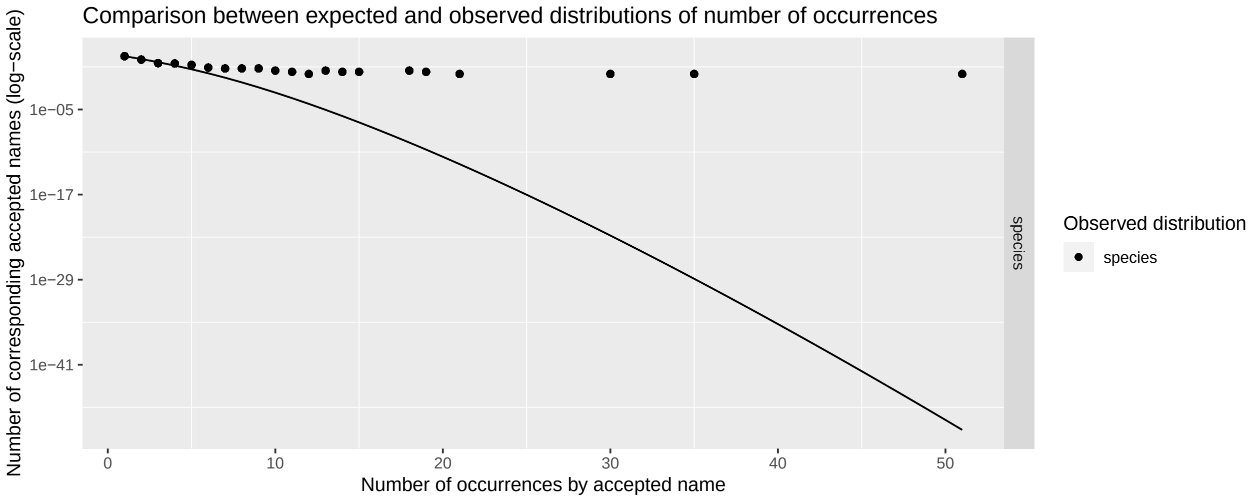
→ There are very few redundancies among the accepted names in collections so aggregating those won't reduce the abundance bias.

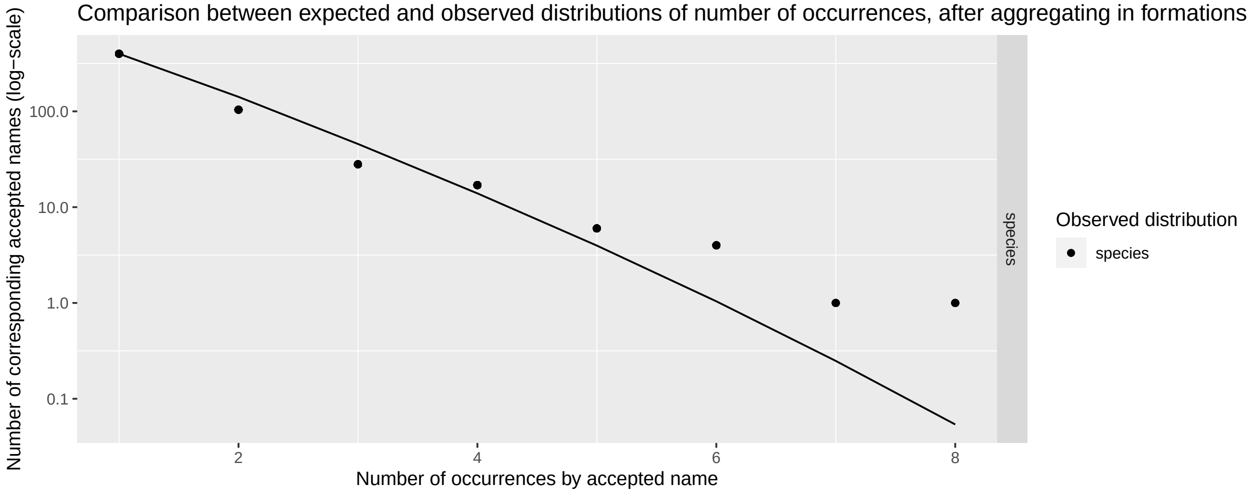
Instead, we may try to **aggregate occurrences with the same accepted name at the level of the geological formation** (ie subsample only one for each).

Aggregate similarly identified occurrences in each formation

```
##                                      Cetacea_occ Cetacea_occ_aggreg removed
## Number of occurrences                       3804               1980    1824
## Number of occurrences (species only)        1436                828     608
```

→ In that case the sub-sampling is big enough to hope correcting our bias.





→ The initial bias is mostly corrected.

```
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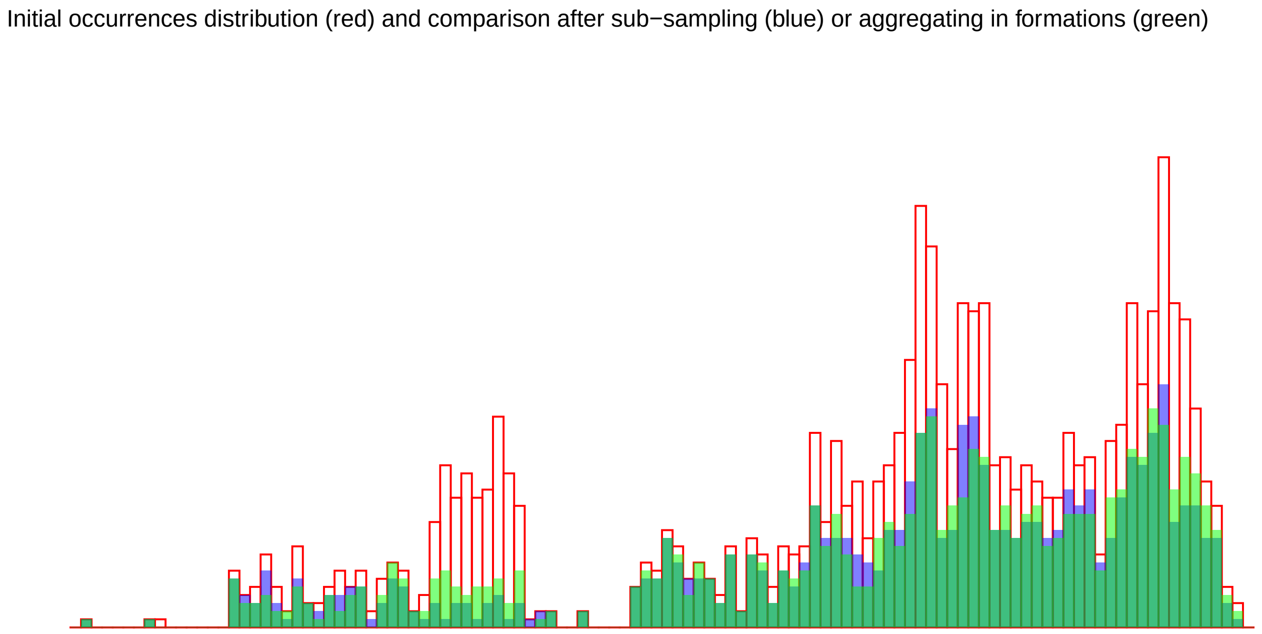
## Warning: Removed 2 rows containing missing values (geom_bar).
```


Initial occurrences distribution (red) and comparison after sub−sampling (blue) or aggregating in formations (green)

→ Comparing with the initial occurrences distribution and with the distribution after our first sub-sampling it appears that both methods lead to very similar distributions. This conforts us about the robustness of those approaches.

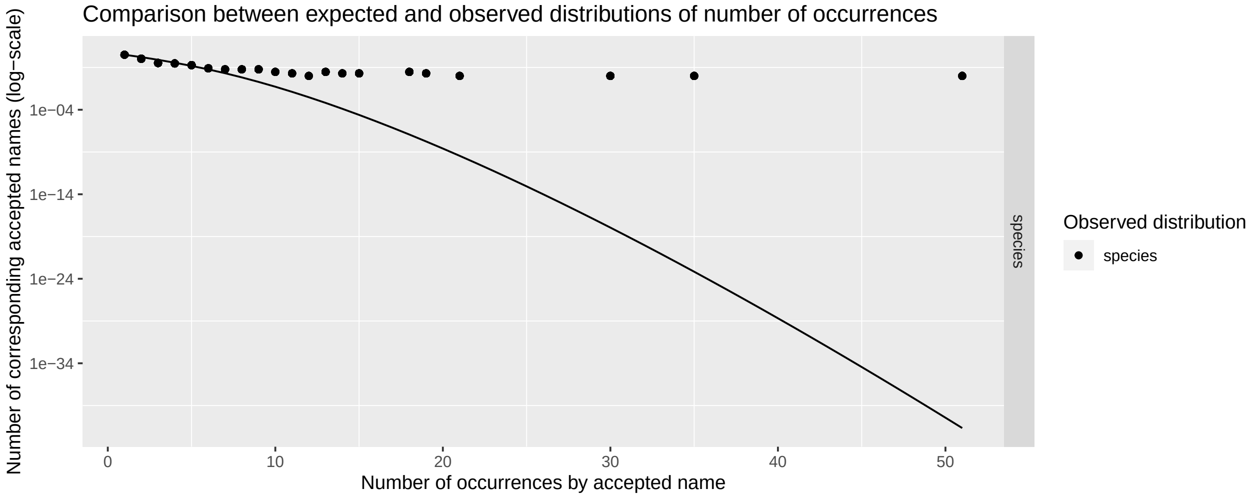
However, we have to take into account the occurrences that do not have any indicated geological formation to subsample them separately.

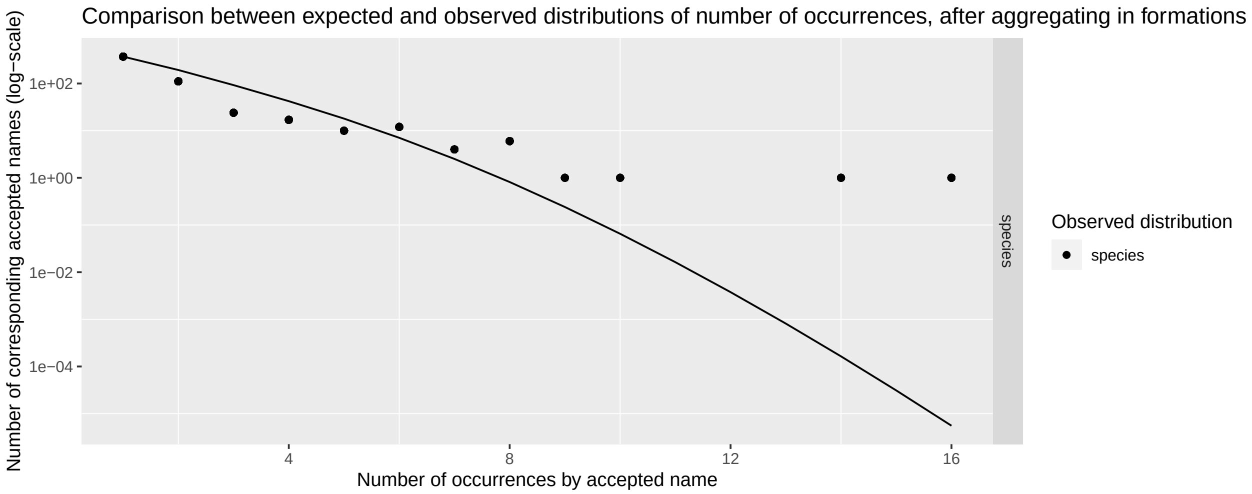
Aggregate occurrences without formation by country + early interval

To approximate geological formation we chose to proceed to the aggregation based on the combination of the country and the early stratigraphic interval.

```
##                                         Cetacea_occ Cetacea_occ_aggreg removed
## Number of occurrences                          3804               2642    1162
## Number of occurrences (species only)           1436                981     455
```

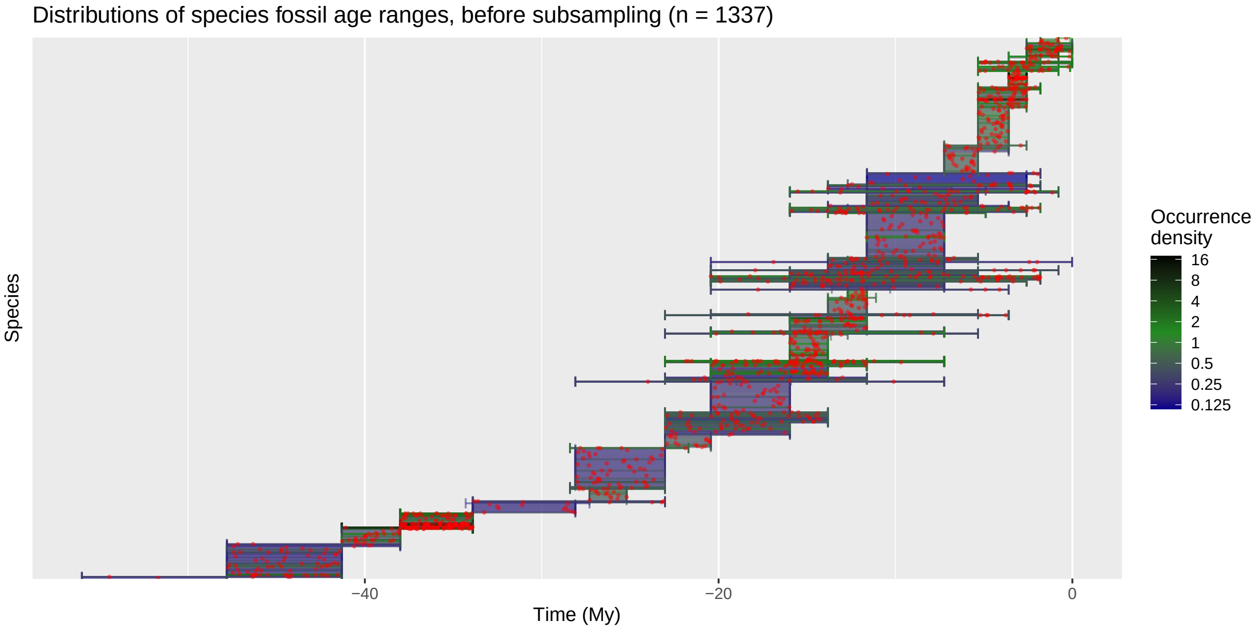
More occurrences remain after aggregating with this new method. Let's compare again with the theoretical distribution :

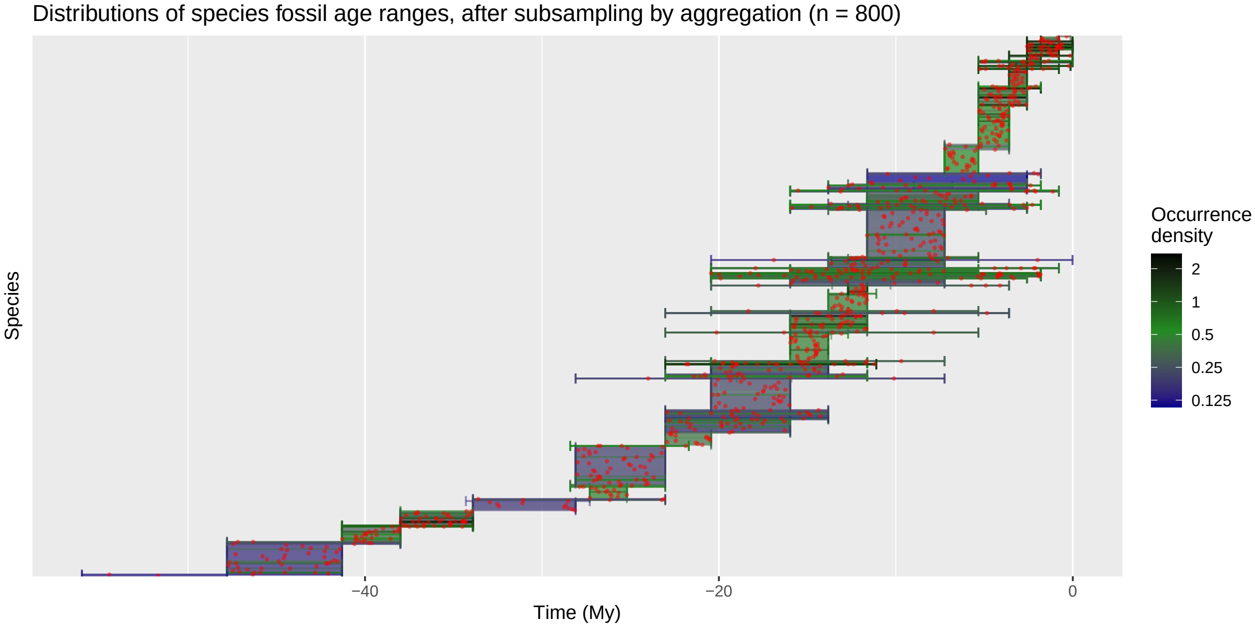

Comparison between expected and observed distributions of number of occurrences



→ The correspondance is still good, except for two taxa :

```
##
##    Scaldicetus grandis Schizodelphis sulcatus
##                     14                     16
```





```
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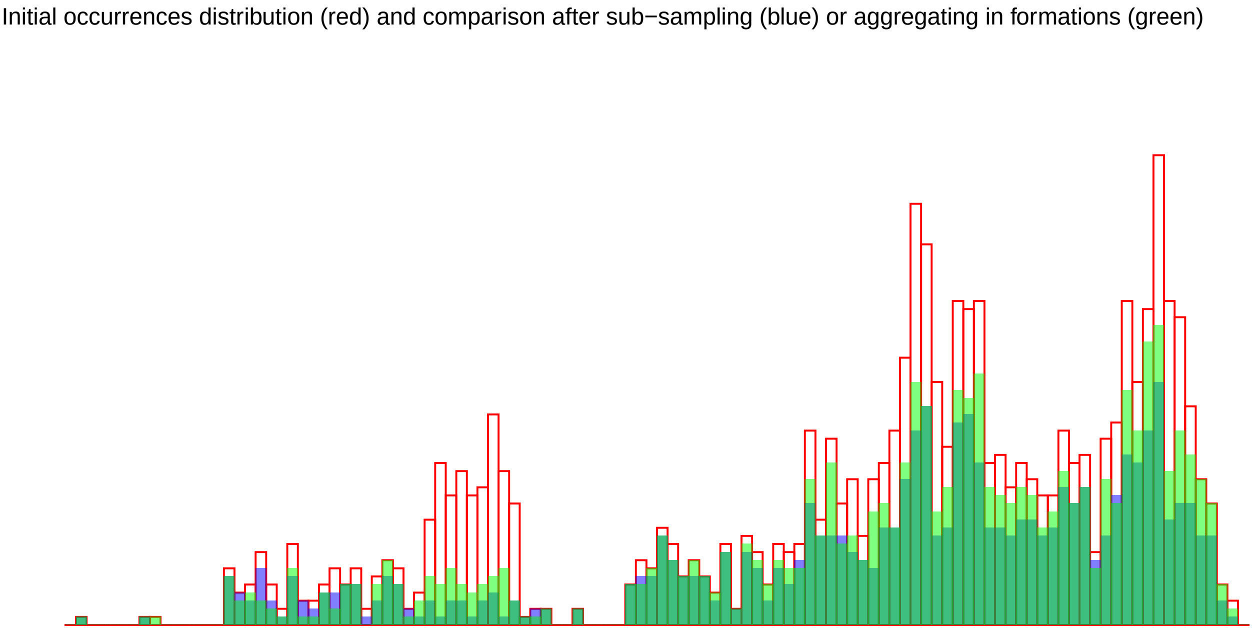

```
## Saving 10 x 5 in image

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```

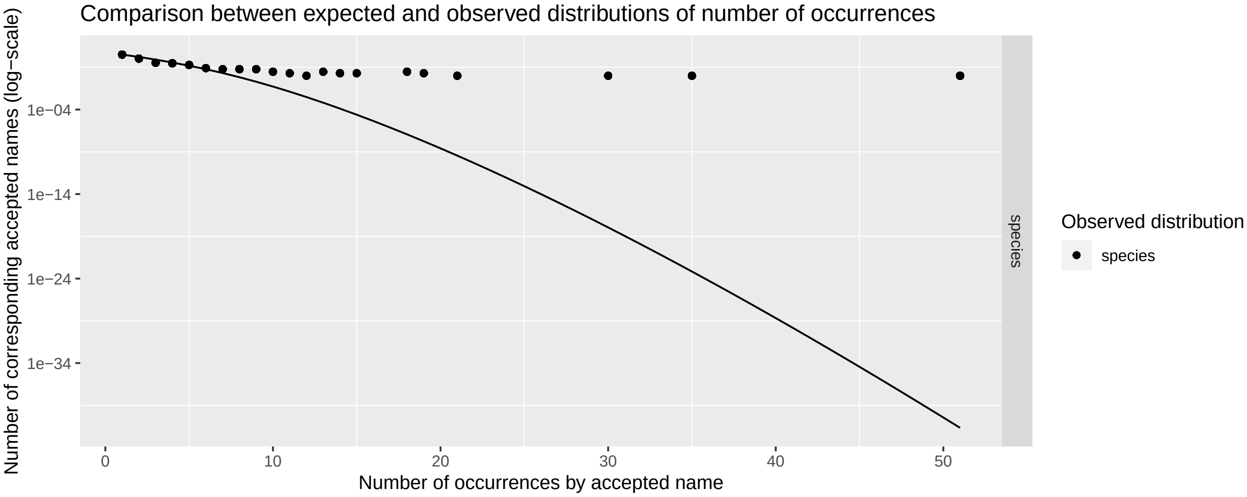
→ Comparing with the initial occurrences distribution and with the distribution after our first sub-sampling it appears that both methods lead to very similar distributions. This conforts us about the robustness of those approaches.

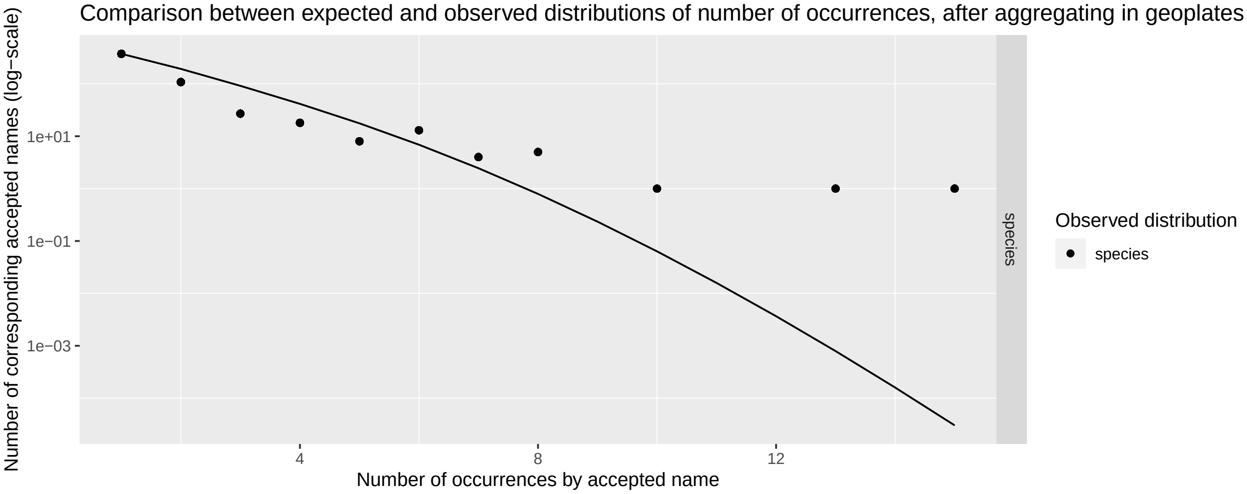
Replacing coutries by gelogical plates seems to make more sens from a palaeontological perspective, so let's try it.

Aggregate occurrences without formation by geoplate + early interval

```
##                                          Cetacea_occ Cetacea_occ_aggreg removed
## Number of occurrences                           3804               2606    1198
## Number of occurrences (species only)            1436                967     469
```

More occurrences remain after aggregating with this new method. Let's compare again with the theoretical distribution :





→ The correspondance is still good, except for two taxa :

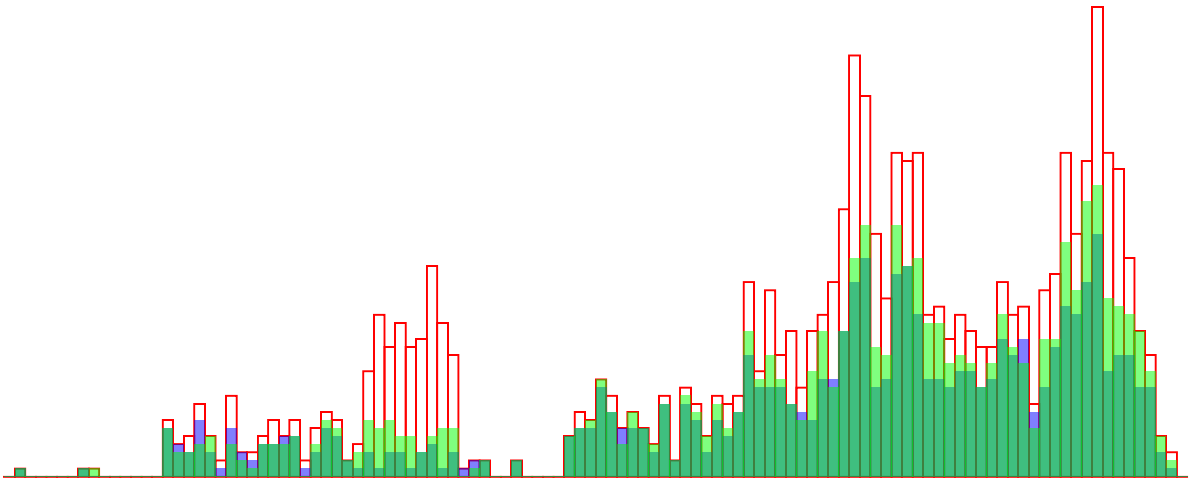
```
##
##    Scaldicetus grandis Schizodelphis sulcatus
##                     13                     15
```

```
## Warning: Removed 2 rows containing missing values (geom_bar).

## Warning: Removed 2 rows containing missing values (geom_bar).

## Warning: Removed 2 rows containing missing values (geom_bar).
```

Initial occurrences distribution (red) and comparison after sub−sampling (blue) or aggregating in geoplates (green)

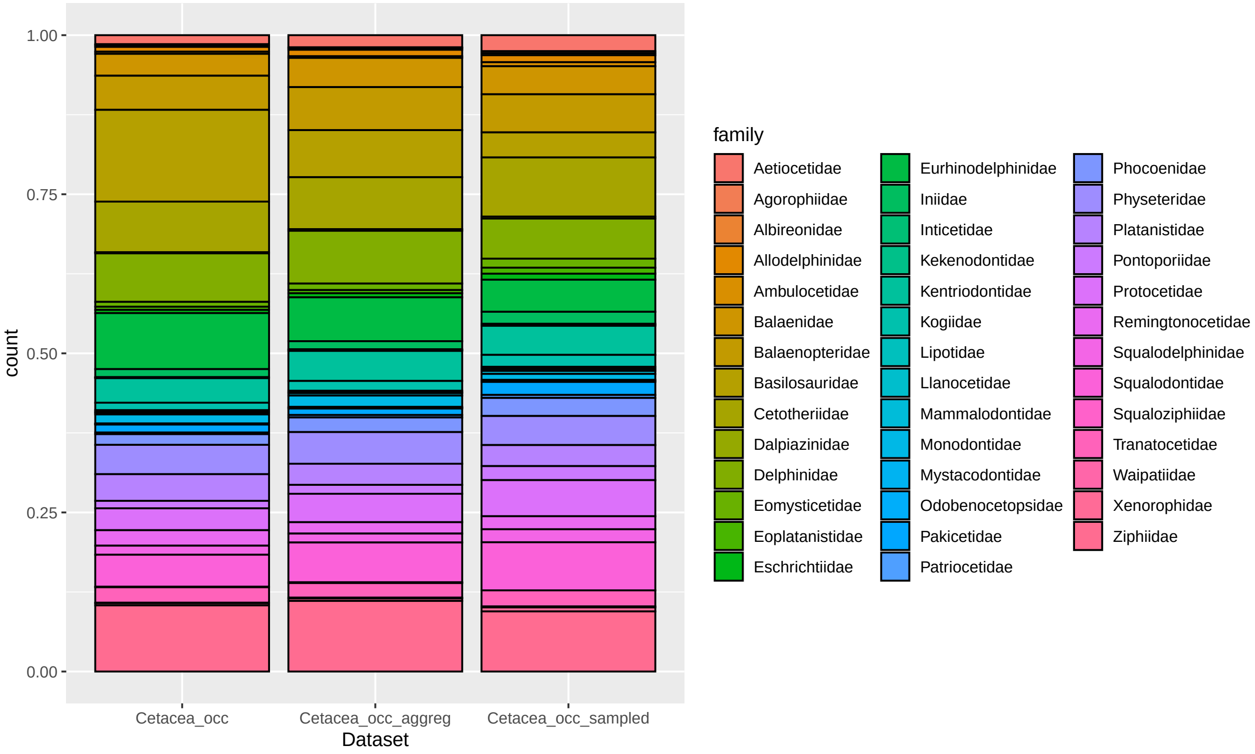


→ Delimiting by geological plates (+ age) instead of countries (+ age) leads to similar distributions, so we will keep it.

Check that the sampling methods do not introduce biases in the repartition between Odontoceti and Mysticeti

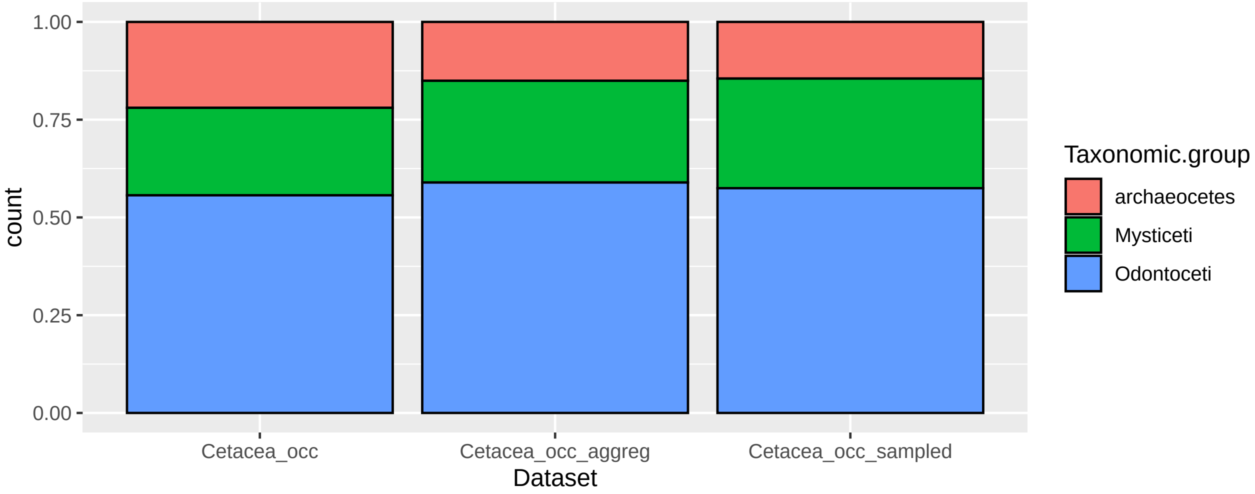
Mystecetes are usually larger than odontocetes, and size is associated with a wider geographic range so since we are subsampling occurrences according to geological formation we may be biasing our data towards more widespread species, therefore towards mystecetes.

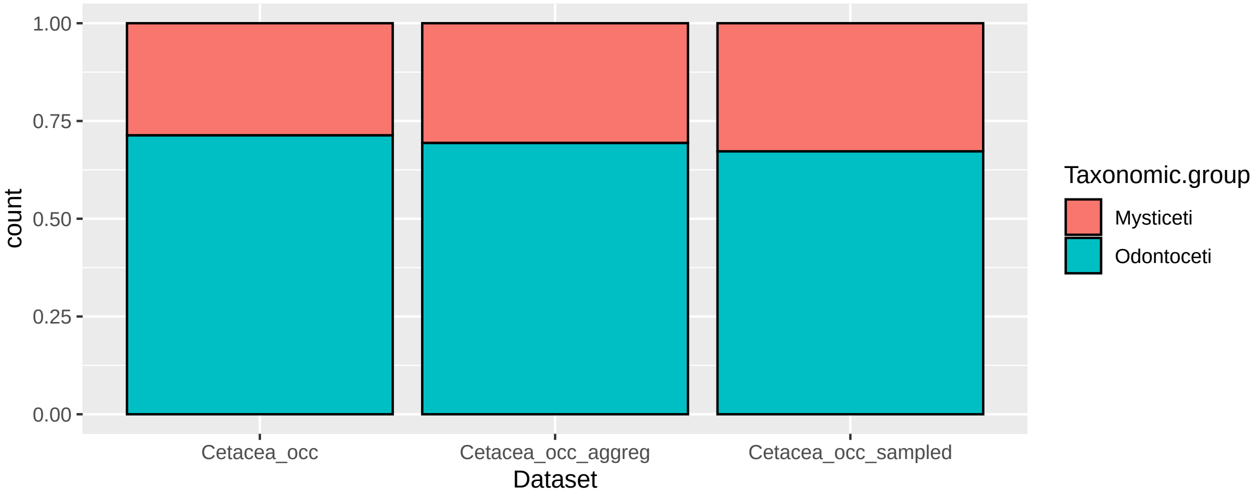
Look at the families first :



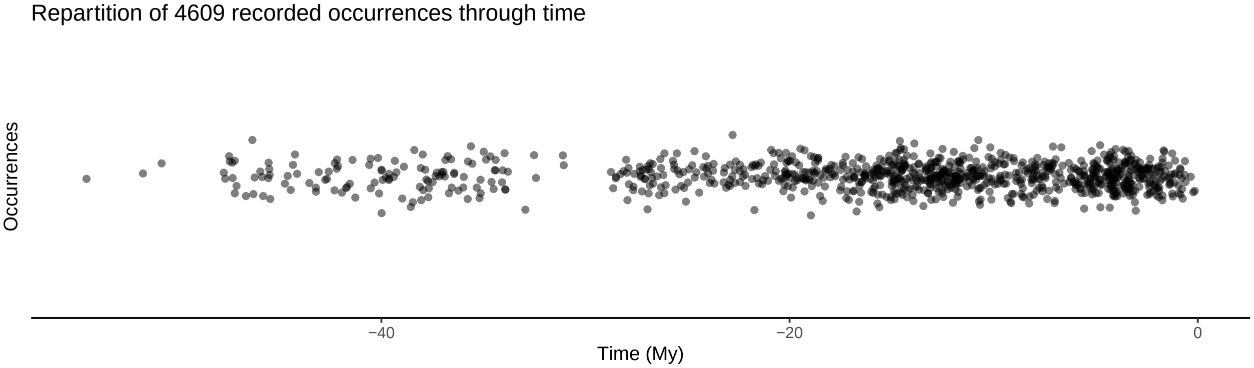
→ The family repartitions vary a bit after subsampling, but because of the limited number of species by family the fact that we corrected the oversampling of some species could have a disproportionate effect.

Let's look rather at a higher taxonomic rank, by importing the topology of cetacean families (from Marx et al. 2016) :





→ There is a smaller proportion of archeocete occurrences after either sampling, because a huge cluster is subsampled around 35 My ago, but this effect is expected. However, for the Mysticeti vs. Odotoceti there is no huge apparent bias, especially with the aggregating method.

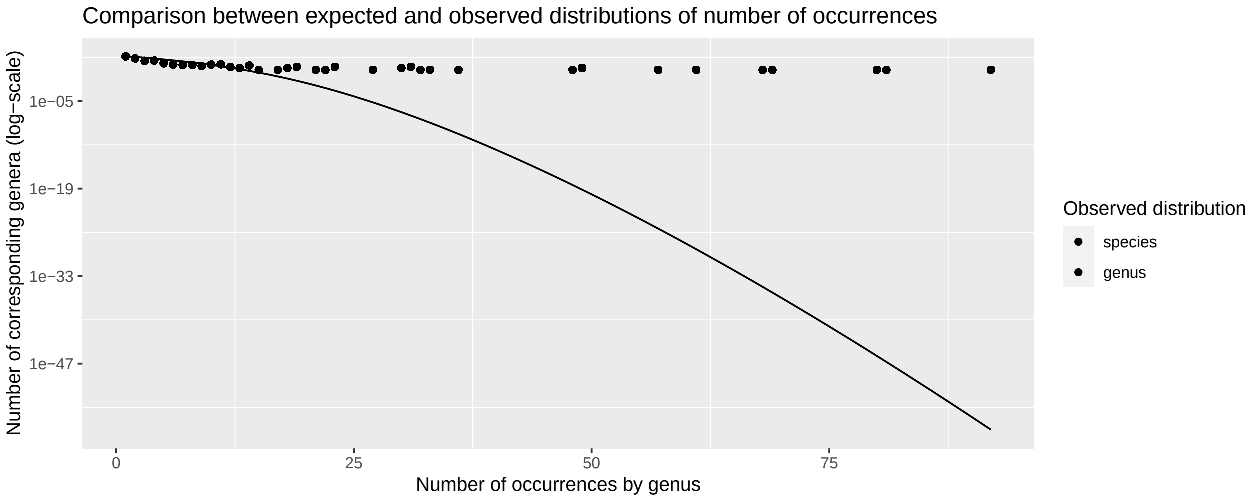


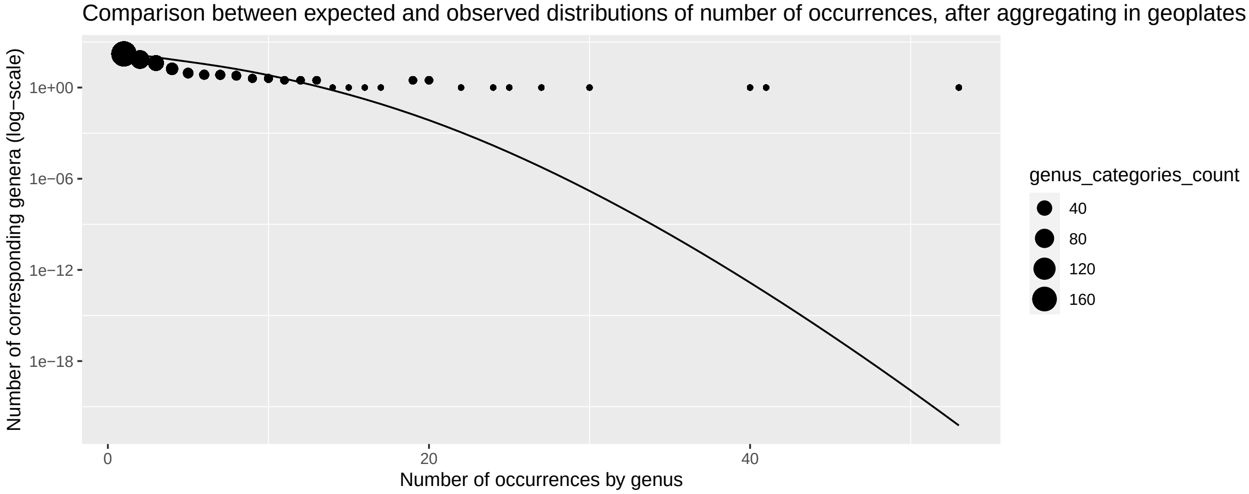
Faster genus-level analysis

Apply the same transformations at the generic level to perform the analysis faster.

```
##                                                  Cetacea_occ
## Number of occurrences                                   3804
## Number of occurrences (species and genera only)         2164
##                                                  Cetacea_occ_aggreg_gen removed
## Number of occurrences                                              1840    1964
## Number of occurrences (species and genera only)                    1303     861
```

More occurrences remain after aggregating with this new method. Let’s compare again with the theoretical distribution :





→ The correspondance is much less improved than with species aggregation because some genera have a lot of occurrences due to their high number of species species :

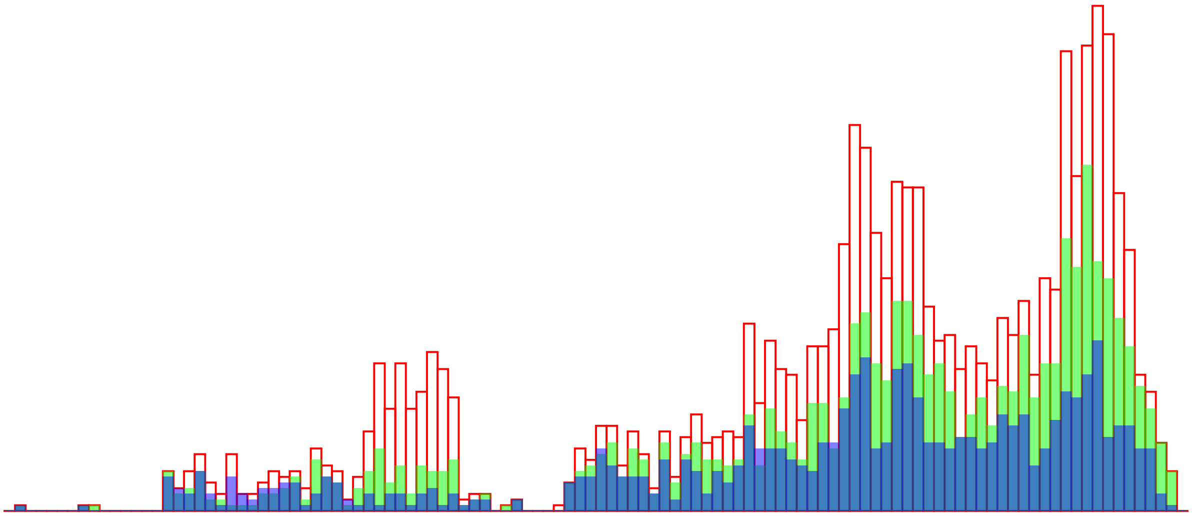
```
##
## Balaenoptera   Kentriodon   Mesoplodon  Scaldicetus    Squalodon
##           53           27           30           41           40
```

```
## Warning: Removed 2 rows containing missing values (geom_bar).

## Warning: Removed 2 rows containing missing values (geom_bar).

## Warning: Removed 2 rows containing missing values (geom_bar).
```

Initial occurrences distribution (red) and comparison after sub−sampling (blue) or aggregating in geoplates (green)



→ Delimiting by geological plates (+ age) instead of countries (+ age) leads to similar distributions, with a bit more occurrences.

Conclusions

- It seems possible to adequately reduce the abundance bias by subsampling the most concentrated intervals, based on a metrics of occurrence density (number of occurrences / time range)
- An alternative sampling method consisting in aggregating the occurrences of the same taxa found in the same geological formation (or the same geoplate + eearly stratigraphic interval if the geological formation is not indicated) seems to work as well, and is more paleontologically relevant
- Using combined ranges by species appears to be more robust
- Very recent samples may have been dated with a more precise method and contain much more fossils, so they should be removed or treated separatadely