BRIEF COMMUNICATIONS ARISING

How foreign is the past?

ARISING FROM S. K. Lyons *et al.* **529,** 80–83 (2016); http://dx.doi.org/10.1038/nature16447

Since Humboldt and Darwin, ecologists have puzzled over what determines community assembly and structure and how community structure may change with time. Human activity is one potential driver. Impacts of modern human societies on the environment and its biota are massive, with many forms of pollution, loss and fragmentation of habitats, and extensive introductions of exotic species changing many ecological and biogeographical patterns. Prehistoric societies might be expected to have had a much lower impact on their environment. However, Lyons and colleagues[1] propose that biotic communities were so fragile that the limited settlements, agriculture, and associated activities 6,000 years ago in North America were sufficient to fundamentally change community-assembly rules. There is a Reply to this Brief Communication Arising by Lyons, S. K. *et al. Nature* **538,** http://dx.doi.org/10.1038/nature20097.

Lyons *et al.*[1] analysed co-occurrence patterns between taxon pairs in 53 fossil (aged 307 million–100 years) and 48 recent (<100 year old) presence–absence matrices, classifying each taxon pair as random, aggregated, or segregated. Lyons *et al.*[1] include 53 modern 'island' datasets in one analysis.

A weighted Loess smoother of the proportion of non-random taxon-pairs that are aggregated in fossil and recent datasets in relation to age (fig. 1 in ref. 1) shows a decrease towards the present day. A break-point analysis of the fossil, recent, and 'island' datasets suggests this decline started 6,000 years ago (extended data fig. 2 in ref. 1).

We were intrigued by these results, so investigated the data and methods used.

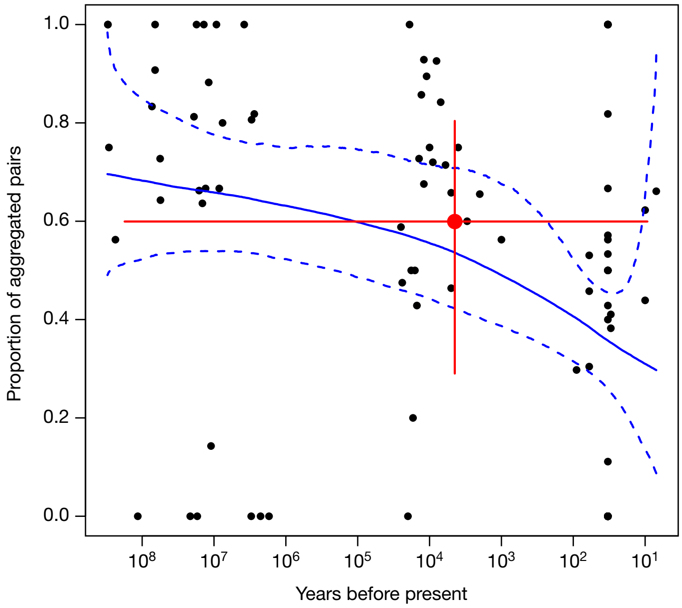


Figure 1 | Break-point re-analysis of the 'no-island' dataset using log[age] as the predictor and a Gaussian link function. The datasets are represented by black dots. The solid blue line is the median estimate for the model prediction from the Markov chain Monte Carlo (MCMC) samples. Dashed blue lines show the 2.5th and 97.5th percentiles of the MCMC prediction. Red dot represents the break point in the model and the lines in the *x* and *y* directions represent the 2.5th and 97.5th percentiles of its sampled values.

The oceanic island datasets included in the break-point analysis typically have a low proportion of aggregated taxon pairs[1], so their inclusion in the break-point analysis is a potential source of bias. The island datasets are not comparable with the fossil datasets, being influenced by natural biogeographical, evolutionary, and ecological processes that reflect strong dispersal limitations rather than by Holocene human activity, although recent human-mediated introductions and extinctions have changed island biota. For this reason they should not have been included in the break-point analysis.

We do not regard the majority of the recent datasets to be appropriate for comparison with the fossil assemblages. Of the 48 recent datasets, two are from the oceanic Canary Islands, and ten are from sky islands. Other dispersal-limited systems such as caves, drainage basins, and jars of artificial lake water at different distances from a Texan lake should also be excluded for the same reasons as the oceanic islands. Several sky-island mammal datasets are related (two are identical; a third is a transposed version of a fourth). Many of the remaining 36 datasets overlap, differing by a few observations or species, or sample the same sites repeatedly (for example, W. Australian camaenids is a subset of species in W. Australian snails, Senoran rodents (scrub) is a subset of sites in Senoran rodents (all sites), the Illinois woodlot birds 1978 and 1979 datasets sample the same sites, and so on). Thus many of these recent datasets cannot be considered independent and their influence will be inflated.

The post-glacial fossil data are dominated by North American pollen data at 1,000 year time slices. Adjacent time slices are likewise not independent.

Lyons *et al.*[1] report that the break-point results were "similar when island data were excluded". In fact, although the break-point age is identical (Extended Data Table 1), the already wide 95% confidence intervals of the break point widen to include the last five million years. This break point is not statistically significant. If the dispersal-limited recent datasets are also excluded (Extended Data Table 1), an early Permian break point is found. This instability reflects the large uncertainties in the break-point analysis.

That the break point has exactly the same age whether or not the island datasets (which constitute one-third of the data) are included may indicate that the break-point analysis failed to fit properly. So we refitted the model using Markov chain Monte Carlo sampling (see Methods). With all the data, models with one break point exhibit higher deviance information criterion scores than models with two, three, or four break points. The credible intervals around the break points are very wide and while these intervals include 6,000 years, there is no clear single event leading to a change in aggregation frequency. When we excluded the modern island data, the 95% credible interval of the break point fills almost the entire temporal extent of the study (Fig. 1). In fact, a model with no break point exhibits a lower deviance information criterion score. The statistical evidence for a mid-Holocene human-induced break point, the central claim of Lyons *et al.*[1], is therefore extremely weak, both in terms of its timing and even of its existence.

Without any break point, the proportion of aggregated pairs shows an exponential decline (that is, linear decline against logarithmic age) over the last 300 million years. This could be an exciting result. However it is more likely an artefact of variations in the number of sites in each dataset, which has a large effect on the proportion of aggregated pairs (Fig. 2). The median number of observations is larger (71) in the

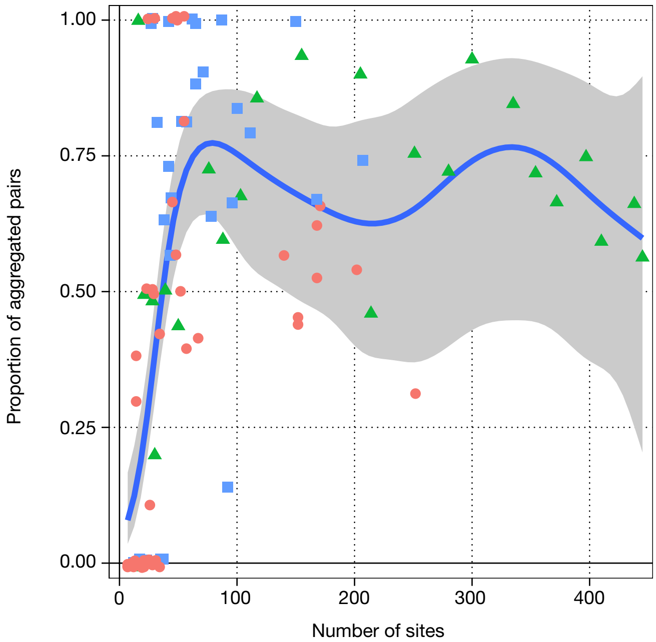


Figure 2 | Effect of number of observations on the proportion of aggregated taxon pairs for the datasets used by Lyons *et al.* Grey band shows the 95% confidence interval of a generalized additive model fitted with a quasi-binomial distribution. Data are jittered for clarity. Red circles show recent (<100 years) datasets; green triangles, shallow fossil; blue squares, deep fossil (>1 million years).

fossil datasets than the modern datasets (28). We explored this potential bias by taking large species presence–absence matrices and randomly sub-sampling them to generate smaller matrices. We then found the number of aggregated and segregated species pairs in each matrix.

With the desert rodent dataset, reducing the number of sites increases the proportion of aggregated pairs (Extended Data Fig. 1a). With three other datasets (Extended Data Fig. 1b–d), the proportion of aggregated pairs increases slightly then strongly declines as the number of sites decreases. Dataset specific nonlinear relationships between the number of sites and the proportion of aggregated pairs make it difficult to correct for this bias, but small datasets (<50–100 sites) should be avoided. Fifty-four per cent of the fossil and recent datasets used in Lyons *et al.*[1] contain <50 sites, as do 96% of the island datasets.

There is a long history in community ecology and island biogeography of disagreements about taxon co-occurrence analyses and their interpretation[2]. Some of the interpretative problems may result from Gotelli and Ulrich's[3] warning about co-occurrence analysis that "perhaps it is asking too much of a statistical analysis to reveal biologically meaningful pairwise associations with no other information than a binary presence–absence matrix". Gotelli and McCabe[4] emphasize that differences between datasets in terms of taxonomy, sampling effort, and site selection can affect the result of co-occurrence analyses and that "such issues cannot be resolved by statistical analyses that are based solely on presence–absence matrices. Simple null models are best viewed as statistical patterns for recognizing non-random patterns … rather than as a critical 'litmus' test for competitive effects". Co-occurrence analysis of presence/absence data may not be a sensitive enough approach to detect changes in community assembly and structure of heterogeneous fossil and recent assemblages. We suggest that inherent differences among the datasets used by Lyons *et al.* are causing biases and introducing artefacts into their analyses. The conclusion that community-assembly rules changed in the mid-Holocene due to human impact in North America cannot be upheld.

Methods

We implemented the break-point model described in Lyons *et al.*[1] for both the entire dataset and excluding the island data. Owing to instabilities in the likelihood estimation algorithm, we implemented the model in JAGS[5] which uses Markov chain Monte Carlo rather than the 'segmented' R package used by Lyons *et al.* This procedure does not change the model, just the fitting mechanism used to parameterize it. We compared models with zero and one break-point using deviance information criterion[6].

For the power analysis, datasets were randomly sub-sampled to generate matrices with fewer sites and a constant number of species. Species co-occurrence analyses were done in an R implementation[7] of Pairs[3] using 20 bins. Ten replicates were performed for each number of sites.

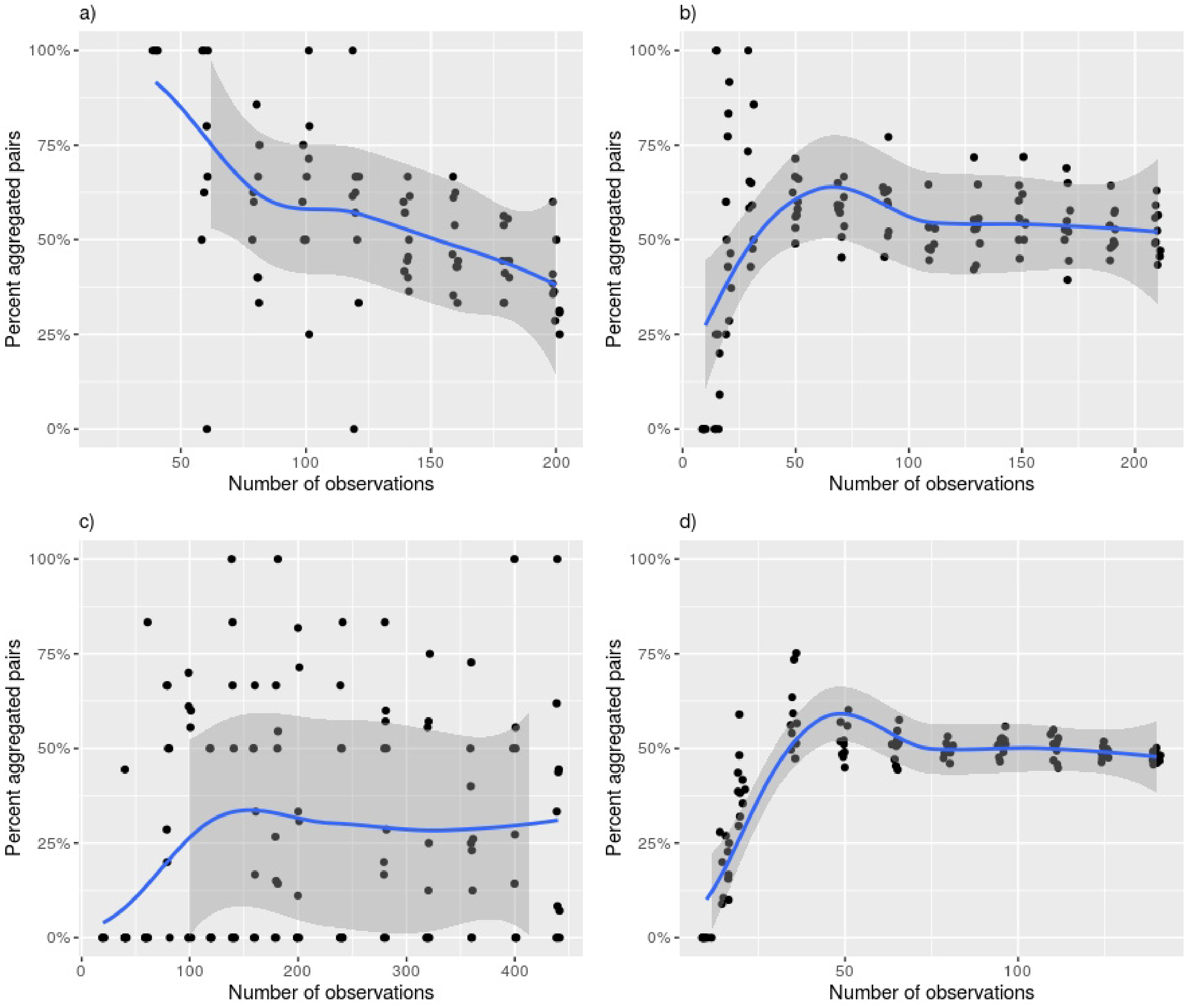
Richard J. Telford[1], Joseph D. Chipperfield[1], Hilary H. Birks[1] & H. John B. Birks[1,2]
[1]Department of Biology, University of Bergen, PO Box 7803, N-5020 Bergen, Norway.
email: richard.telford@uib.no
[2]Environmental Change Research Centre, University College London, London WC1E 6BT, UK.

1. Lyons, S. K. *et al.* Holocene shifts in the assembly of plant and animal communities implicate human impacts. *Nature* **529,** 80–83 (2016).
2. Sanderson, J. G. & Pimm, S. L. *Patterns in Nature. The Analysis of Species Co-occurrences.* (Univ. Chicago Press, 2015)
3. Gotelli, N. J. & Ulrich, W. The empirical Bayes approach as a tool to identify non-random species associations. *Oecologia* **162,** 463–477 (2010).
4. Gotelli, N. J. & McCabe, D. J. Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecology* **83,** 2091–2096 (2002).
5. Plummer, M. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003),* March 20–22, Vienna, Austria (2003).
6. Spiegelhalter, D. J., Best, N. G., Carlin, B. P. & van der Linde, A. Bayesian measures of model complexity and fit. J. R. *Stat. Soc. Series B Stat. Methodol.* **64,** 583–639 (2002).
7. von Gagern, M., von Gagern, M. & Schmitz Ornés, A. Problems with bins: a critical reassessment of Gotelli and Ulrich's Bayes approach using bird data. *Acta Oecol.* **69,** 137–145 (2015).

Author Contributions All authors discussed the manuscript. R.J.T. investigated the modern datasets and ran the power tests. J.D.C. carried out the break-point analyses. R.J.T., H.H.B., and H.J.B.B. contributed to the first draft. All authors edited the final draft.

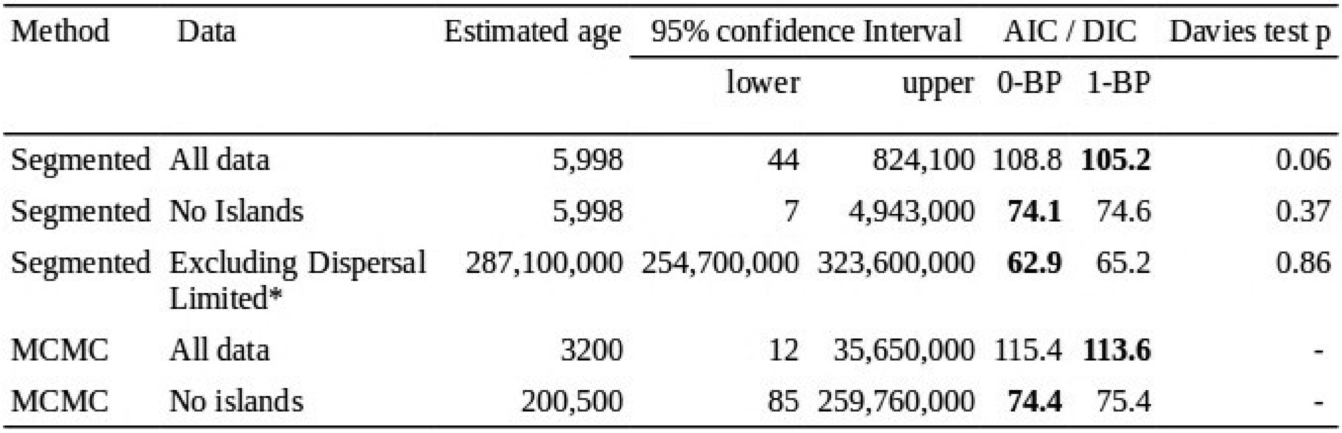
Competing Financial Interests Declared none.

doi:10.1038/nature20096



Extended Data Figure 1 | Effect of number of observations on percentage of aggregated taxon pairs for four datasets used by Lyons *et al.*[1] a–d, US desert rodents (**a**), Holocene mammals (**b**), 1,000-year-old North American pollen (**c**), and 1950 Wisconsin understorey vegetation (**d**). Grey band shows 95% confidence interval of a local regression smoother fitted with a quasi-binomial distribution.

Extended Data Table 1 | Estimated age (years) of the break point and its 95% confidence interval (credible interval for MCMC model) for different subsets of the data



Method	Data	Estimated age	95% confidence Interval		AIC / DIC		Davies test p
			lower	upper	0-BP	1-BP	
Segmented	All data	5,998	44	824,100	108.8	**105.2**	0.06
Segmented	No Islands	5,998	7	4,943,000	**74.1**	74.6	0.37
Segmented	Excluding Dispersal Limited*	287,100,000	254,700,000	323,600,000	**62.9**	65.2	0.86
MCMC	All data	3200	12	35,650,000	115.4	**113.6**	-
MCMC	No islands	200,500	85	259,760,000	**74.4**	75.4	-

Akaike information criterion (AIC) for segmented models and deviance information criterion[6] (DIC) for MCMC models with zero or one break point (BP). Lowest AIC/DIC highlighted in bold. *P* value of a Davies test with one break point. The Davies test is conservative.

*Dispersal-limited datasets are six US montane mammal datasets; terrestrial cave invertebrates; two Canary island beetles datasets; Andean butterflies; Great-Basin fish; and aquatic organisms in jars of artificial lake water.

Lyons *et al.* reply

REPLYING TO R. J. Telford *et al.* *Nature* **538,** http://dx.doi.org/10.1038/nature20096 (2016)

In the accompanying Comment[1], Telford *et al.* claim that many of the modern datasets we used previously[2] were inappropriate for the analysis, and that the pattern through time is uninteresting and probably the result of differences in sample size (number of sites in each data set). We find their criticisms to be flawed for several reasons.

We disagree with the claim of Telford *et al.*[1] that many of our modern datasets are inappropriate for comparison with fossil datasets The contemporary landscape is highly fragmented[3,4]. Excluding modern assemblages that are relicts or in patchy habitats is a subjective exercise and would leave few, if any, modern ecosystems to analyse; another indication that the present is different. Moreover, some of our fossil plant data sets represent local communities from edaphically distinct habitat islands[5–7], making them comparable to modern dispersal-limited systems. The datasets were selected because of their age, not because they demonstrated human influence. The only objective classification is island versus mainland, as used by Lyons *et al.*[2] Nonetheless, we redid our break-point analysis removing successively larger amounts of the modern data sets as proposed by Telford *et al.*[1] Specifically, we eliminated data sets with small sample sizes and those that were subsets of sites, species, or habitats from other datasets (see Supplementary Information). We did not delete any fossil pollen assemblages because they are separated by 1,000 to 20,000 years, do not necessarily contain the same cores, and vary in their geographic extent. They are not subsets of one another, even if some of the genera and sites may recur. These new analyses gave comparable results to our previous findings[2], with consistent differences in the proportion of aggregated species pairs through time and a consistent Holocene break point (Extended Data Table 1).

Telford *et al.* also misconstrue our use of the break-point analysis. We did not use it as a formal statistical hypothesis test. Nor did we argue that the decline in aggregated species pairs through time was literally represented by a function with two linear segments. Rather, we used the break-point analysis to identify the approximate time the decline became more pronounced. Using a different break-point algorithm, Telford *et al.*[1] find a mid-Holocene break point with wide confidence intervals as we did previously[2]. They report the most parsimonious model is one that does not have a break point but instead an "exponential decline" in the proportion of aggregated pairs through time. Thus, their new analysis confirms the following results: a) the proportion of aggregated species pairs shows a prominent decline over the last 300 million years; b) the decline is non-linear; c) the decline becomes steeper in the Holocene.

Having confirmed our previous core results[2], Telford *et al.*[1] argue that sampling is responsible. However, their data supporting a sample size effect are highly inconsistent. Two of the four datasets in their extended data fig. 1 (modern Wisconsin understory plants and Holocene mammals) showed a significant effect of decreasing proportion of aggregations with lower sample size (linear model, $P < 0.05$), one (1,000-year-old North American pollen) showed no significant effect, and one (US desert rodents) showed a significant effect in the opposite direction (proportion of aggregations increased with lower sample size).

Using data from Telford *et al.* simulations[1], we note that the purported sample size effect in their extended data fig. 1 is found only at low sample sizes (rarefying to ten samples). Even slightly elevated sampling removes this effect; when rarefying to 20, two datasets were non-significant and two showed a relationship in the opposite direction (Extended Data Fig. 1). Redoing our analyses while eliminating datasets with less than 10, 20 or even 50 sites does not change our results substantially (Extended Data Table 1).

A more direct test of the effect of sampling is to stratify the data sets into three groups: Deep Time (>1 million years ago; $n = 29$ data sets), Shallow Time (1 million–100 years ago; $n = 24$), and Modern (<100 years ago; $n = 46$). In these groupings, both Deep Time and Modern data sets have similar sample sizes ($P = 0.37$), but they differ significantly in the proportion of aggregated pairs ($P < 0.01$; Extended Data Fig. 2). Similarly, while Deep and Shallow Time data sets are significantly different in their sample sizes ($P < 0.001$), the per cent aggregations are not significantly different ($P = 0.90$). Together, this indicates that the significant reduction in per cent aggregated species pairs through time is driven by a sudden shift downward towards the Modern. Limiting analysed datasets to those more acceptable to Telford *et al.*[1], we still find significantly fewer aggregations in modern versus fossil data sets and a Holocene break point (Extended Data Table 1). Our key finding[2], that modern communities represent a unique state in the history of life, remains unchanged.

Author D.W. of ref. 2 did not participate in this Reply.

S. Kathleen Lyons[1], Joshua H. Miller[2], Kathryn L. Amatangel[3], Anna K. Behrensmeyer[4], Antoine Bercovici[1], Jessica L. Blois[4], Matt Davis[5], William DiMichele[1], Andrew Du[6], Jussi T. Eronen[7], J. Tyler Faith[8], Gary R. Graves[9,10], Nathan Jud[11], Conrad Labandeira[1,12,13], Cindy V. Looy[14], Brian McGill[15], David Patterson[6], Silvia Pineda-Munoz[1], Richard Potts[16], Brett Riddle[17], Rebecca Terry[18], Anikó Tóth[1], Werner Ulrich[19], Amelia Villaseñor[6], Scott Wing[1], Heidi Anderson[20], John Anderson[20] & Nicholas J. Gotelli[21]

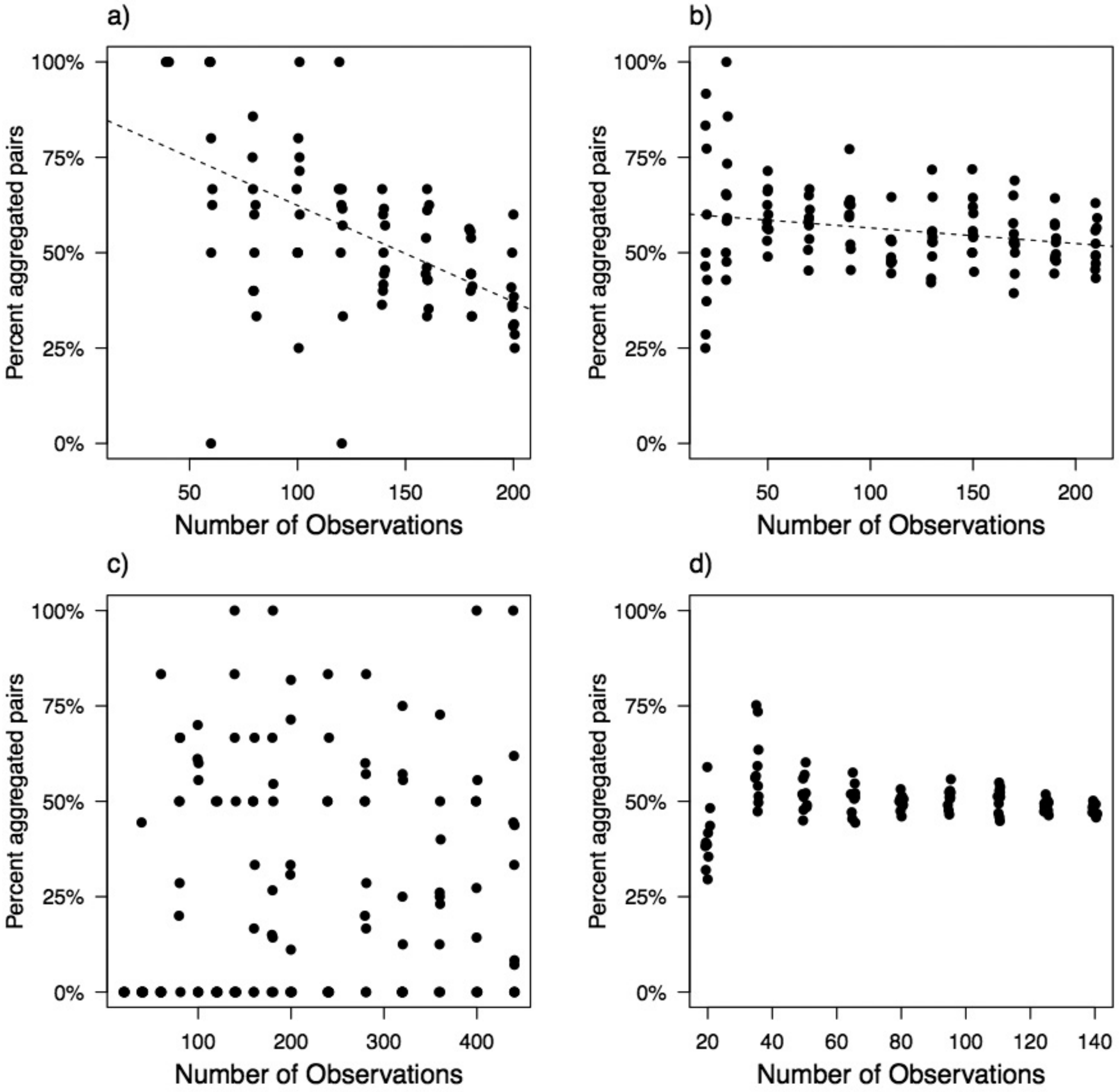
[1]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington DC 20013, USA.
email: lyonss2@si.edu
[2]Department of Geology, University of Cincinnati, Cincinnati, Ohio 45221, USA.
[3]Department of Environmental Science and Biology, The College at Brockport – SUNY, Brockport, New York 14420, USA.
[4]School of Natural Sciences, University of California, Merced, 5200 North Lake Road, Merced, California 95343, USA.
[5]Department of Geology and Geophysics, Yale University, New Haven, Connecticut 06520, USA.
[6]Hominid Paleobiology Doctoral Program, Center for the Advanced Study of Hominid Paleobiology, Department of Anthropology, George Washington University, Washington DC 20052, USA.
[7]Department of Geosciences and Geography, University of Helsinki, 00014 Helsinki, Finland.
[8]School of Social Science, The University of Queensland, Brisbane, Queensland 4072, Australia.
[9]Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington DC 20013, USA.
[10]Center for Macroecology, Evolution and Climate, University of Copenhagen, Copenhagen 2100, Denmark.
[11]Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, USA.

[12]Department of Entomology, University of Maryland College Park, College Park, Maryland 20742, USA.
[13]Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing 100048, China.
[14]Department of Integrative Biology and Museum of Paleontology, University of California Berkeley, Berkeley, California 94720, USA.
[15]School Biology and Ecology & Sustainability Solutions Initiative, University of Maine, Orono, Maine 04469, USA.
[16]Department of Anthropology, Human Origins Program, National Museum of Natural History, Smithsonian Institution, Washington DC 20013, USA.
[17]School of Life Sciences, University of Nevada–Las Vegas, Las Vegas, Nevada 89154, USA.
[18]Department of Integrative Biology, Oregon State University, Corvallis, Oregon 97731, USA.
[19]Chair of Ecology and Biogeography, Nicolaus Copernicus University, Lwowska 1, 87-100 Torun, Poland.
[20]Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg 20150, South Africa.
[21]Department of Biology, University of Vermont, Burlington, Vermont 05405, USA.

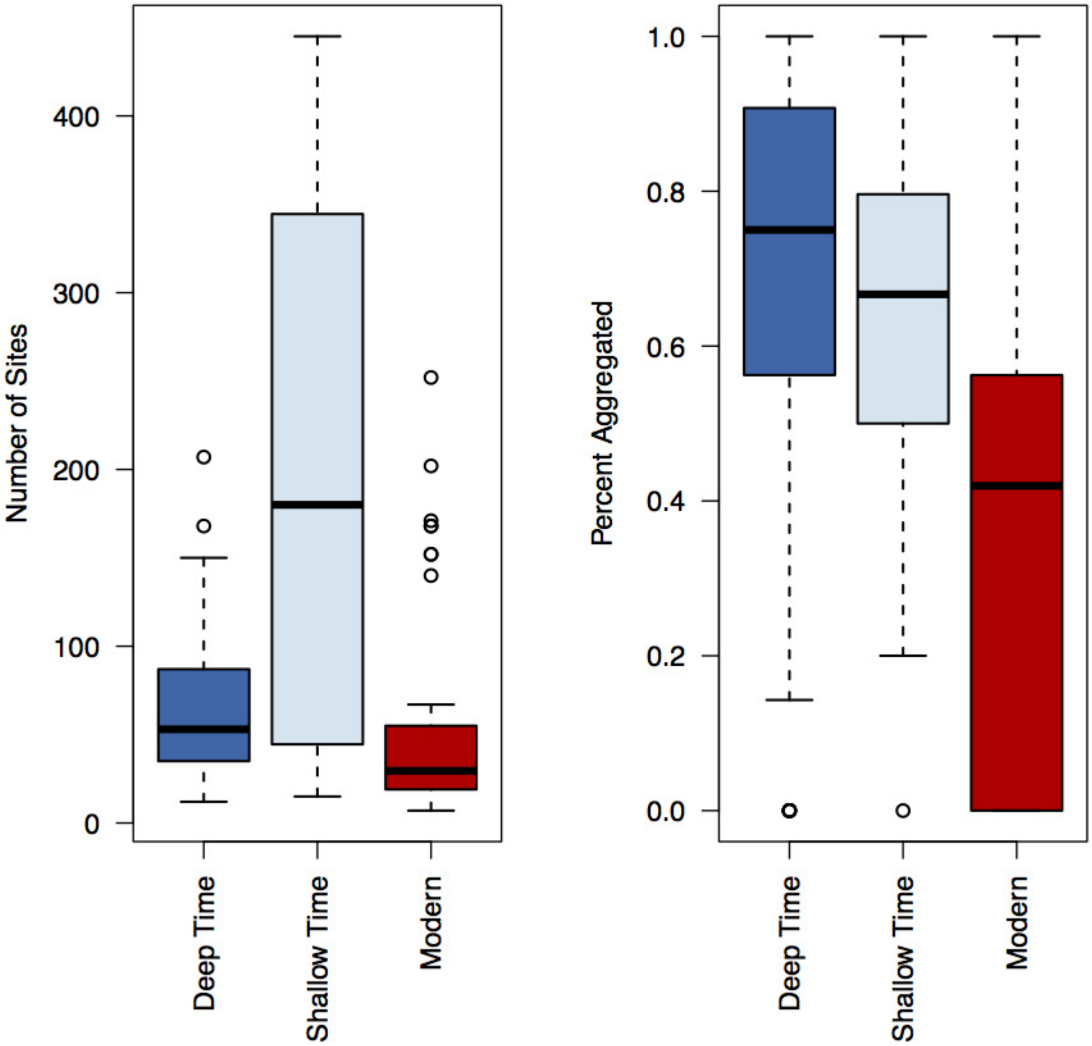
1. Telford, R. J., Chipperfield, J. D., Birks, H. H. & Birks, H. J. B. How foreign is the past? *Nature* **538**, http://dx.doi.org/10.1038/nature20096 (2016).
2. Lyons, S. K. *et al.* Holocene shifts in the assembly of plant and animal communities implicate human impacts. *Nature* **529,** 80–83 (2016).
3. Law, B. S. & Dickman, C. R. The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. *Biodivers. Conserv*. **7,** 323–333 (1998).
4. McDonald, R. I., Kareiva, P. & Formana, R. T. T. The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biol. Conserv.* **141,** 1695–1703 (2008).
5. Greb, S. F. & DiMichele, W. A. (eds) *Wetlands through Time* Vol. 399 (The Geological Society of America 2006).
6. DiMichele, W. A., Philips, T. L. & Olmstead, R. G. Opportunistic evolution: abiotic environmental stress and the fossil record of plants. *Rev. Palaeobot. Palynol.* **50,** 151–178 (1987).
7. Wing, S. L., Alroy, J. & Hickey, L. J. Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **115,** 117–155 (1995).

Supplementary Information is available in the online version of the paper.

doi:10.1038/nature20097



Extended Data Figure 1 | Results from subsetting analyses rarefying to 20 sites instead of 10 as done by Telford *et al.*[1] a–d, Datasets are US desert rodents (**a**), Holocene mammals (**b**), 1,000-year-old North American pollen (**c**) and 1950 Wisconsin understory vegetation (**d**). Lines indicate a significant linear regression at $P < 0.05$. Panels without lines are non-significant.



Extended Data Figure 2 | Box plots showing the number of sites and proportion of aggregated species pars with the data stratified into three groups: Deep Time (>1 million years ago Ma; $n = 29$ data sets), Shallow Time (1 million–100 years ago; $n = 24$), and Modern (<100 years ago; $n = 46$). Deep Time and Modern datasets each differ significantly in the number of sites compared to Shallow time, but Deep Time and Modern datasets do not differ significantly from one another (left; $P = 0.37$). By contrast, there is a significant difference between Deep Time and Modern datasets in the proportion of aggregated species pairs ($P < 0.01$). Even if there is an effect of sample size on pairs analysis, it cannot explain our previous findings[2].

Extended Data Table 1 | Results of break-point analysis and ANOVAs showing a consistent difference in the proportion of aggregated pairs in modern versus fossil data sets and a consistent Holocene break point

Datasets	mean proportion of aggregated species pairs			p (anova)	Breakpoint (yrs)
	Deep fossil	Shallow fossil	Modern/Historical		
All original data included	0.63 [N=29]	0.64 [N=24]	0.33 [N=50]	<0.001	6000
Corrected data only	0.63 [N=29]	0.64 [N=24]	0.37 [N=46]	<0.001	6002
Corrected data; overlapping datasets removed	0.63 [N=29]	0.64 [N=24]	0.30 [N=32]	<0.001	6008
Corrected data; overlapping datasets removed; Telford filtered	0.63 [N=29]	0.64 [N=24]	0.34 [N=25]	<0.001	6000
Corrected data; overlapping datasets removed; >=10 sites	0.63 [N=29]	0.64 [N=24]	0.33 [N=29]	<0.001	6003
Corrected data; overlapping datasets removed; Telford filtered; >=10 sites	0.63 [N=29]	0.64 [N=24]	0.35 [N=24]	0.0016	6001
Corrected data; overlapping datasets removed; >=20 sites	0.68 [N=27]	0.66 [N=22]	0.40 [N=22]	0.0020	6999
Corrected data; overlapping datasets removed; Telford filtered >=20 sites	0.68 [N=27]	0.66 [N=22]	0.41 [N=19]	0.0049	6998
Corrected data; overlapping datasets removed; >=50 sites	0.79 [N=15]	0.71 [N=18]	0.53 [N=8]	0.0046	10000
Corrected data; overlapping datasets removed; Telford filtered >=50 sites	0.79 [N=15]	0.71 [N=18]	0.53 [N=8]	0.0046	10000

We first corrected errors in the categorization of modern datasets as land or island (see Supplementary Information). Each row shows the results for successive data reductions proposed by Telford *et al.*[1], with sample sizes for the reduced modern data sets given in parentheses. 'Telford filtered' refers to datasets Telford *et al.*[1] rejected for reasons other than overlap with other datasets or errors. >=10, >=20 and >=50 refer to additional filtering that removes datasets with fewer than 10, 20 or 50 sites, respectively. The final column gives the date of the estimated break point for each dataset variation.