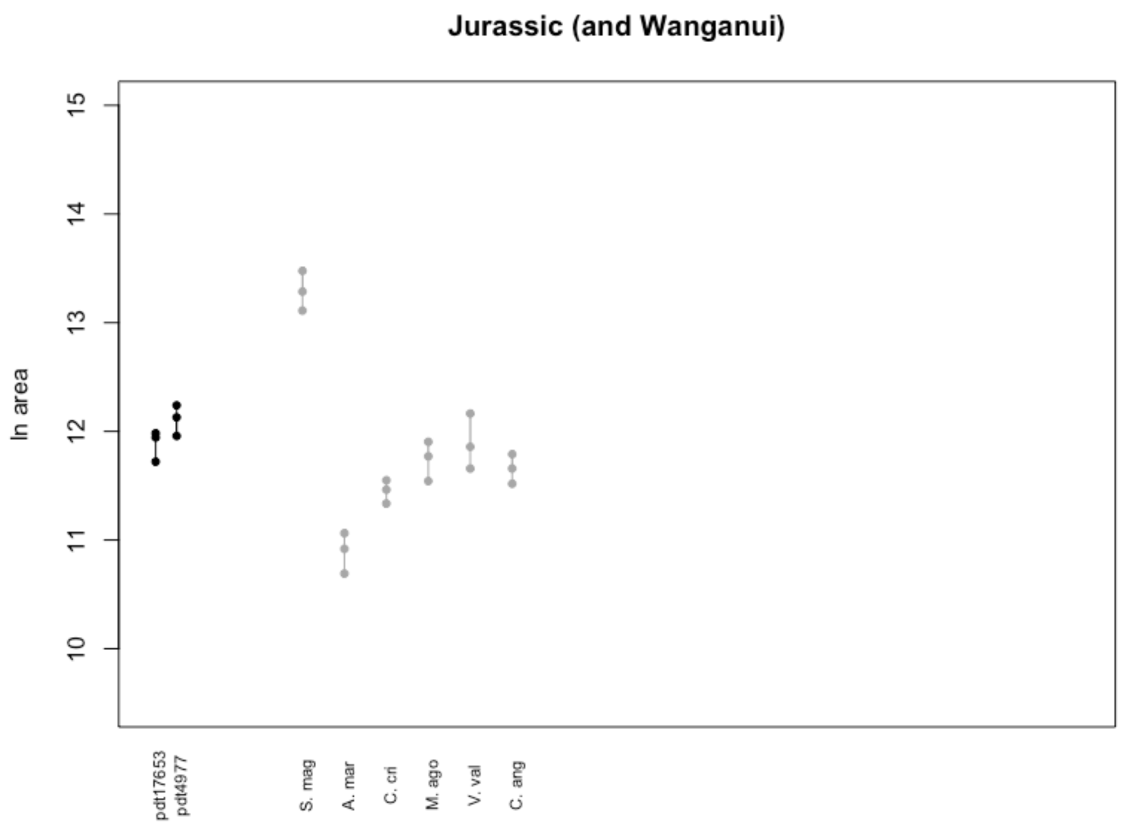
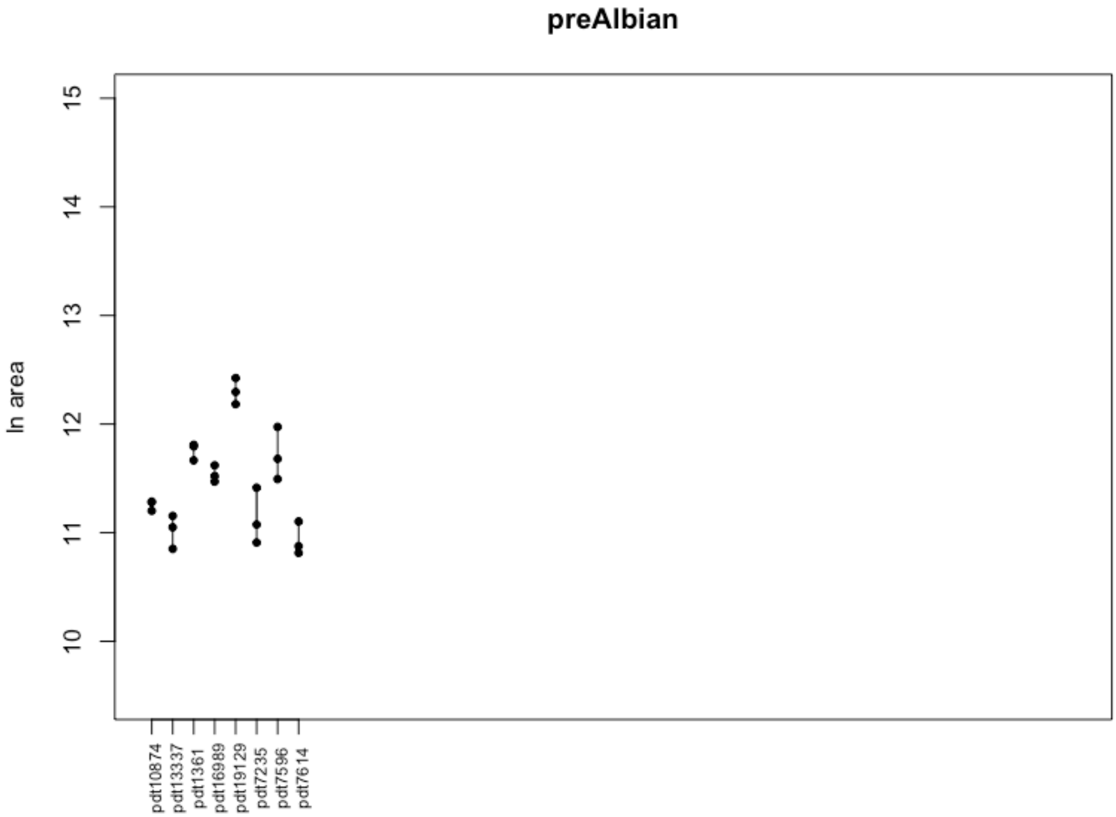
Supplementary material for MS (Evolution)

Cope's Rule in a modular organism: Directional evolution without an overarching macroevolutionary trend

Fig. S1. Zoid area measurements for each species. Natural log (ln area μm^2) of the three haphazardly selected zooids for each named image on the x-axis are shown. Repeat measurements of the areas of select colonies as shown as red (second measurement) and blue (third measurement) dots where available. Note that there is no temporal order within each of the named geological time interval (as assigned in the original metadata of the image files) and some have multiple plots. On the first plot we also show the median and interquartile range of measurements from 180 zooids each from six time intervals (ranging from 2.3 Ma to 0 Ma) of six species from New Zealand (data from Liow et al. 2017). S. mag = *Steginoporella magnifica;* A. mar = *Aimulosia marsupium;* C. cri. = *Crepidacantha crinispina;* M. ago = *Microporella agonistes;* V. val = *Valdemunitella valdemunita*; C .ang = *Calloporina angustipora.* The second time interval is simply labeled 'pre-Albian' because we only have 8 cheilostomes for several geological stages (from the Berriasian to the Aptian, i.e. 145 to 113 million years ago).

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ln area
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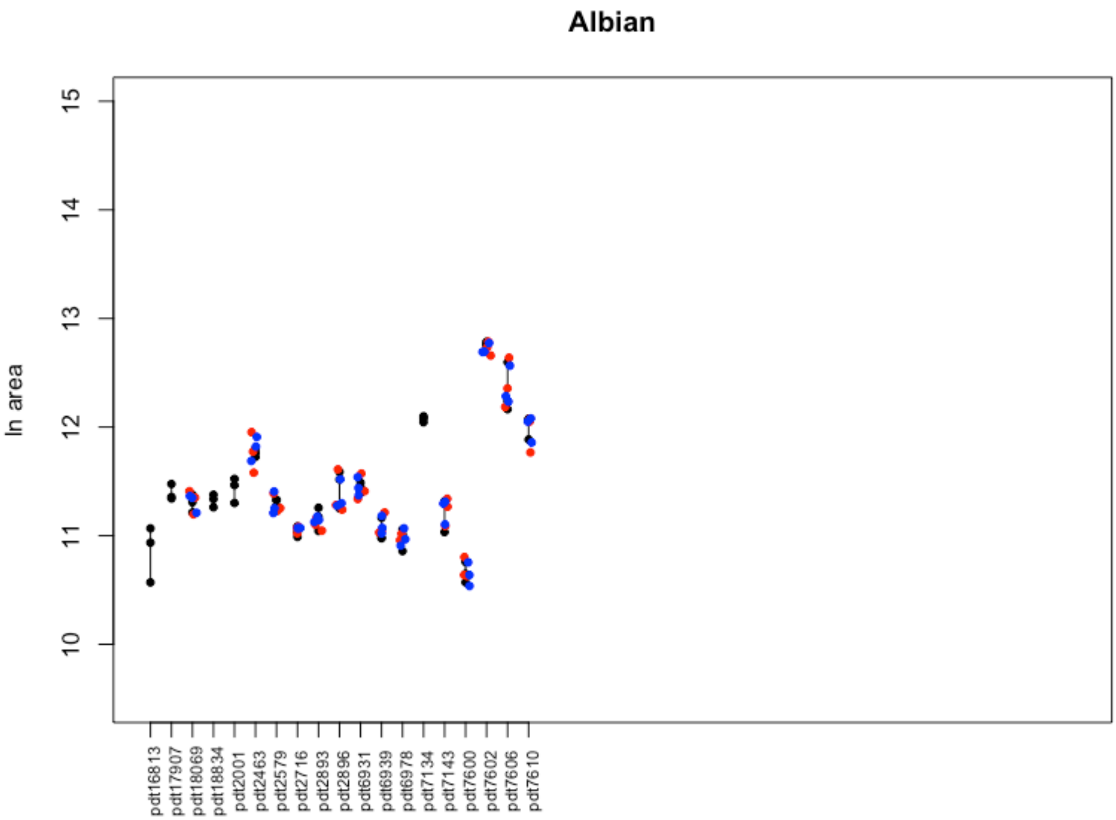
Albian
ln area
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11
12
13
14
15
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pdt18834
pdt2001
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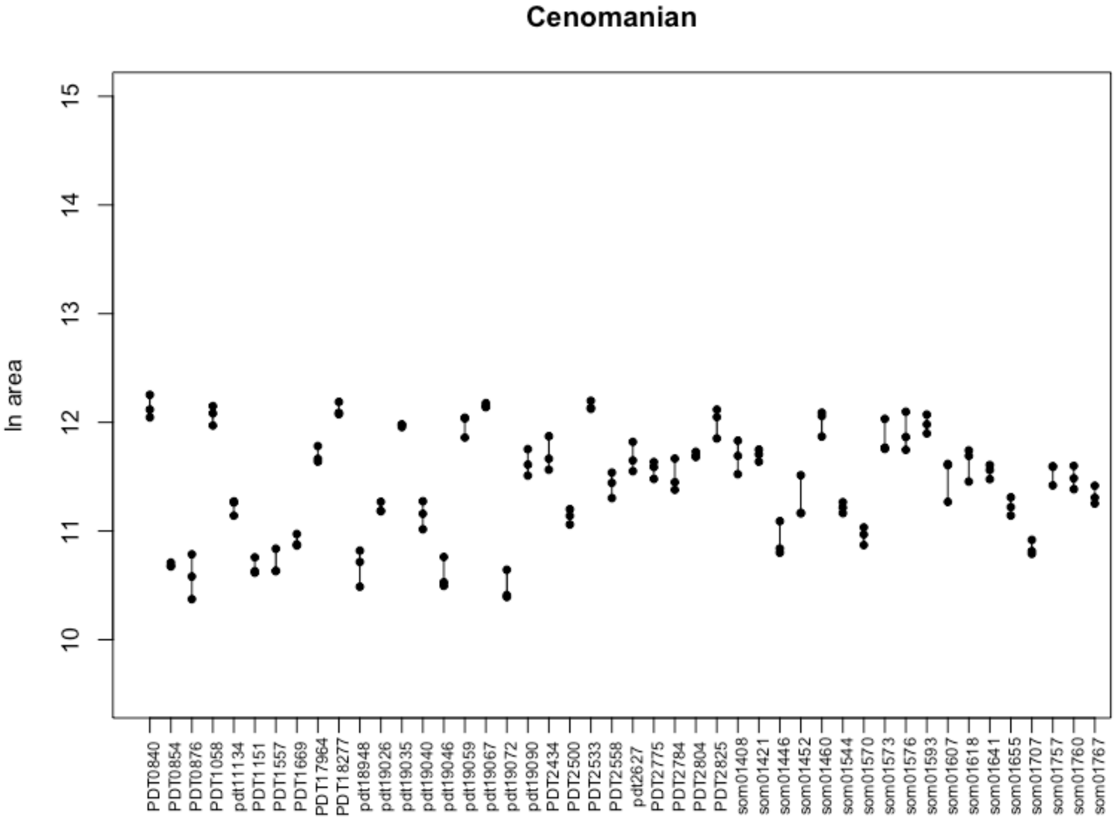
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ln area
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13
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pdt19040
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pdt19059
pdt19067
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som01544
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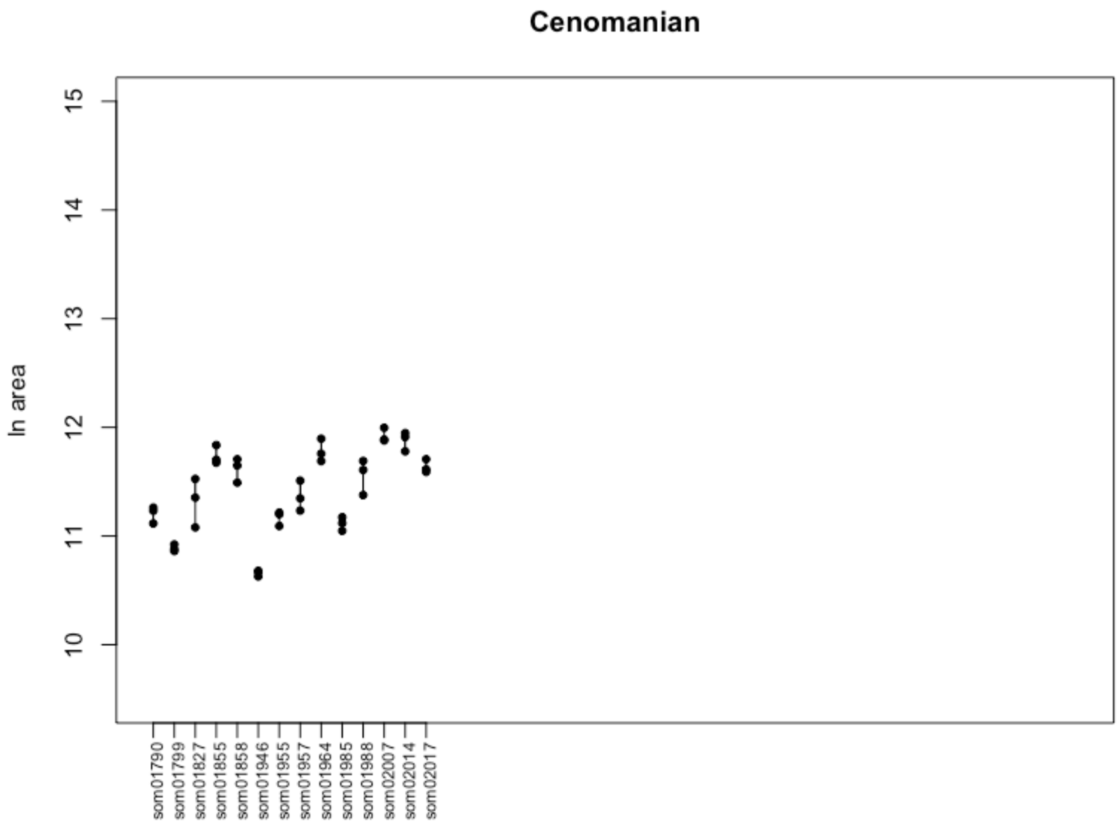
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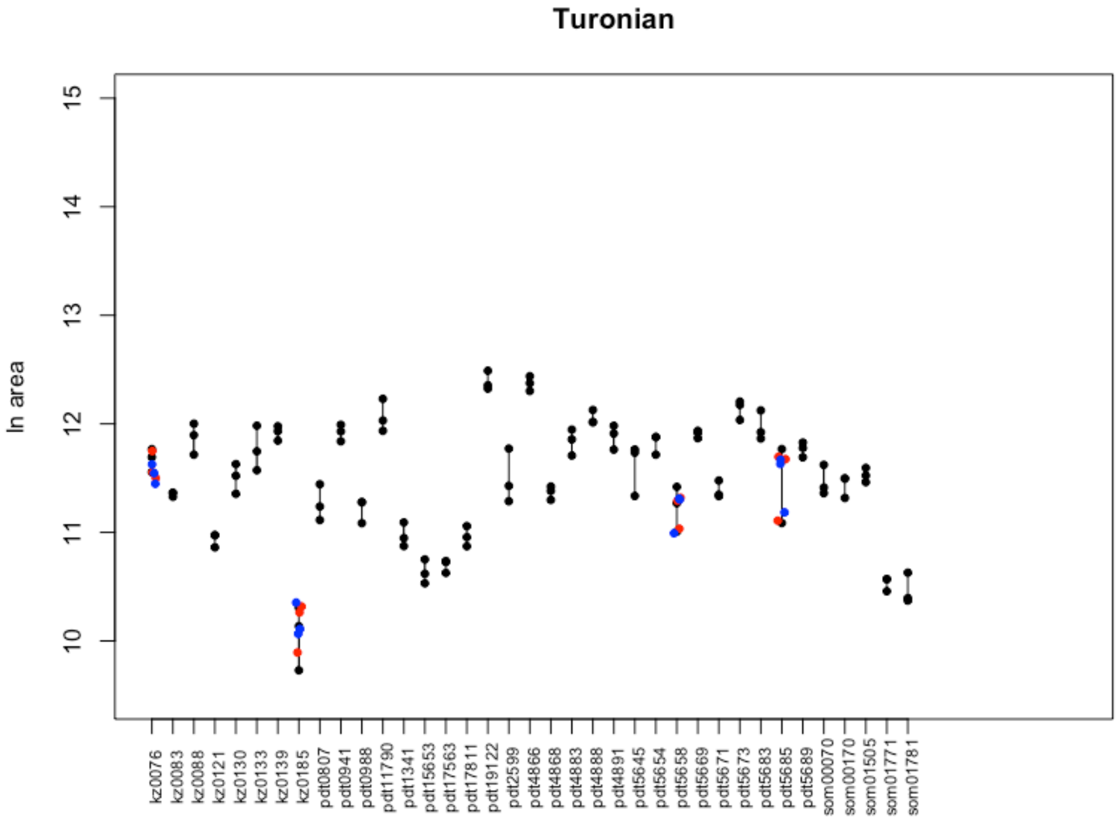
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ln area
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12
13
14
15
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kz0083
kz0088
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kz0139
kz0185
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pdt0941
pdt0988
pdt11790
pdt1341
pdt15653
pdt17563
pdt17811
pdt19122
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pdt5654
pdt5658
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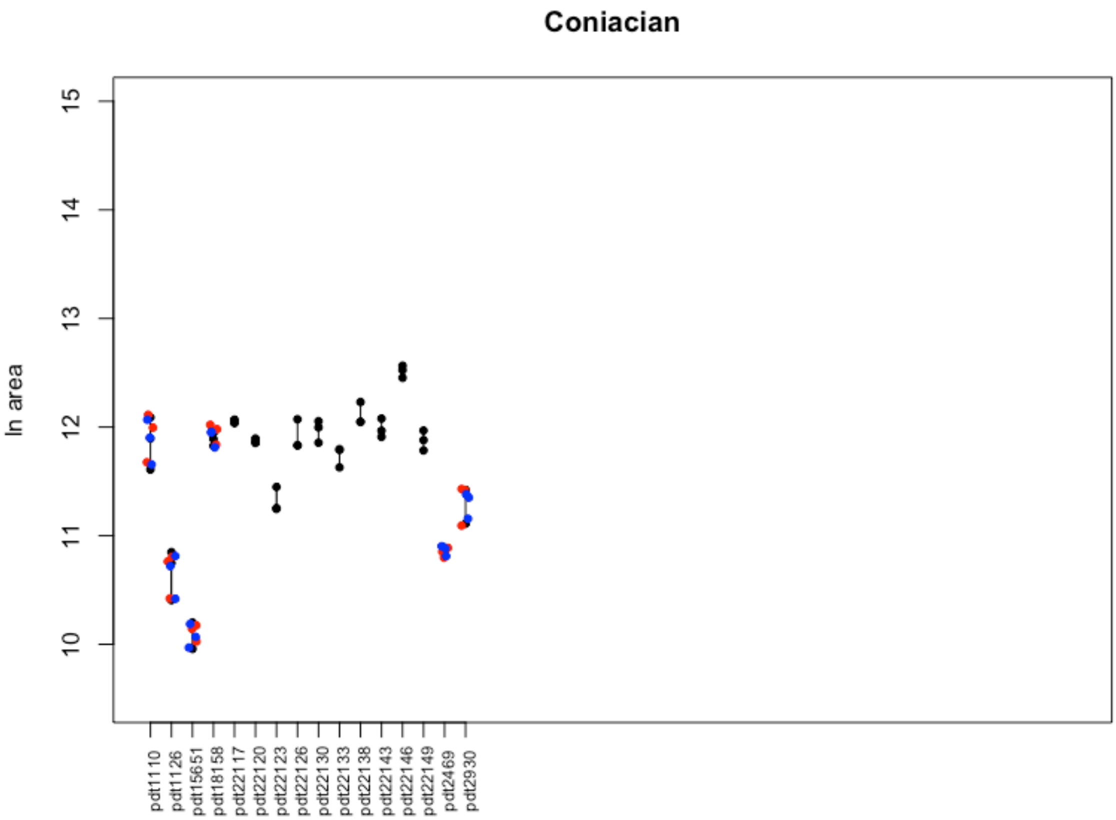
Coniacian
ln area
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12
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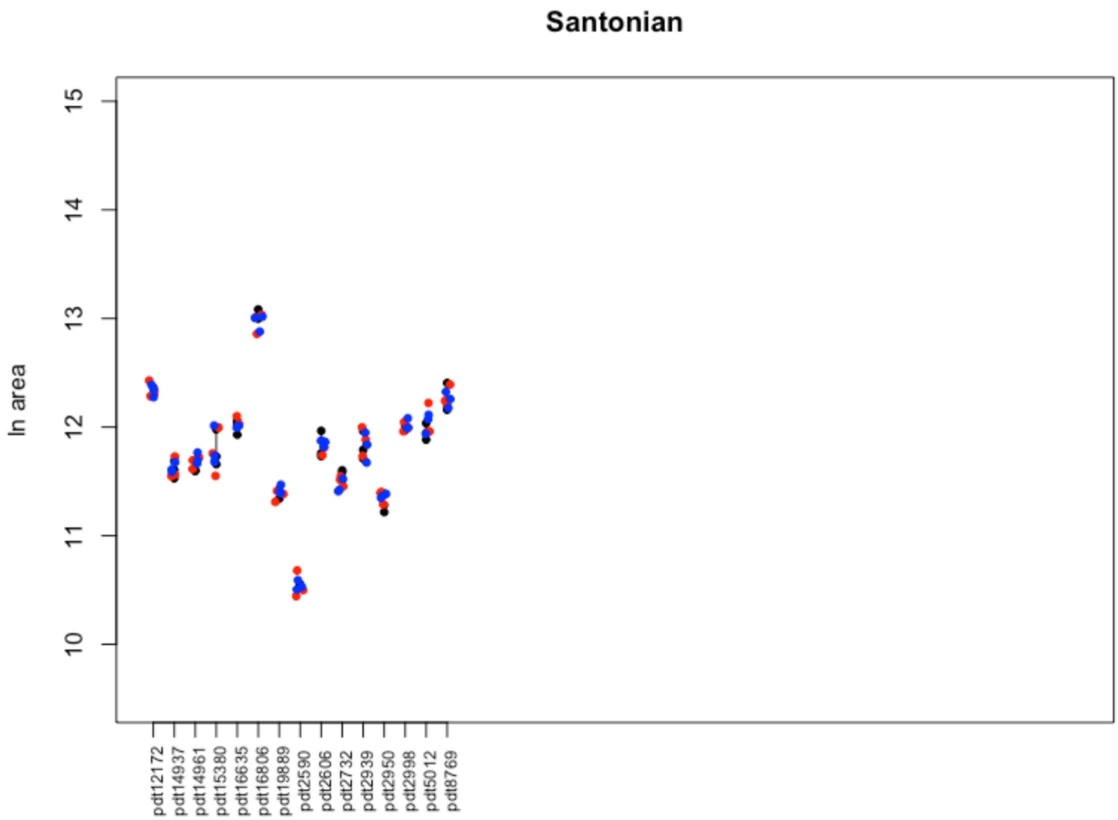
Santonian
ln area
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13
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15
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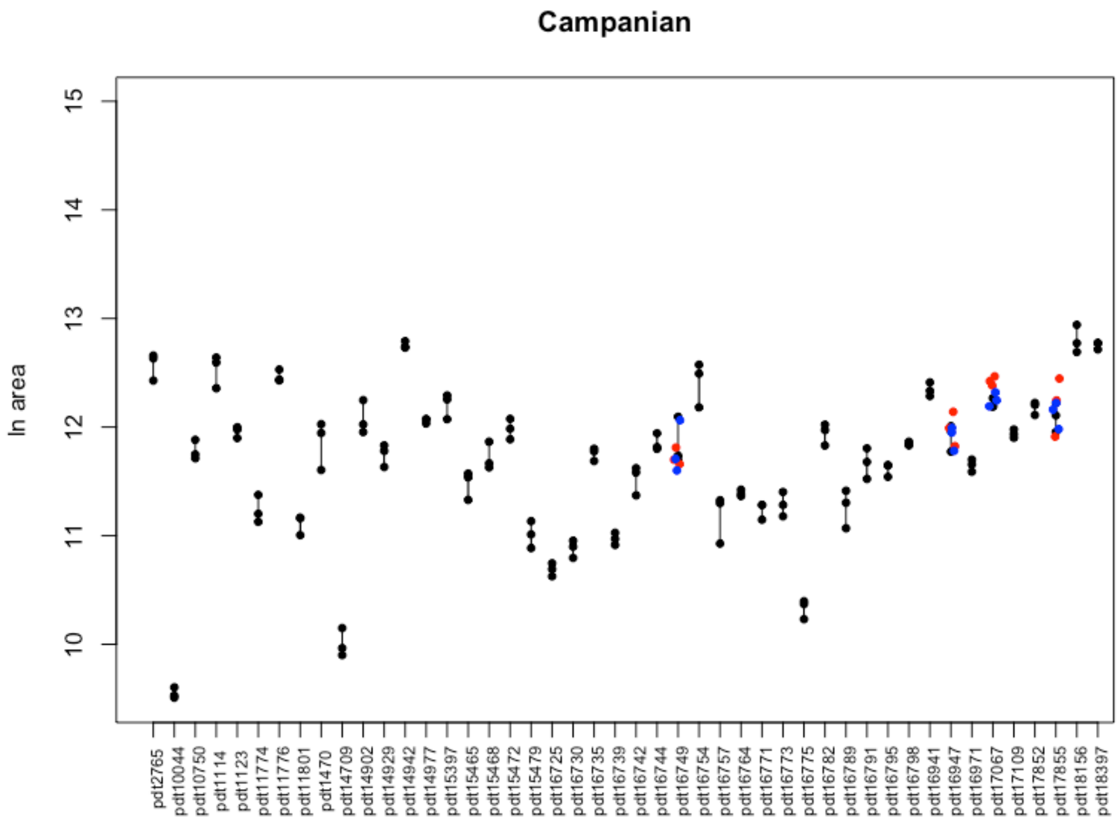
Campanian
ln area
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11
12
13
14
15
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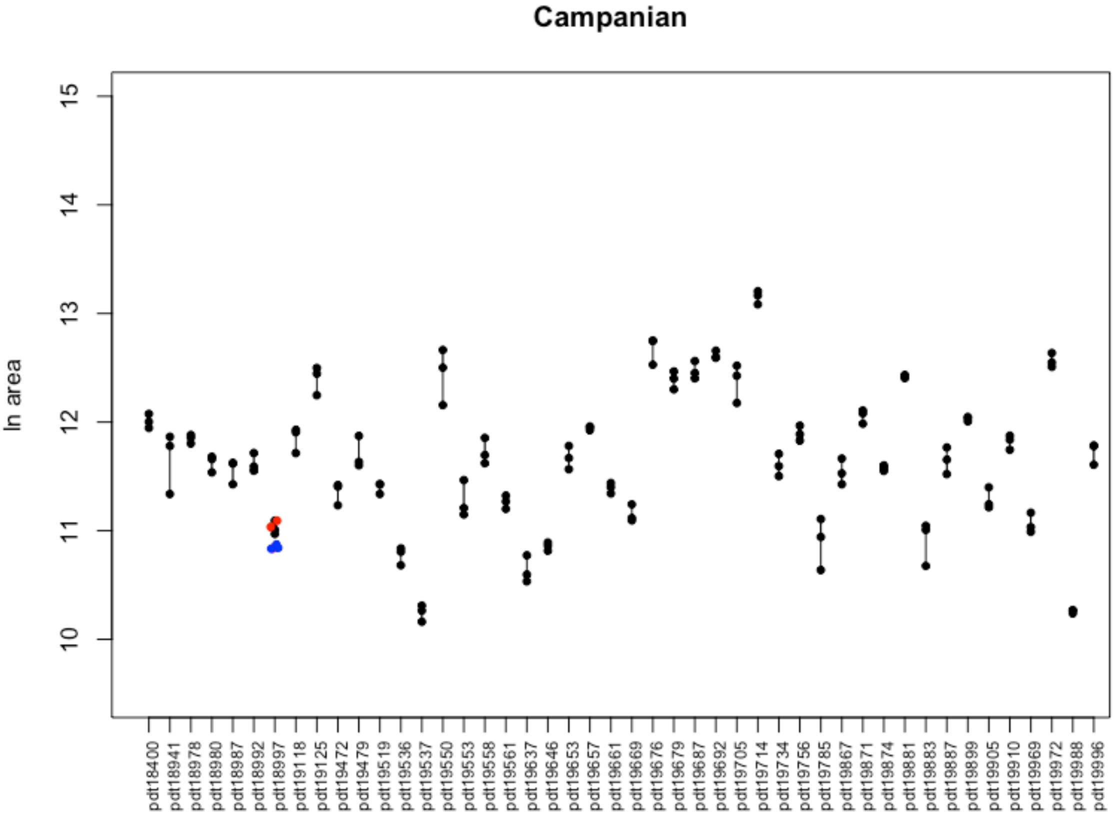
Campanian
ln area
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12
13
14
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pdt19867
pdt19871
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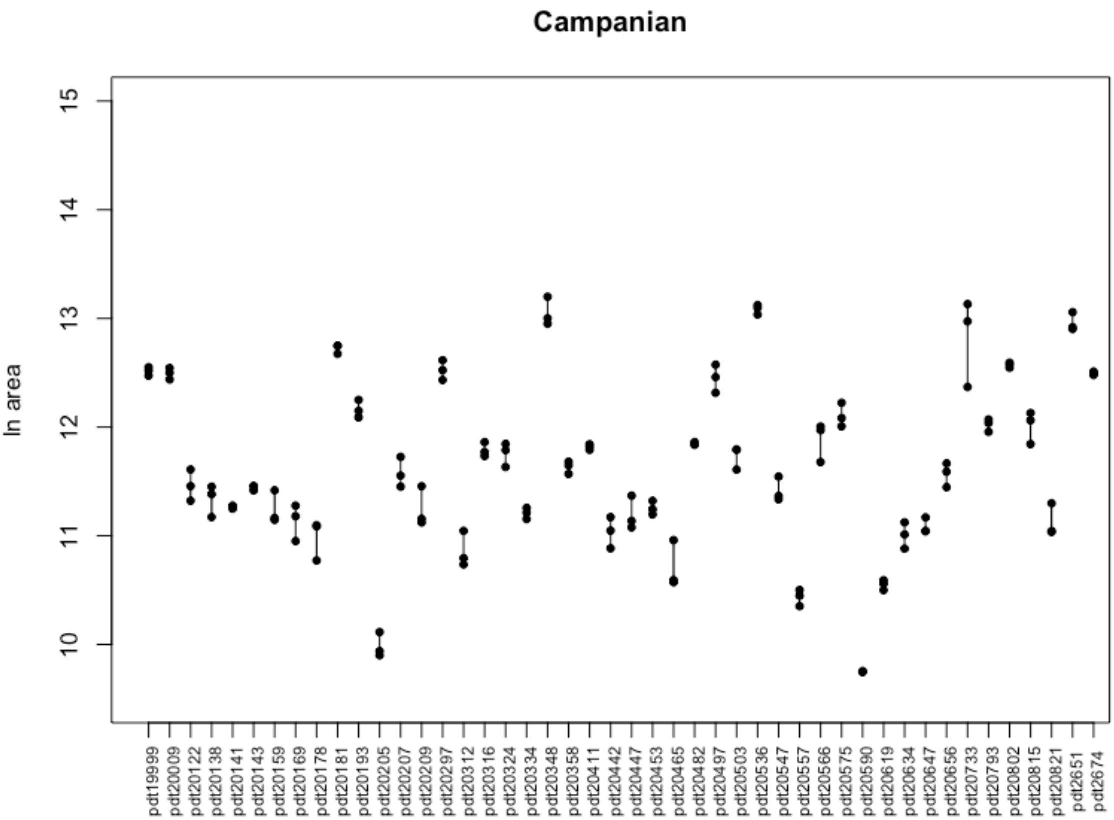
Campanian
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pdt20193
pdt20205
pdt20207
pdt20209
pdt20297
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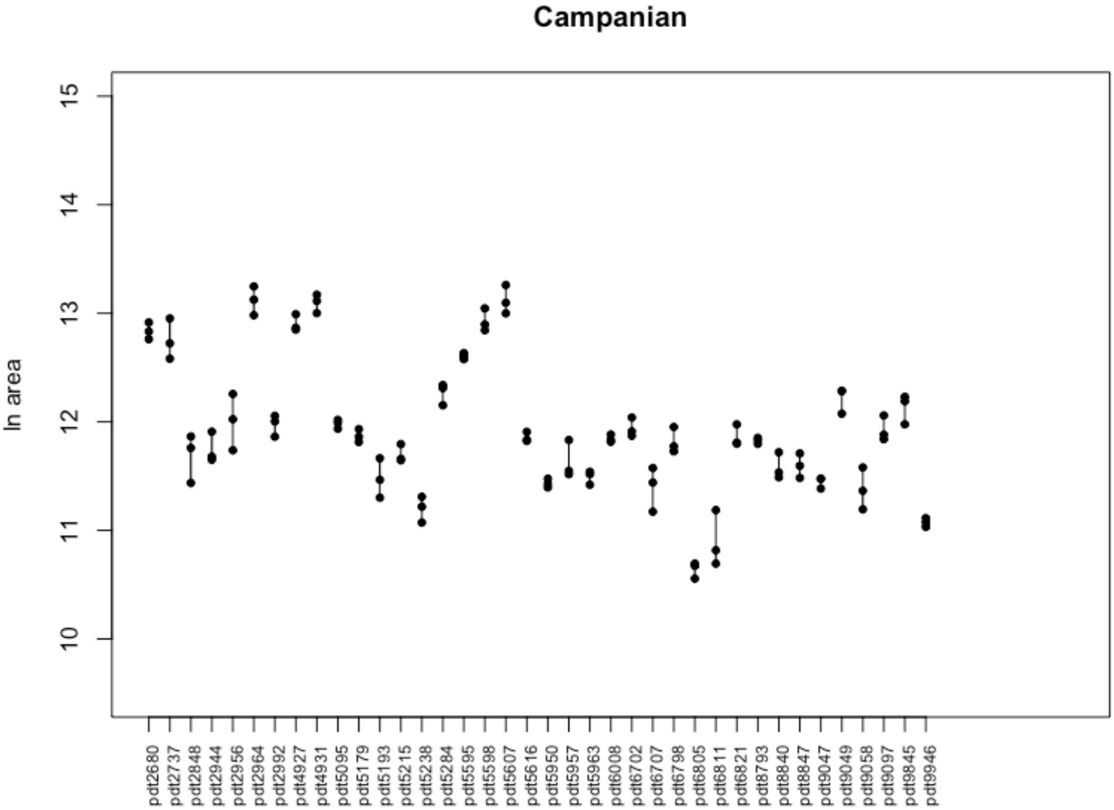
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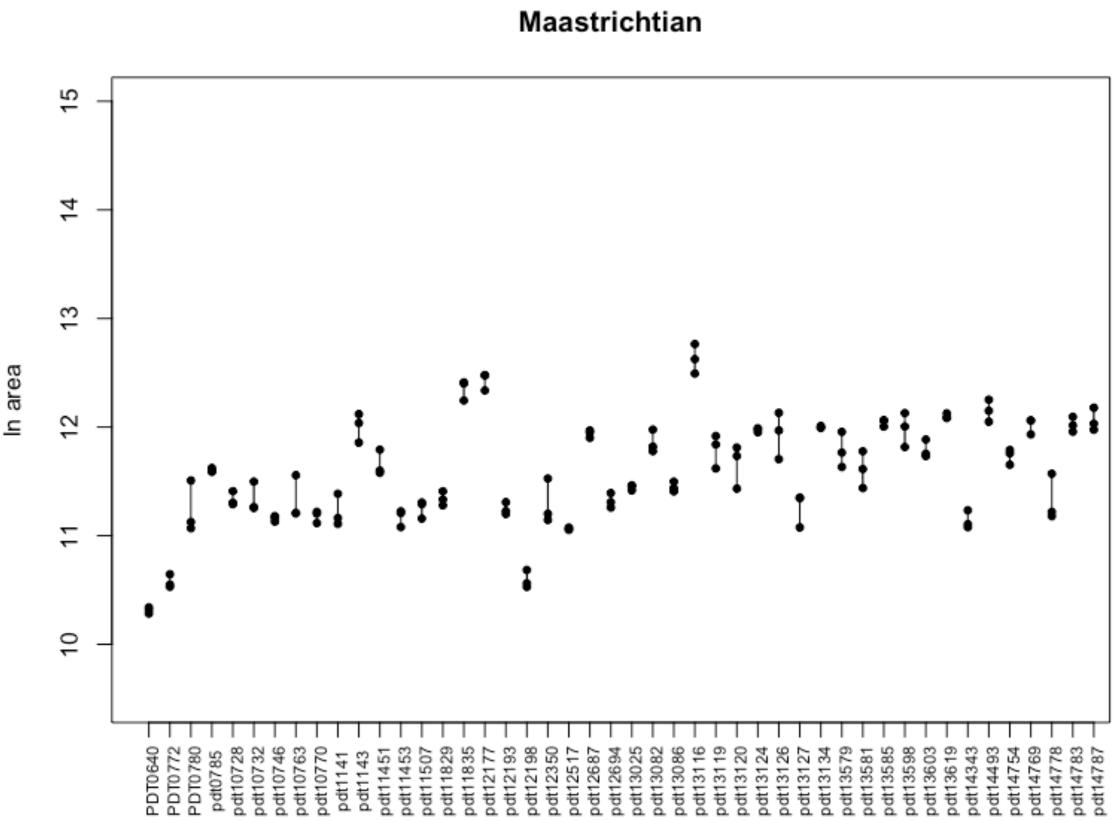
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12
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14
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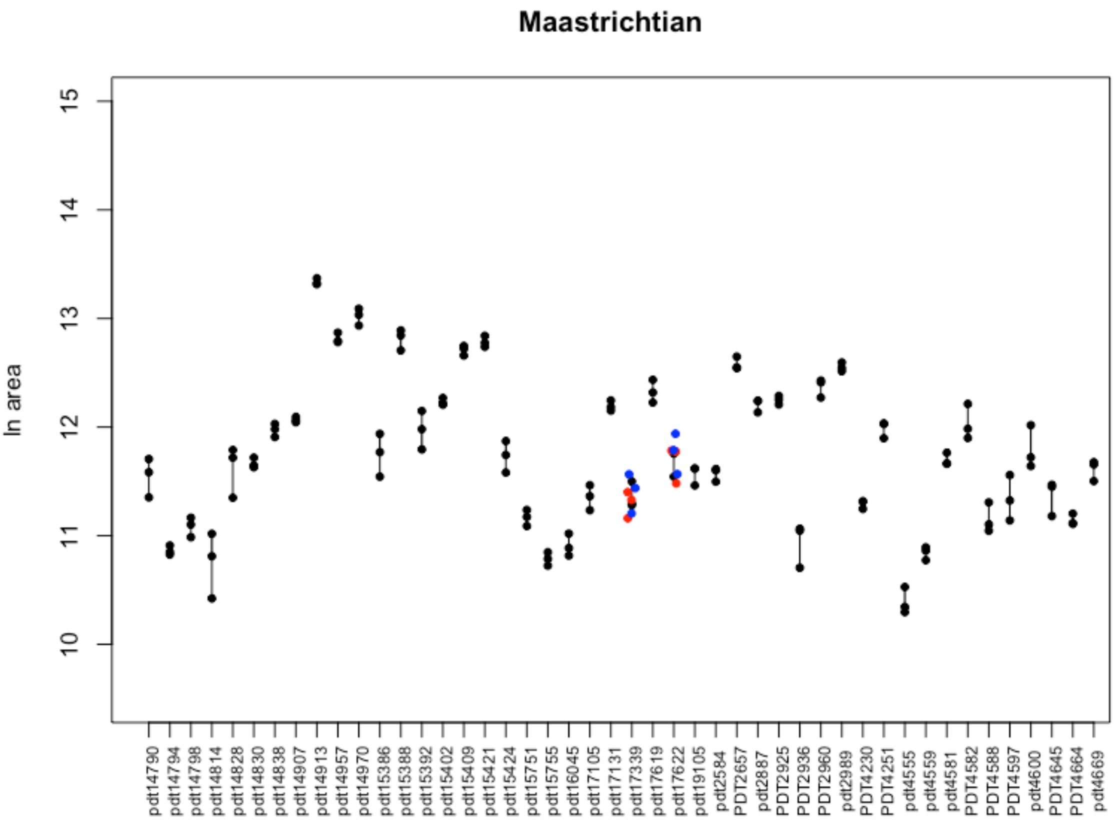
Maastrichtian
ln area
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11
12
13
14
15
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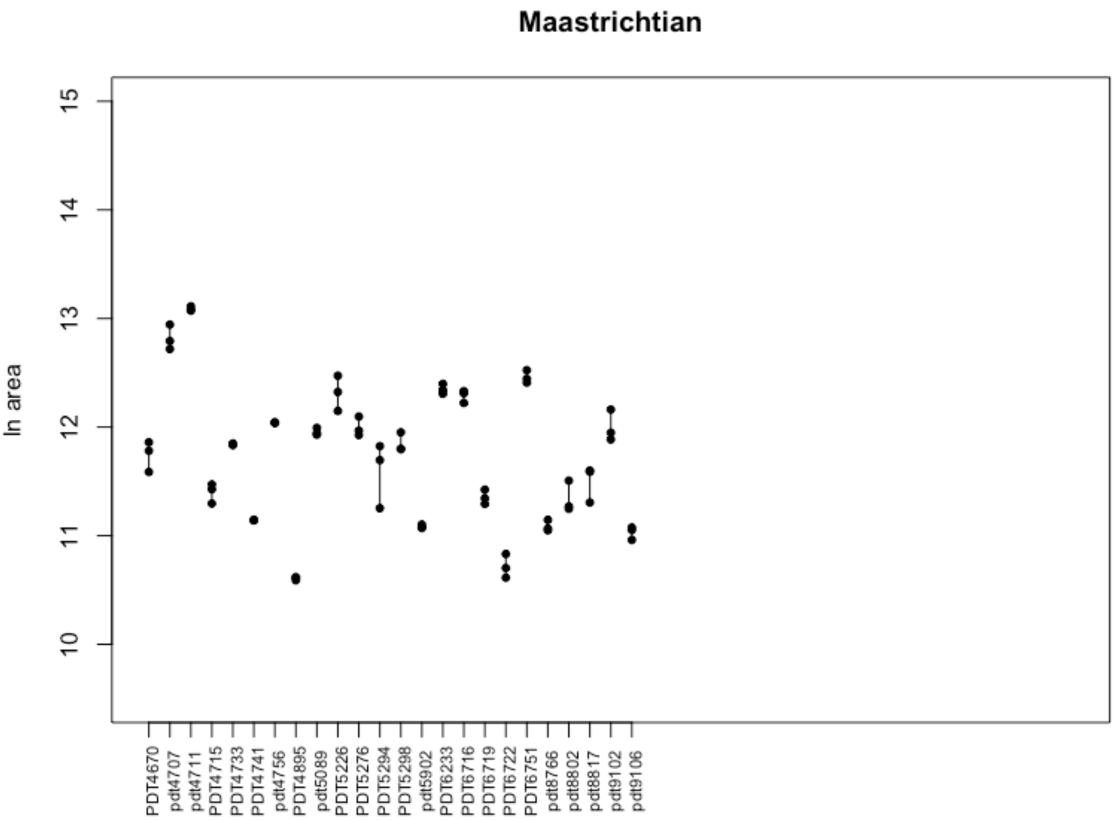
37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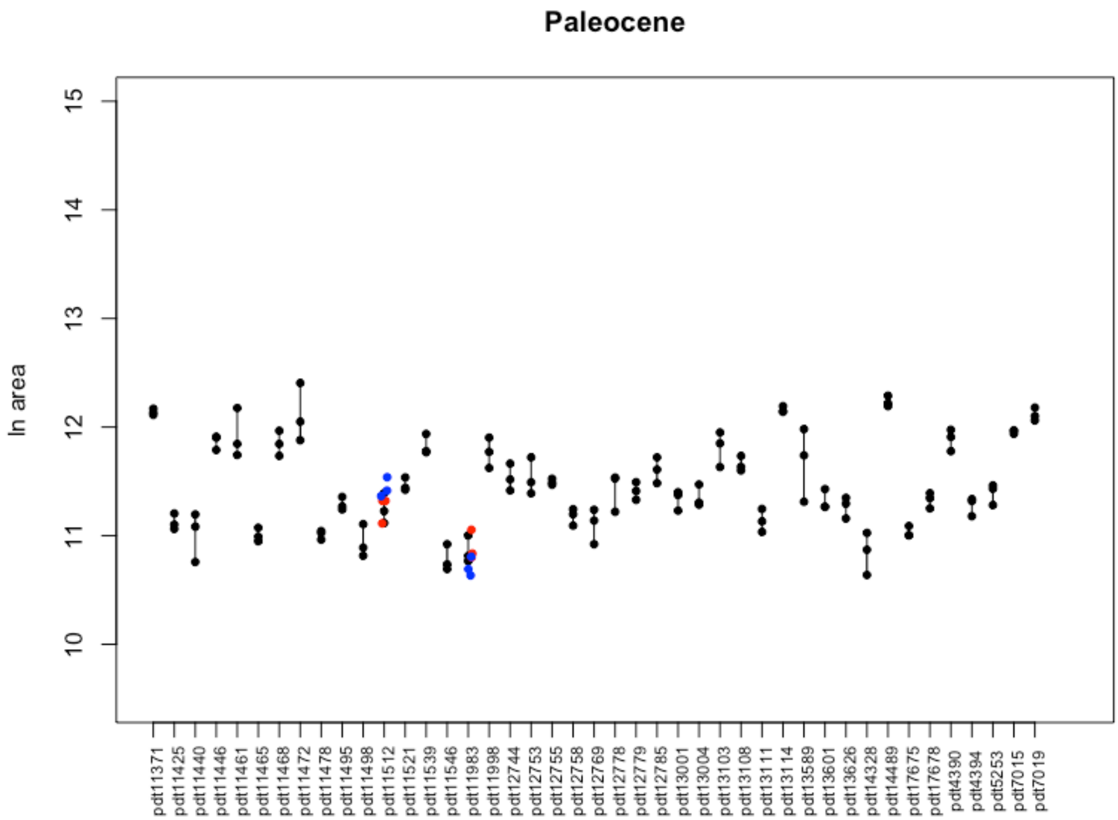
38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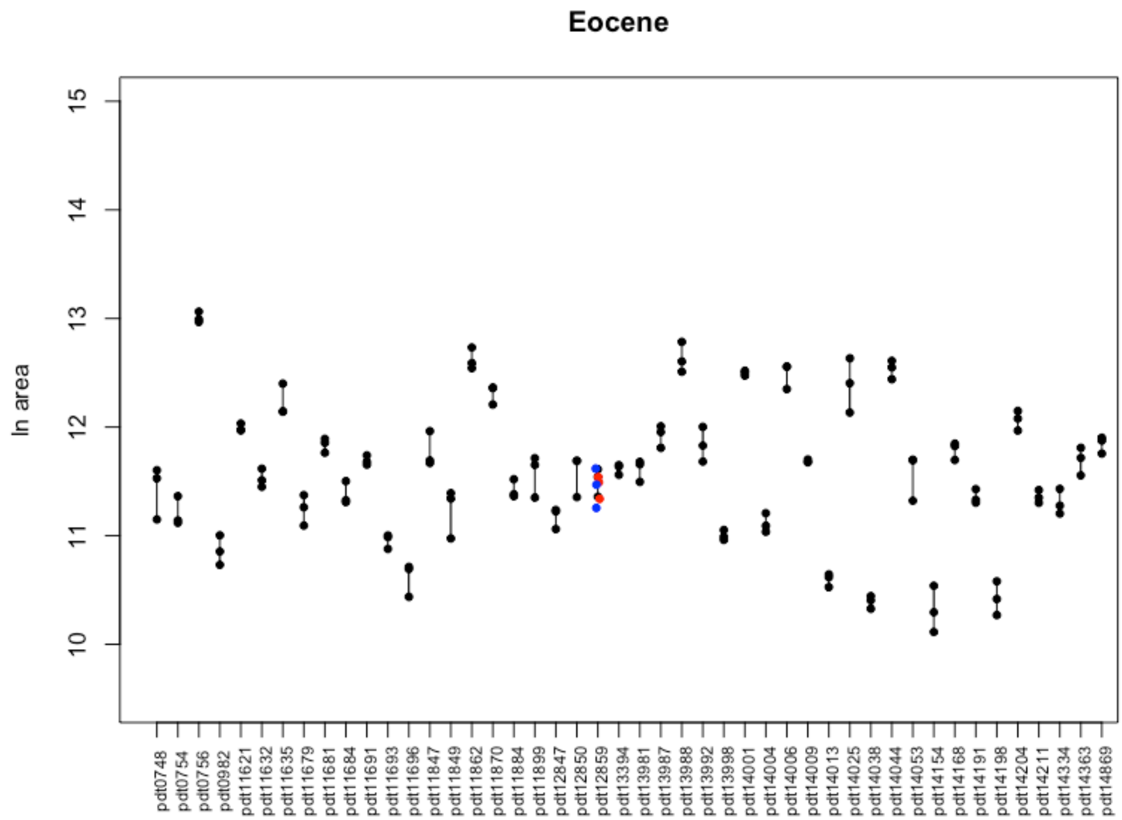
39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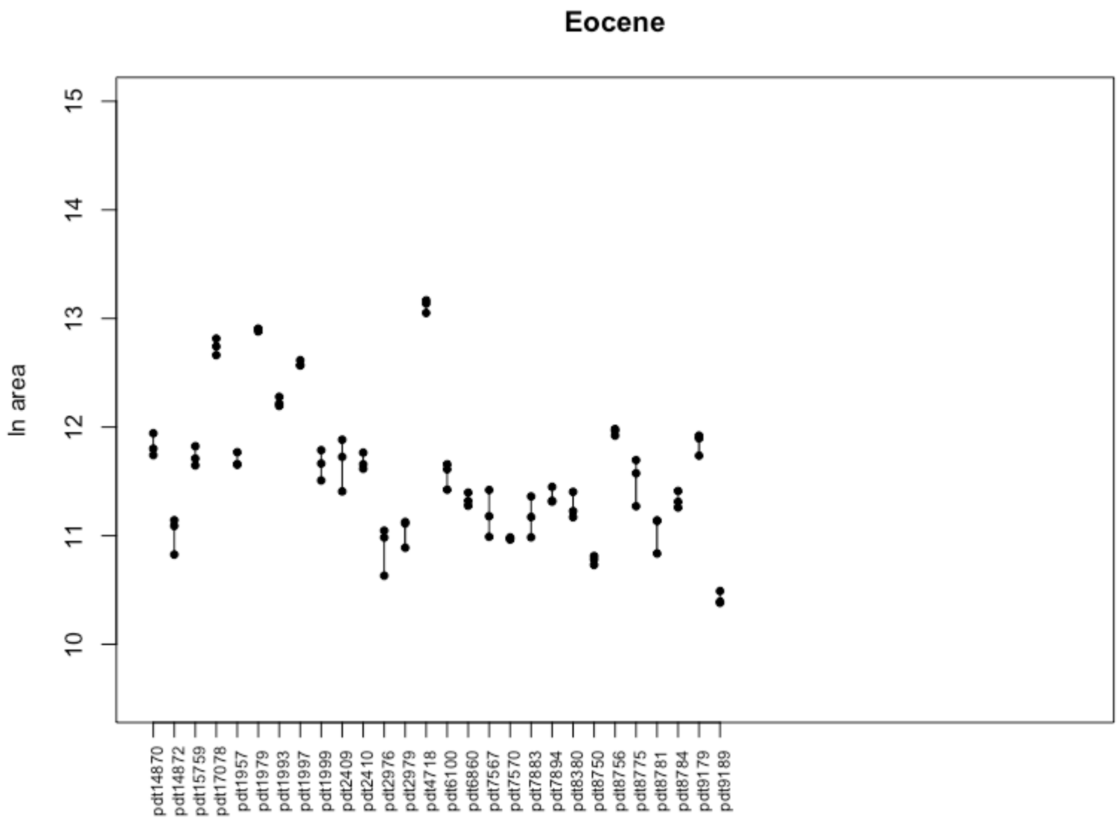
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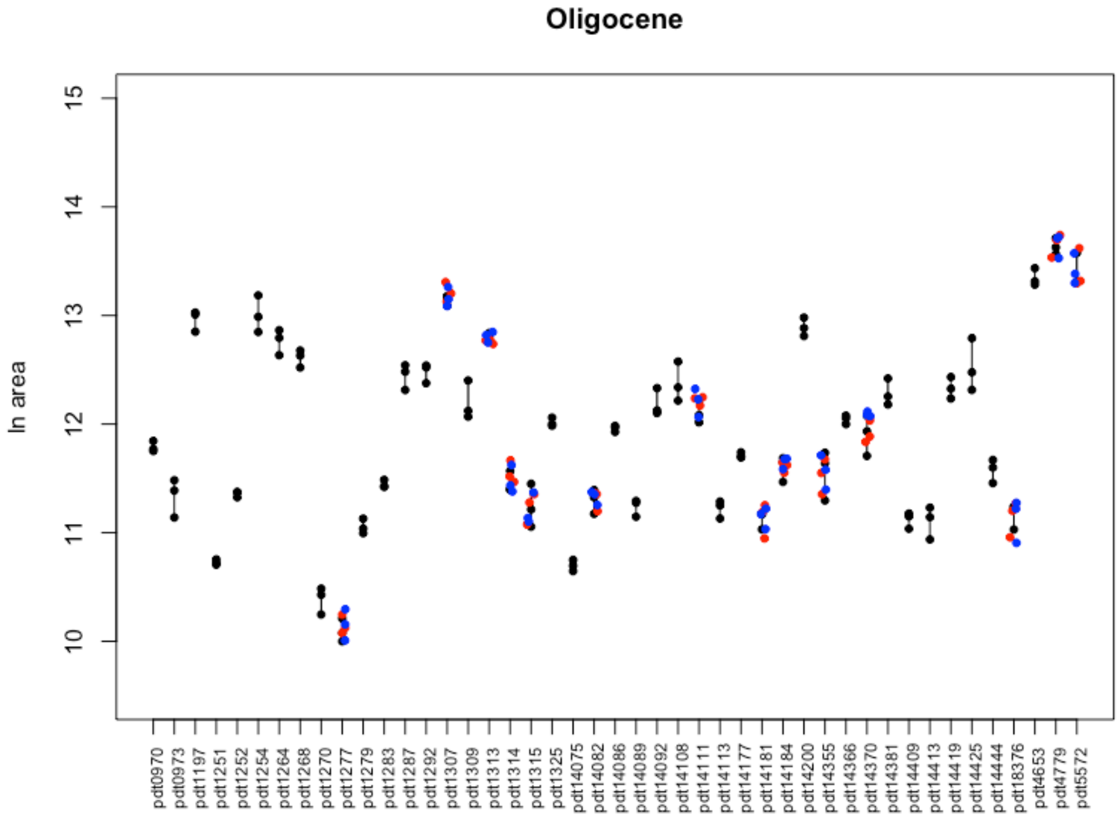
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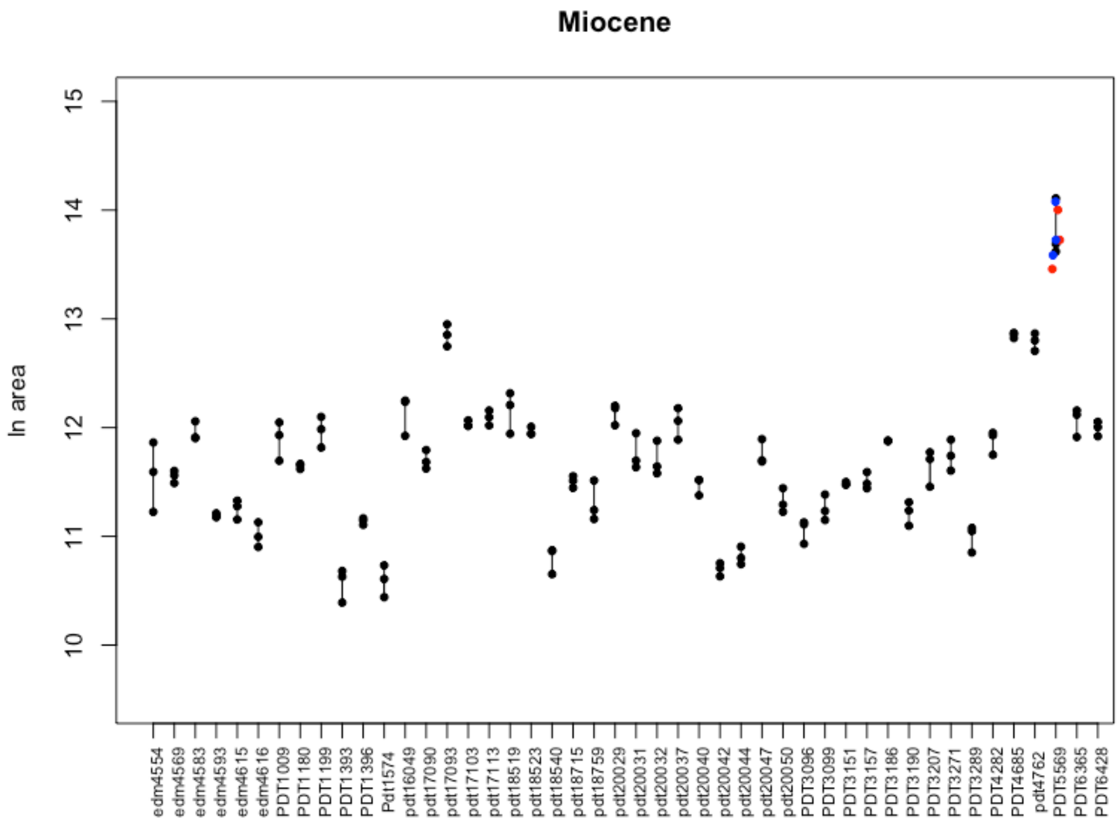
42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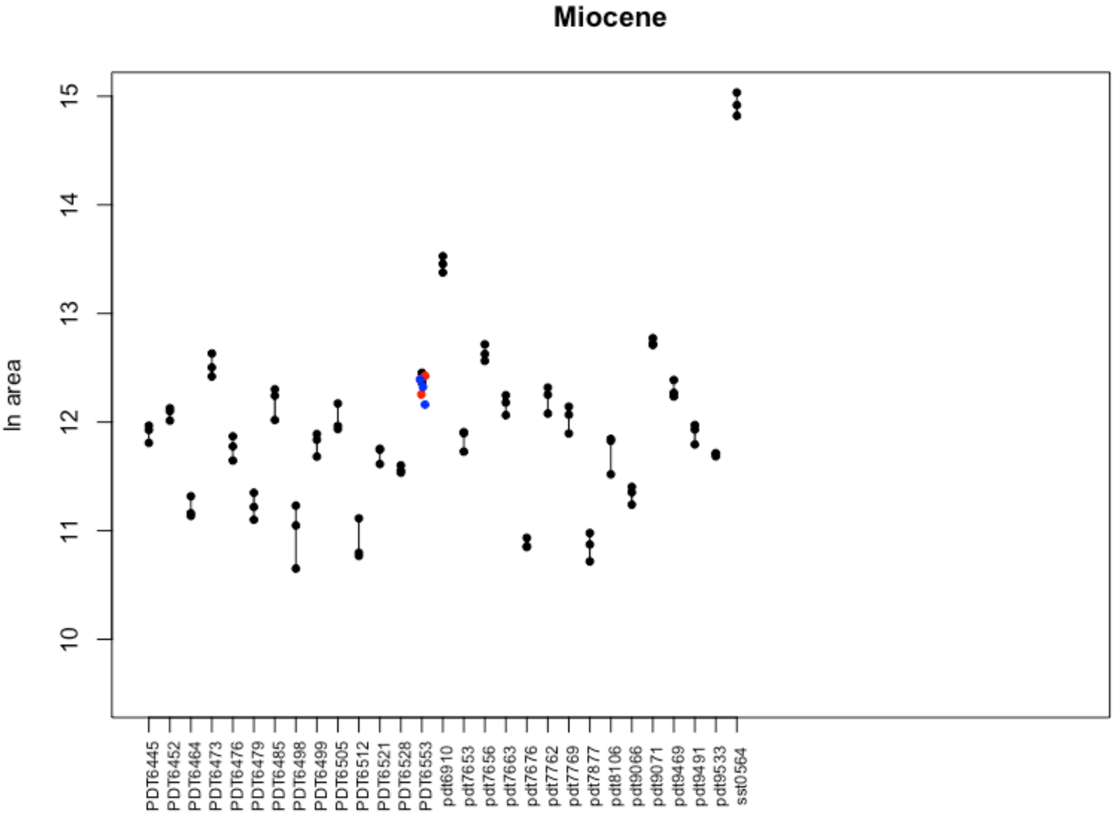
43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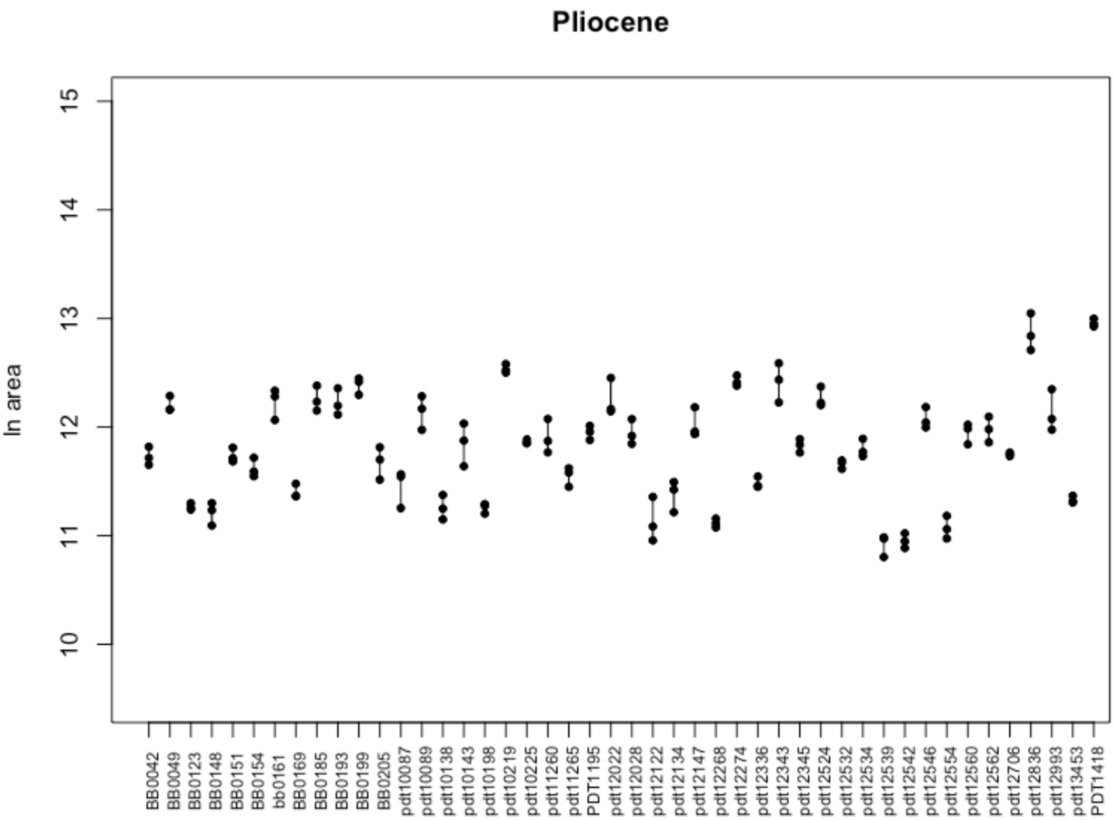
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ln area
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BB0205
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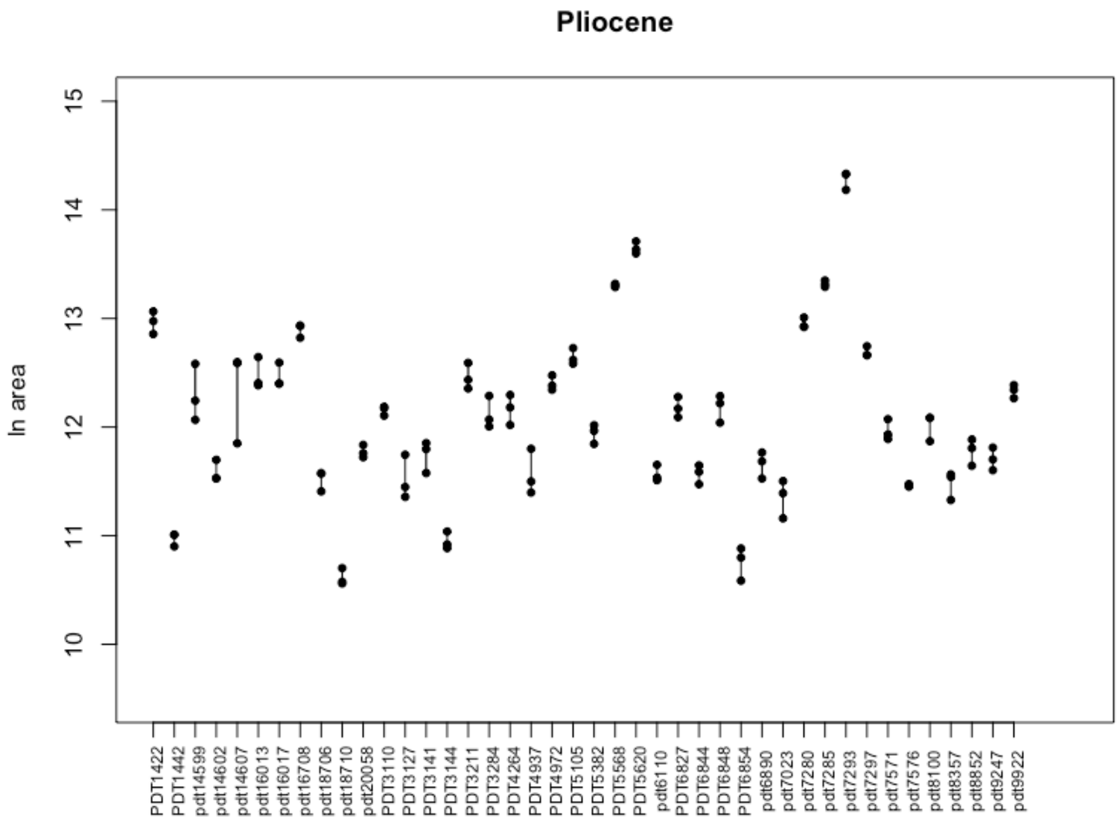
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pdt18706
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PDT3127
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PDT3144
PDT3211
PDT3284
PDT4264
PDT4937
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PDT5105
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PDT6827
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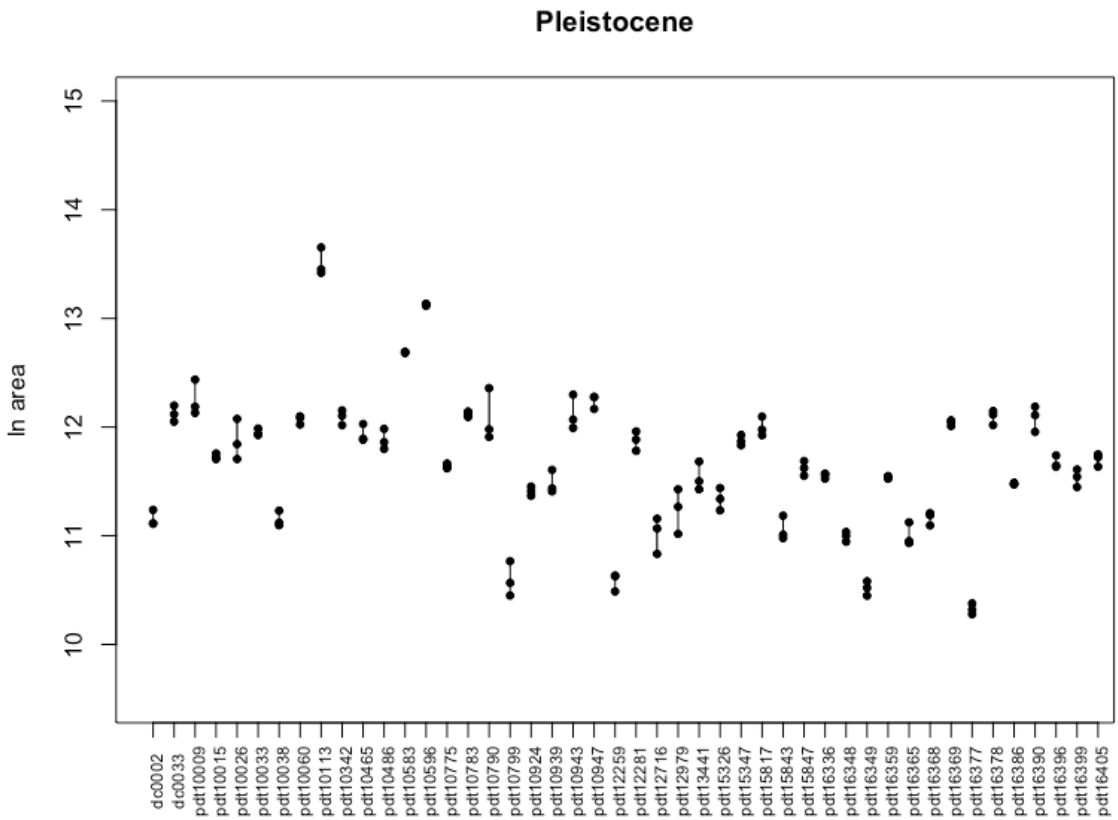
Pleistocene
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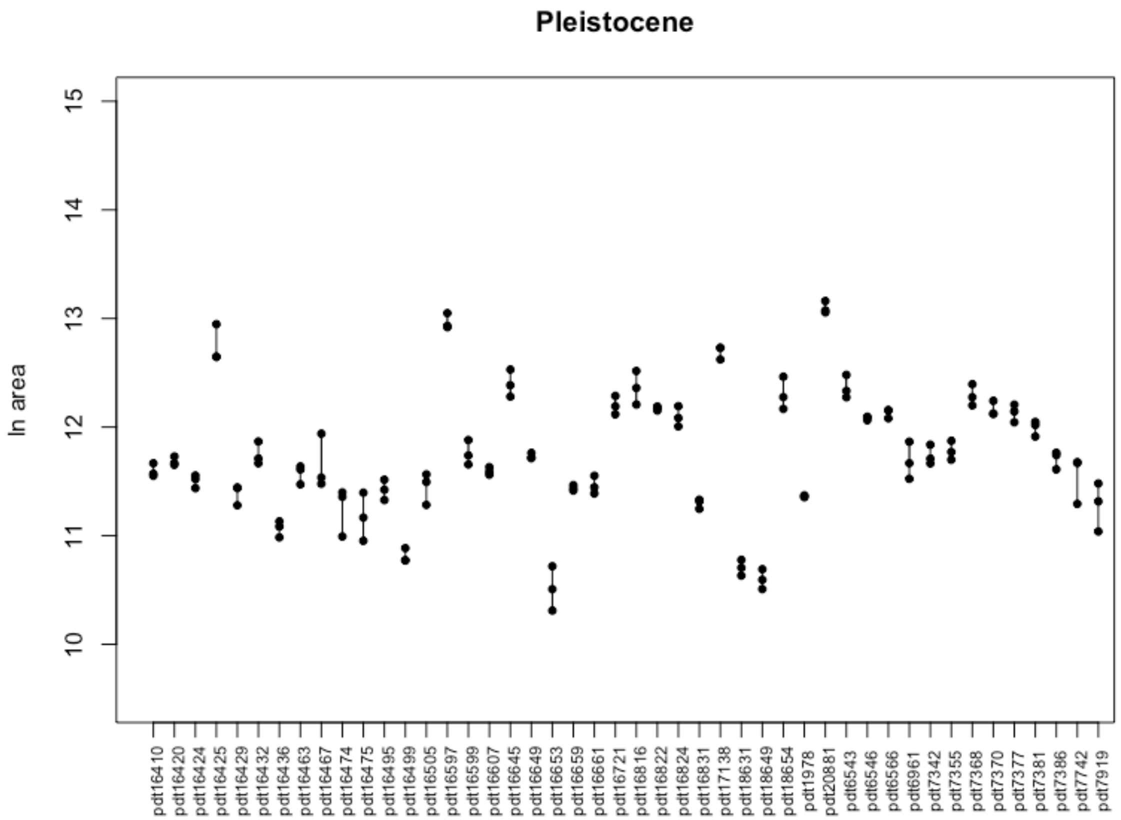
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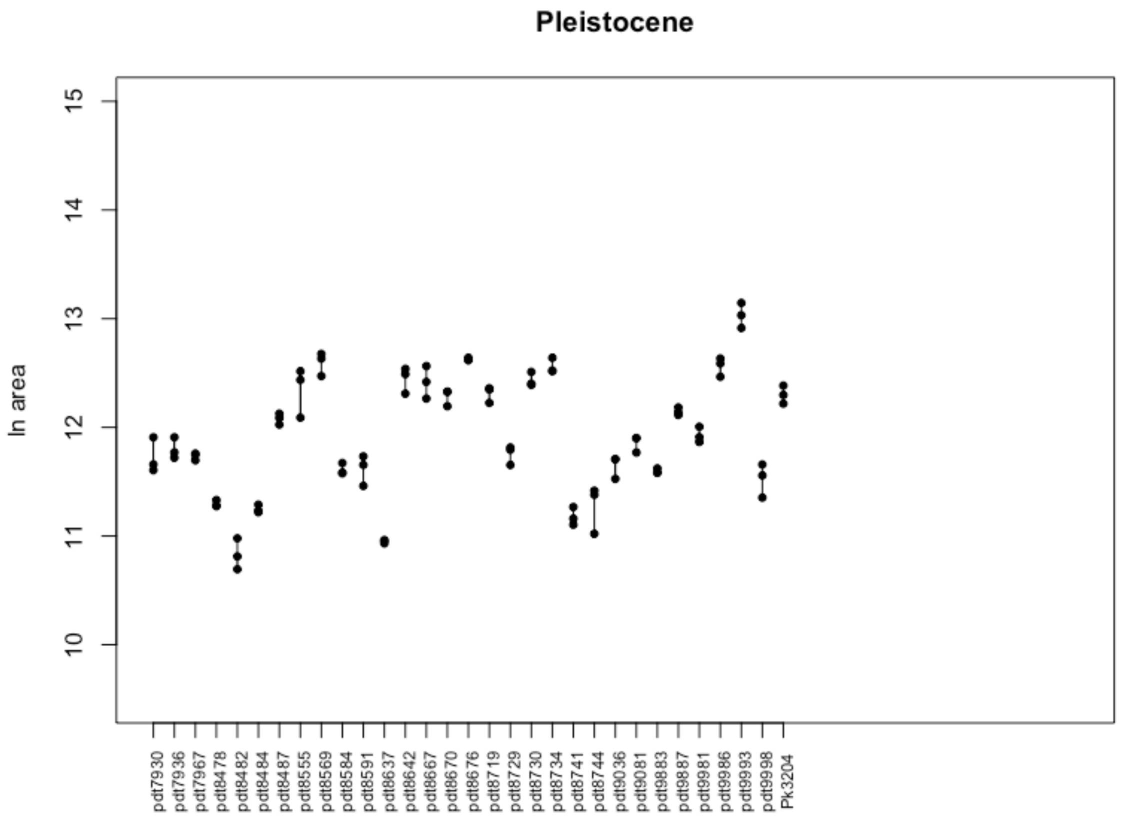
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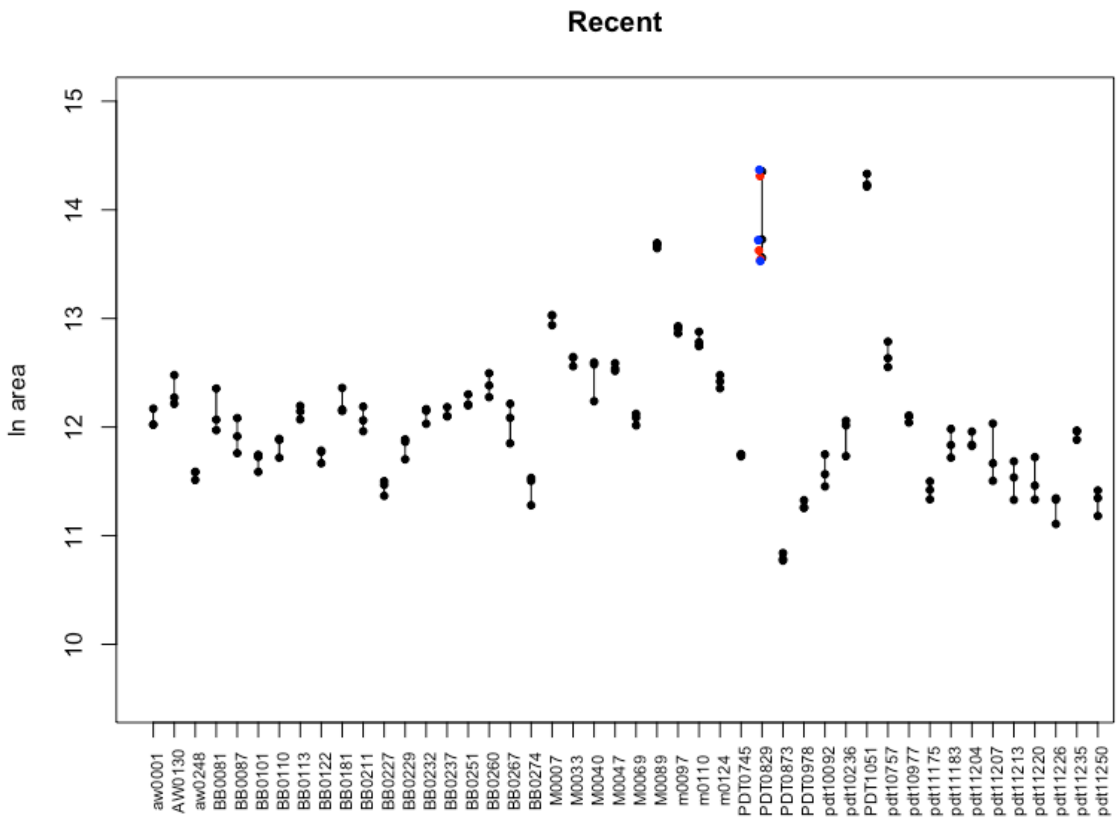
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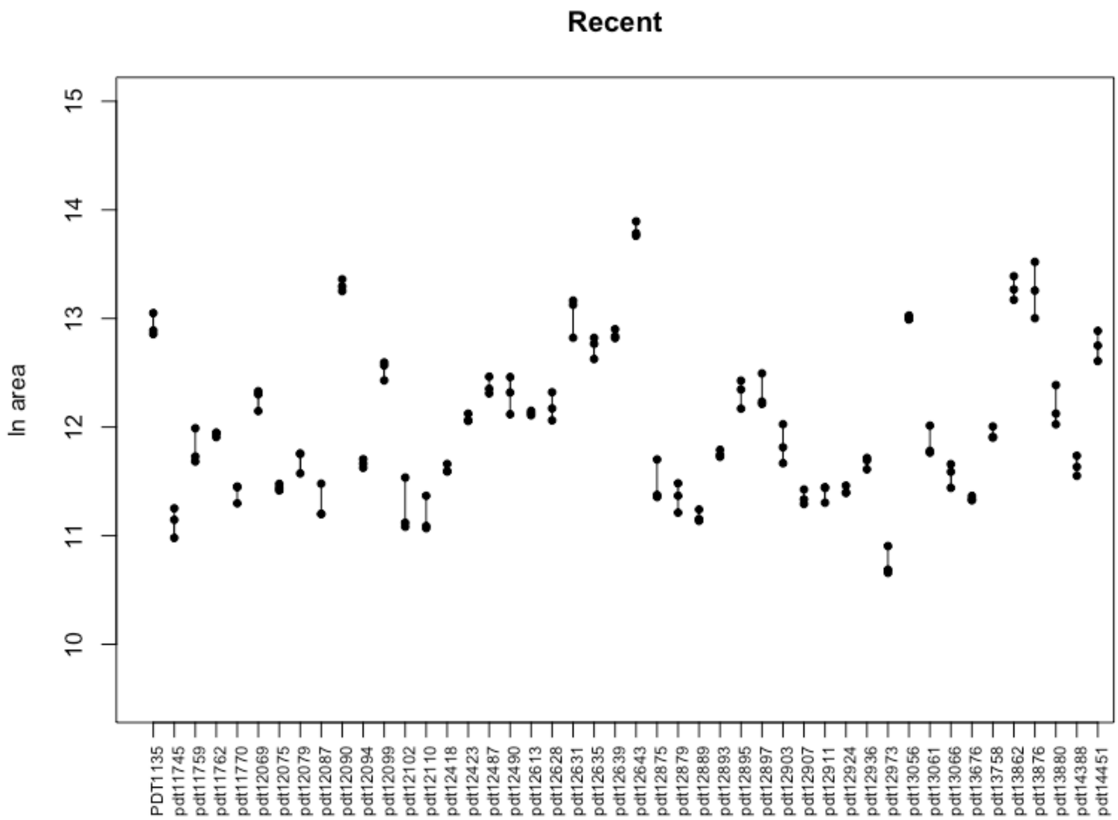
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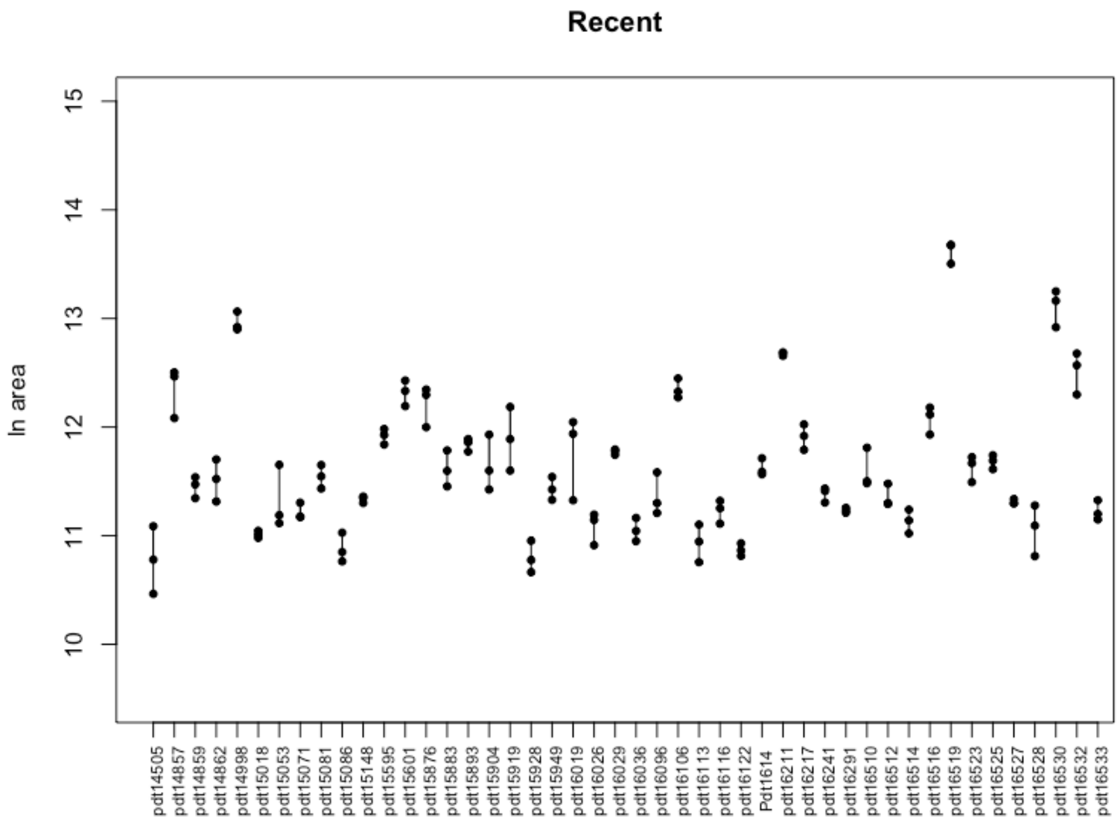
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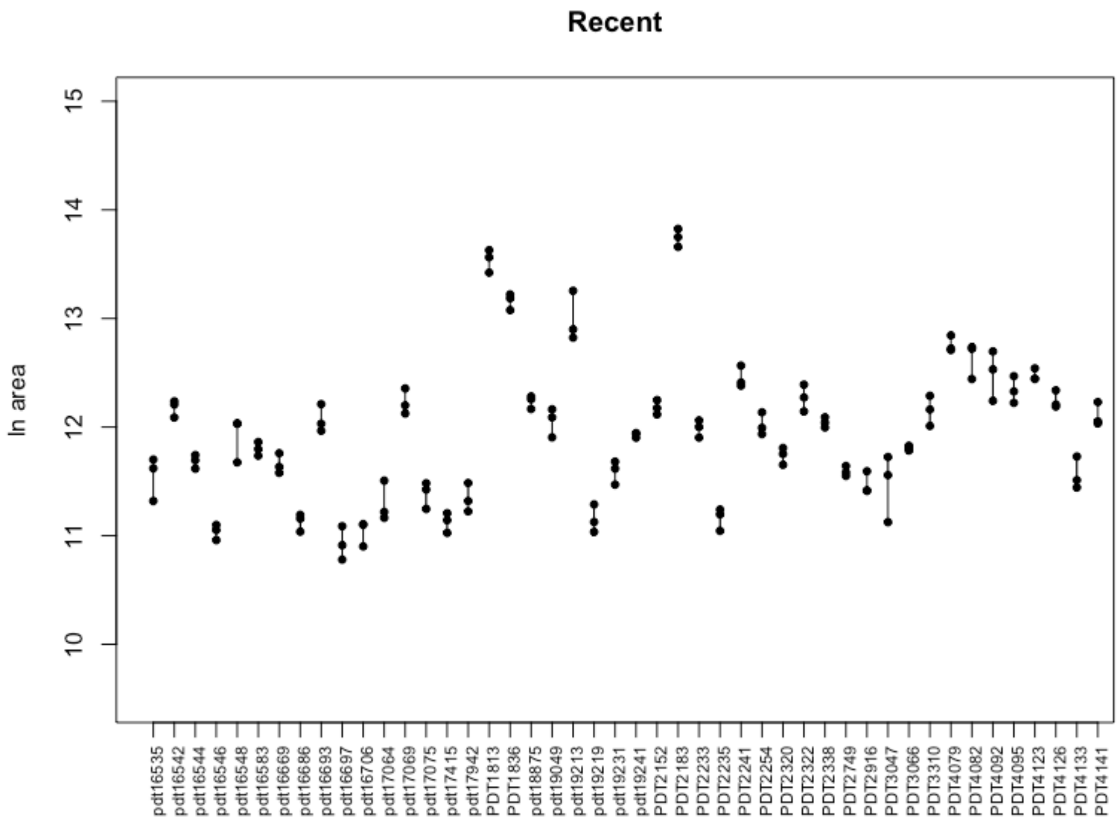
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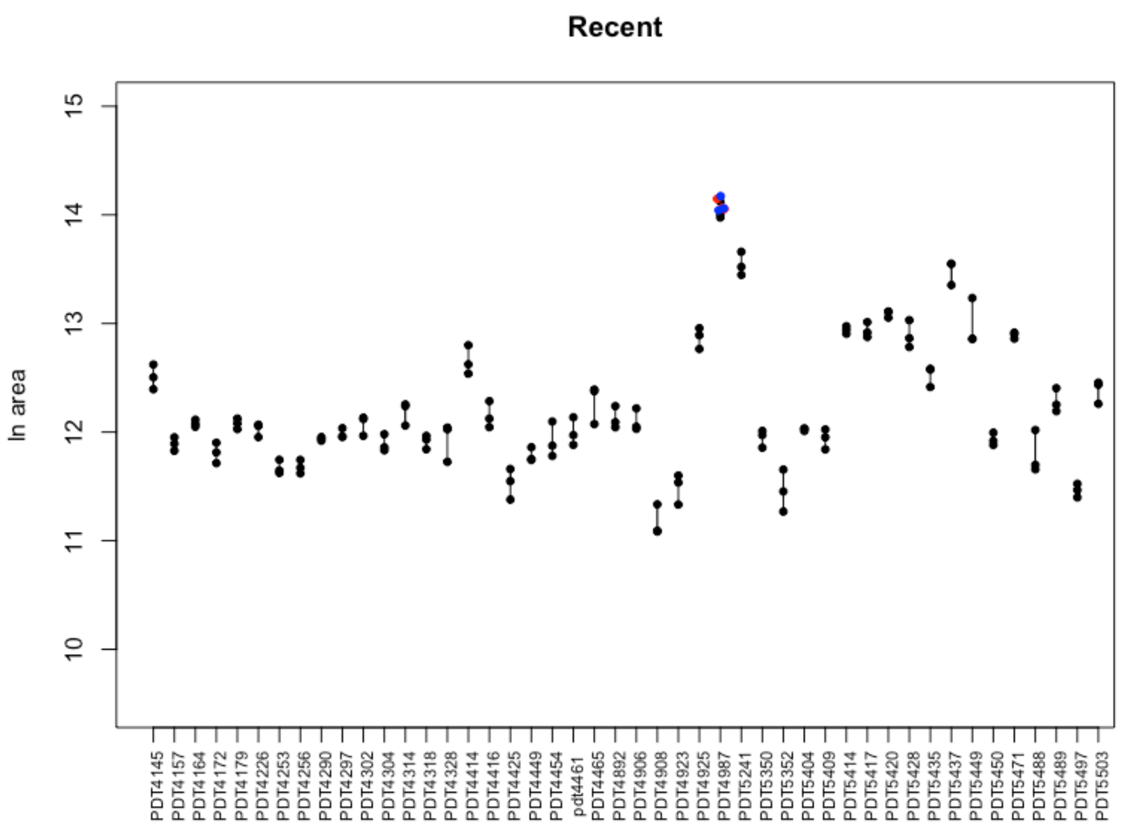
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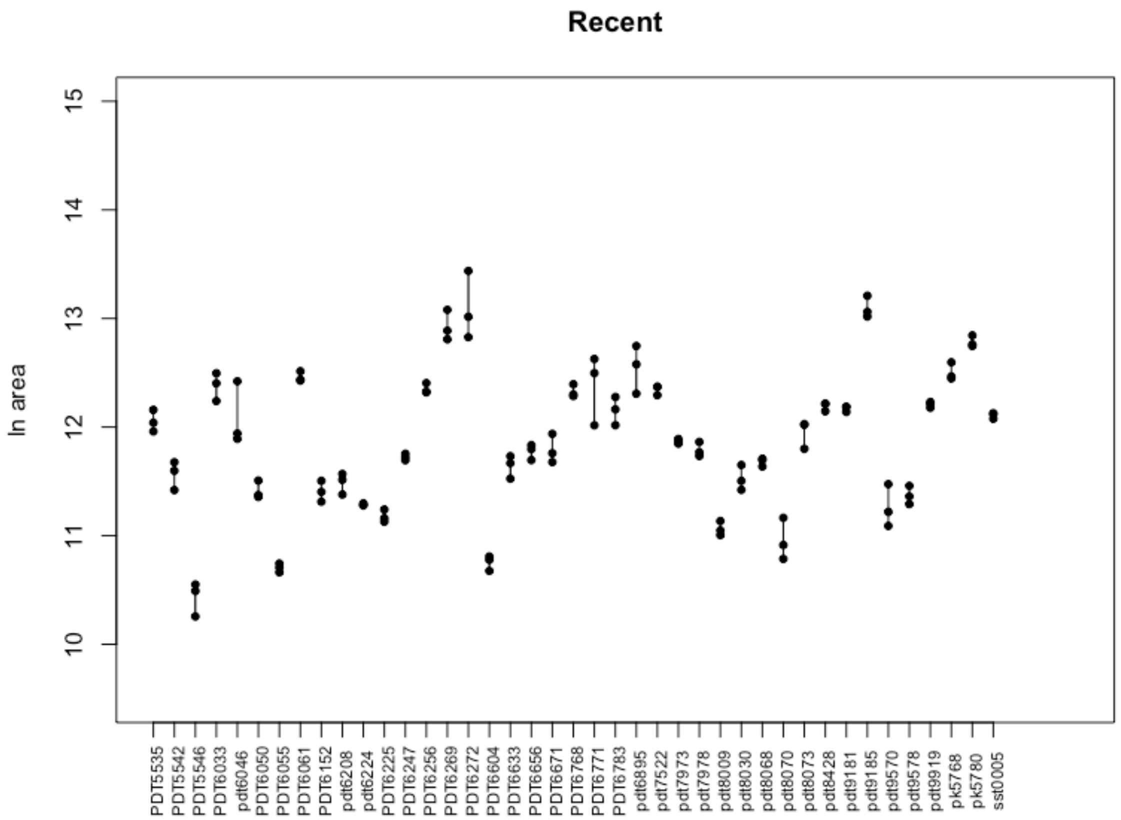
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pk5780
sst0005

55

Fig. S2. Length, width, area relationships. Each point represents a measurement of a zooid (natural logged in µm or µm^2) , from only the first measurement of any species (N = 3504). Zooid areas are square-rooted to reduce it to one dimension, except in the last panel. Red lines are fitted linear models and r.sq are adjusted r-squared values from the linear fit. Note that both length and width are reasonable proxies for area, but that length and width do not correlate well with each other. However, length times width is a good proxy for area (adjusted r-square = 0.958).

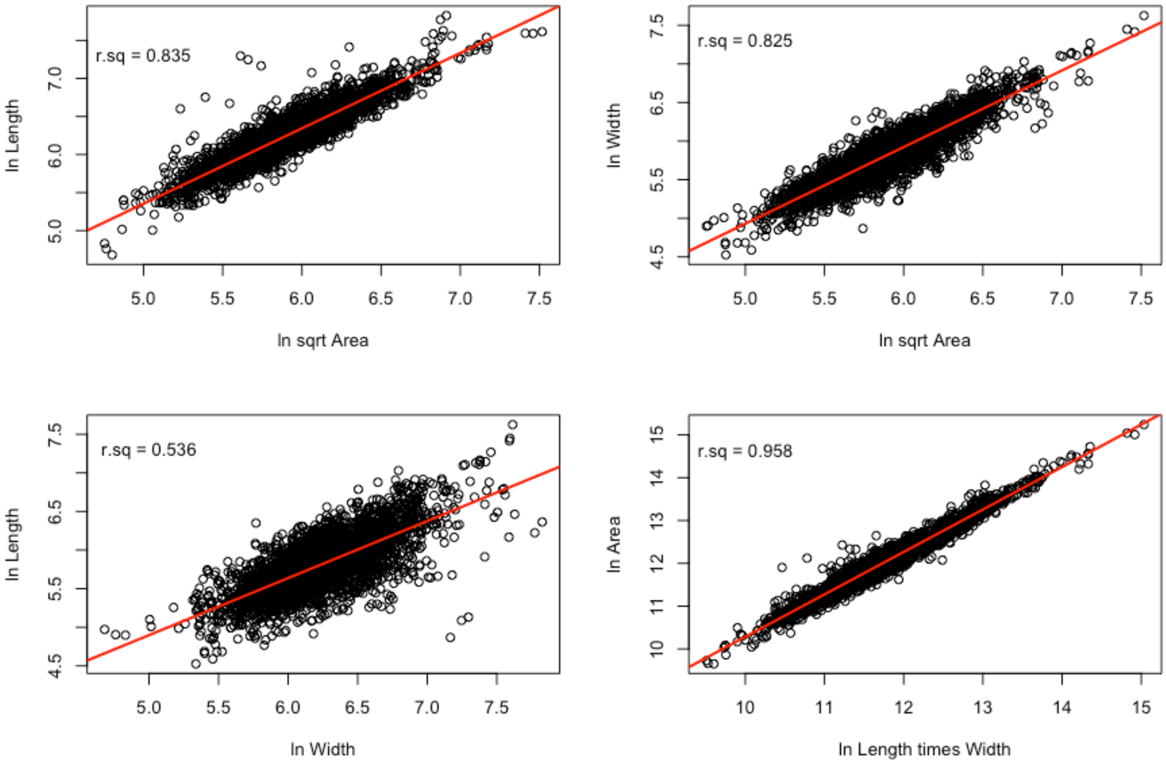


Fig. S3. Distribution of ln zooid area. A histogram showing the species means of all 1168 species. The grand median is 11.74 (plotted in blue) while the grand mean is 11.76 µm^2.

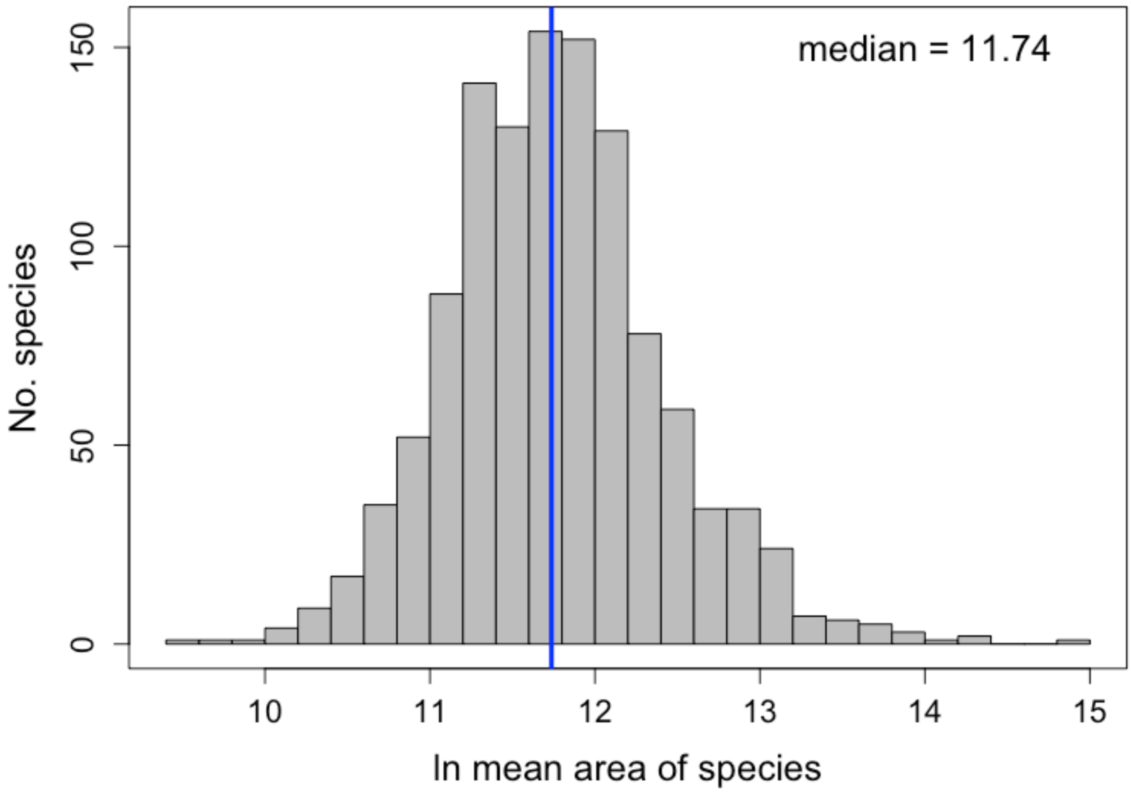
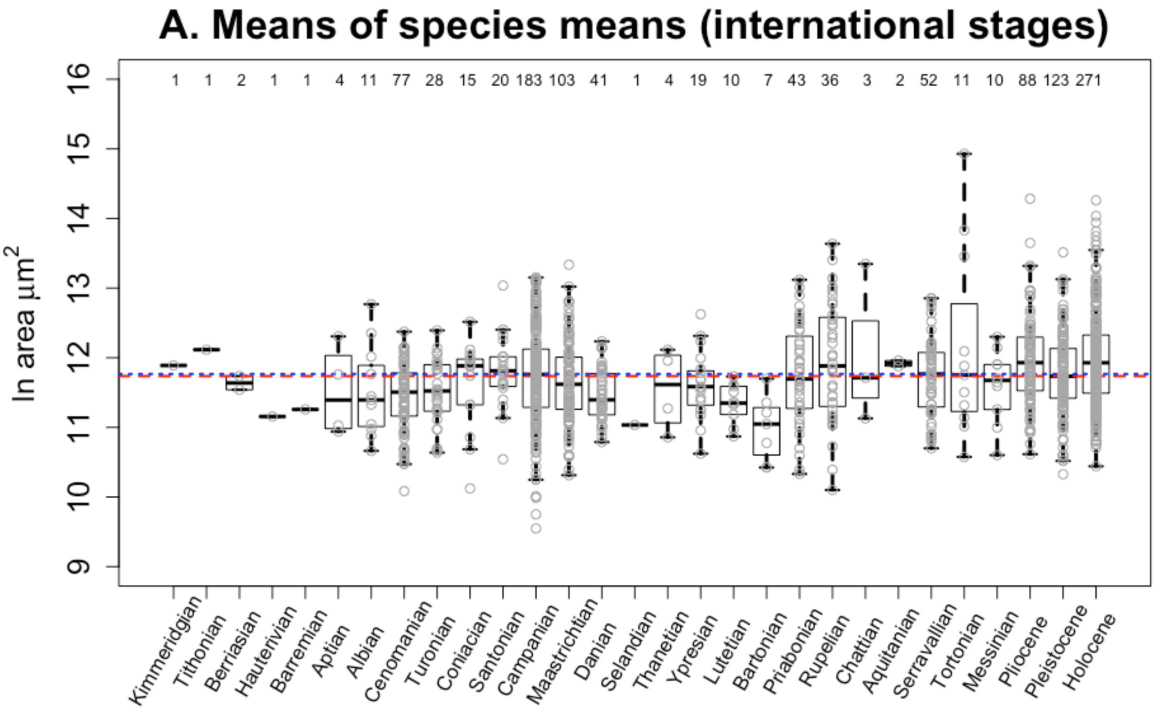


Fig. S4. Autozooid area over time. A. Boxplots of mean ln area µm^2 of cheilostome species sampled within international geological stages. B. The same data for 11 million year (myr) time intervals equivalent to one of the defaults used by the Paleobiology Database. As in main text Fig. 2, boxes show interquartile ranges (IQR) while whiskers extend to 1.5 times IQR. Grey open circles are individual species means. Numbers above the boxes are the number of species represented in the given time interval. The red lines are the grand median while the blue lines are the grand means.



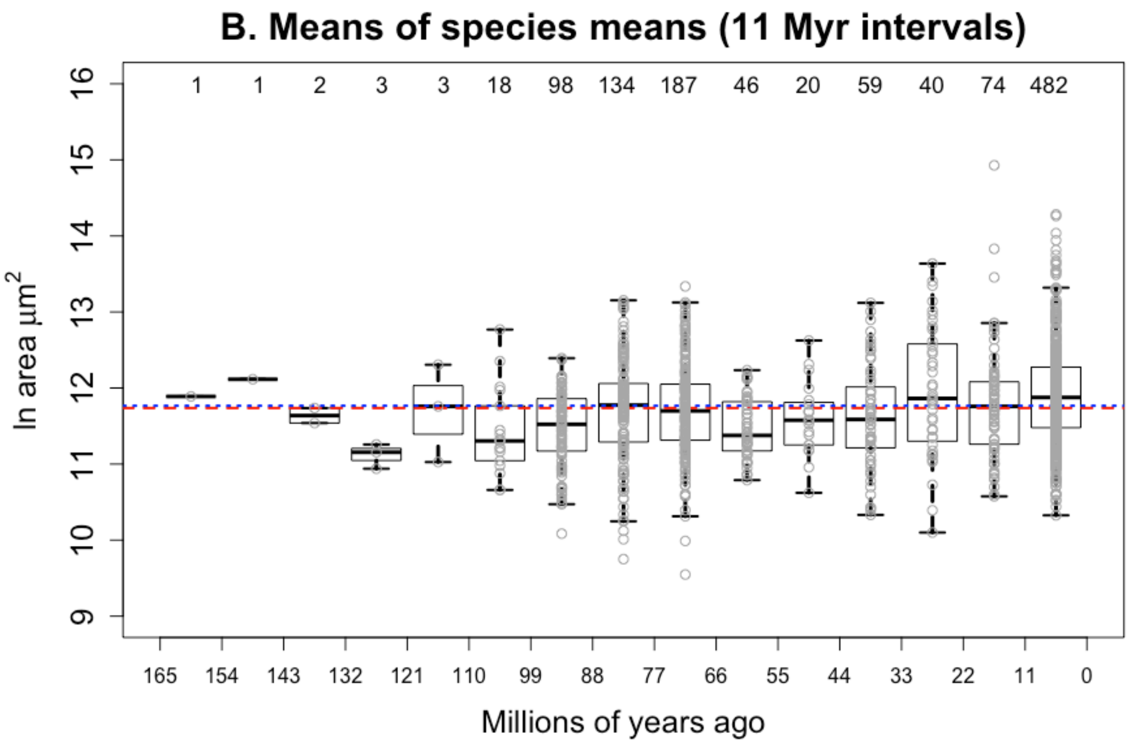


Table S1. Phenotypic change model weights. The first column indicates the models used. The column '10-million-year bins' shows model weights for data where the ln zooid area data are averaged in evenly spaced 10-million-year bins (data as in main text Fig. 2). The column 'Stages bins' shows model weights for data where the ln zooid area are averaged in international geological stages (as in Fig. S4A). The column '11-million year bins' shows model weights for data where the ln zooid area data are averaged in evenly spaced 11-million-year bins (data as in Fig. S4B). The column 'Runs' shows means (and standard deviations in parentheses) of 1000 model weights when ages of species are drawn from the duration of the geological stage they were found in (see main text). The best models are in bold.

Models	**10-million-year bins**	**International stages**	**11-million-year bins**	**Runs**
Unbiased Random Walk (URW)	0.090	0.003	0.193	**0.342** (0.169)
Generalized Random Walk (GRW)	0.031	0.001	0.067	0.119 (0.575)
Stasis	**0.571**	**0.812**	**0.712**	0.249 (0.204)
Strict Stasis (SS)	0	0	0	0 (0)
Ornstein Uhlenbeck model (OU)	0.309	0.185	0.028	0.288 (0.233)

Fig. S5. Average probabilities of larger descendants within genera. Each point (jittered to show overlapping points) plots the average binomial probability of having larger descendants in putative AD pairs in a genus, versus the number of species available for comparisons within that genus. Two of the most data-rich genera are labeled.

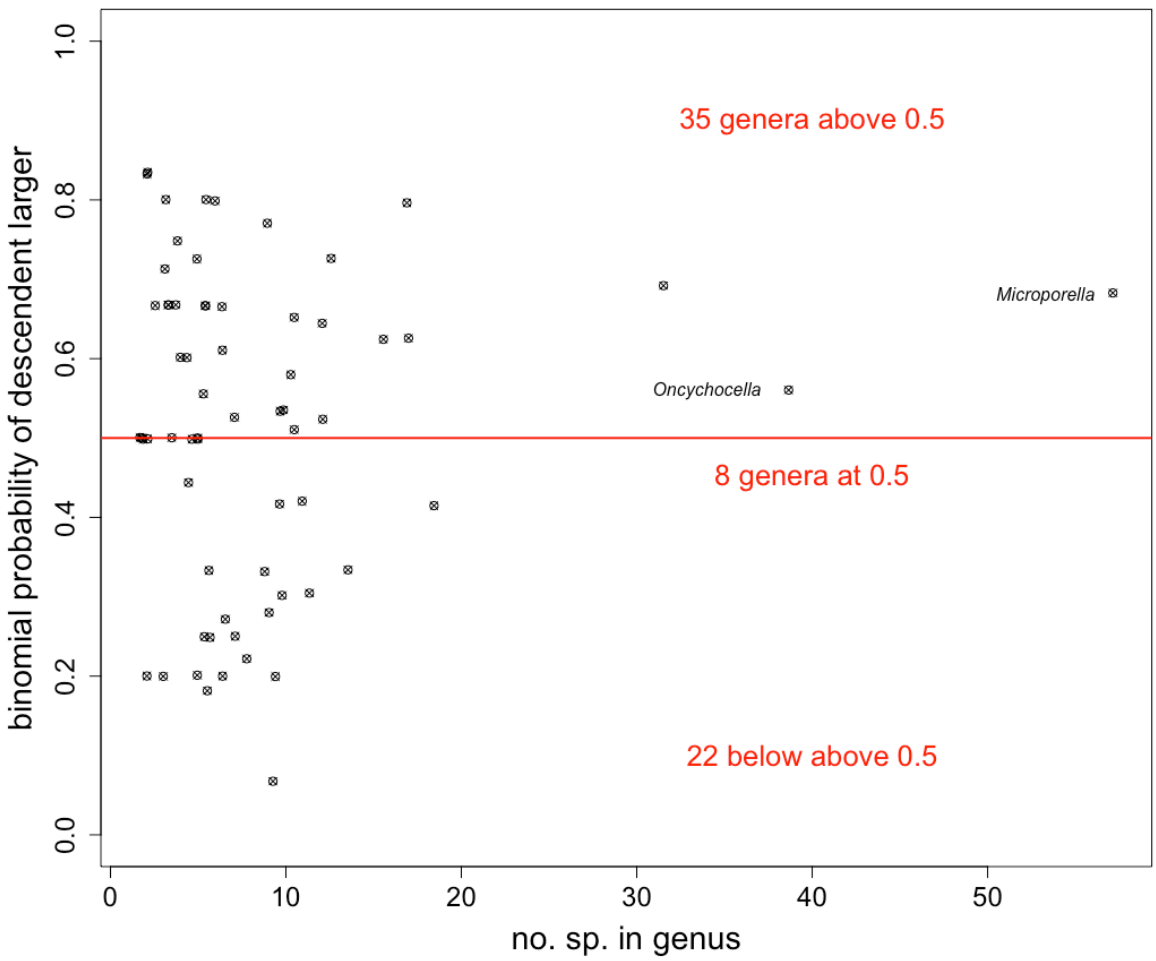


Table S2 A comparison of basic random effects models. Comparing four different random effects models indicated in the first column indicated using R notation. The columns are degree of difference (df), Akaike Information Criteria (AIC), followed by estimates for the fixed effect of log zooid area and standard error in parentheses, then random effect variances for species, repeat measurements in species, time (geologic stages) and residuals. Note that the third model includes time as fixed effects (hence the cell for random effects is empty). The df is 13 rather than 19 for the third model because some time intervals have no repeat measurements and are hence dropped from the analyses. Note that these analyses is based only on the colonies that have repeat measurements. The bold model is the best but the model with double asterisks is what will be used (see Table S3).

Model	df	AIC	Fixed (area)	Random (species)	Random (repeats)	Random (Time)	Residuals
~ (1|species/repeat)	5	-758	11.72 (0.10)	0.708	0.016	NA	0.0041
~ (1 | species)**	3	-365	11.72 (0.10)	0.712	NA	NA	0.0163
~ Time + (1 | species)	13	-381	11.46 (0.17)	0.415	NA		0.0163
~ (1 | Time) + (1 | species)	4	-368	11.81 (0.23)	0.509	NA	0.419	0.0163

Table S3 A comparison of mixed models including paleolatitude and growth forms. Comparing five different random effects are indicated using R notation (first column). The five rows under "two colony forms" include only the most common forms, namely encrusting sheet (N= 854) and erect colonies (N = 249). The five rows under "four colony forms" include also encrusting runners (N = 31) and free-living colonies (N = 33). The columns are degree of difference (df), Akaike Information Criteria (AIC). Note that this analysis is based only all colonies that can be assigned to a latitude. The bold model is the best one in each case, as also confirmed by an Anova analysis.

Model	df	AIC
Two colony forms		
~ (1 | Time) +(1 | species)	4	291
~ Form+(1 | Time) +((1 | species)	5	291
~PaleoLat+(1 | Time) +((1 | species)[§,+]	5	258
~PaleoLat +Form+(1 | Time) +((1 | species)[§]	6	244
~PaleoLat *Form+(1 | Time) +((1 | species)[§]	6	246
Four colony forms		
~ (1 | Time) +(1 | species)	4	328
~ Form+(1 | Time) +((1 | species)	7	311
~PaleoLat+(1 | Time) +((1 | species)	5	272
~PaleoLat +Form+(1 | Time) +((1 | species)*	8	264
~PaleoLat *Form+(1 | Time) +((1 | species)	11	267

[§]These three models have different slightly different AICs but are not significantly different in a anova test and hence the simplest model has been highlighted as the overall best model.

[+]Estimates for the best model from two colony forms data: zooid size (fixed effect) = 11.20 (std error = 0.09); latitude (fixed effect) = 0.012 (std error = 0.002); time (random effect variance) = 0.035 (std. dev = 0.18); species (random effect variance) = 0.37 (std. dev = 0.61); residual variance = 0.015 (std. dev = 0.12)

[*] Estimates for the best model from four colony forms data: zooid size (fixed effect) = 11.20 (std error = 0.09); latitude (fixed effect) = 0.012 (std error = 0.002); Free-living (fixed effect) = -0.40 (std. error = 0.12); Runner (fixed effect) = -0.03 (std. error = 0.12); Encrusting Sheet (fixed effect) = 0.04 (std. error = 0.05) time (random effect variance) = 0.031 (std. dev = 0.18); species (random effect variance) = 0.37 (std. dev = 0.61); residual variance = 0.015 (std. dev = 0.12). Hence, encrusting sheets are have marginally larger zooids than erect colonies while runners and free-living forms have somewhat smaller zooids than erect colonies.

Table S4. A comparison of mixed models for change in area from ancestor to descendent. Comparing three different random effects models indicated in the first column indicated using R notation, where shift indicates the change in latitude and abs.time.diff is the absolute difference in time between the putative ancestor and descendent (using estimates to the closest million years). The columns are degree of difference (df), Akaike Information Criteria (AIC), followed by estimates for the fixed effects of change in log zooid area and standard error in parenthesis, shift in (paleo)latitude, and absolute time difference between ancestor and descendent followed by genus random effects and the residuals. The bold model is the best one.

Model	df	AIC	Fixed (change in area)	Fixed (shift in latitude)	Fixed (time transpired)	Random (Genus)	Residual
~(1|genus)	3	8064	-0.061 (0.029)			0.04	0.44
~shift+(1|genus)	4	8065	-0.060 (0.029)	0.0005 (0.0006)		0.04	0.44
~shift+(1|genus)+ abs.time.diff	5	8067	- 0.061 (0.030)	0.0005 (0.0007)	2.96e-06 (5.98e-04)	0.04	0.44

Fig. S6. Shift in latitude versus change in ln zooid size (from Ancestor to Descendent). Each point represents a putative AD pair. The blue line is the null hypothesis, while the dotted red line is the estimated fit from the second model in Table S4. These are indistinguishable.