

**PROCEEDINGS OF  
THE ROYAL SOCIETY B**

BIOLOGICAL SCIENCES

**The Origin of Tetrapod Herbivory: Effects on Local Plant  
Diversity**

Journal:	<i>Proceedings B</i>
Manuscript ID	RSPB-2020-0124.R3
Article Type:	Research
Date Submitted by the Author:	12-May-2020
Complete List of Authors:	Brocklehurst, Neil; University of Oxford, Kammerer, Christian; North Carolina Museum of Natural Sciences Benson, Roger; University of Oxford, Department of Earth Sciences; Natural History Museum, Department of Palaeontology
Subject:	Ecology < BIOLOGY, Evolution < BIOLOGY, Palaeontology < BIOLOGY
Keywords:	Paleozoic, Herbivore, Tetrapod, Plant, Diversity
Proceedings B category:	Palaeobiology

SCHOLARONE™  
Manuscripts

**Author-supplied statements**

Relevant information will appear here if provided.

***Ethics***

*Does your article include research that required ethical approval or permits?:*

This article does not present research with ethical considerations

*Statement (if applicable):*

CUST\_IF\_YES\_ETHICS :No data available.

***Data***

*It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:*

Yes

*Statement (if applicable):*

All data is included in the electronic supplementary material

***Conflict of interest***

I/We declare we have no competing interests

*Statement (if applicable):*

CUST\_STATE\_CONFLICT :No data available.

***Authors' contributions***

This paper has multiple authors and our individual contributions were as below

*Statement (if applicable):*

Conceived study: NB

Collected data: NB, CFK

Analysed data: NB

Wrote paper: NB, CFK, RJB

## **The Origin of Tetrapod Herbivory: Effects on Local Plant Diversity**

Neil Brocklehurst<sup>1</sup>, Christian F Kammerer<sup>2</sup>, Roger J Benson<sup>1</sup>

1 – Department of Earth Sciences, University of Oxford, South Parks Road, Oxford, UK

2 – North Carolina Museum of Natural Sciences, 11 West Jones Street, Raleigh, North Carolina, USA

## Abstract

The origin of herbivory in the Carboniferous was a landmark event in the evolution of terrestrial ecosystems, increasing ecological diversity in animals but also giving them greater influence on the evolution of land plants. We evaluate the effect of early vertebrate herbivory on plant evolution by comparing local species richness of plant palaeofloras with that of vertebrate herbivores and herbivore body size. Vertebrate herbivores became diverse and achieved a much greater range of body sizes across the Carboniferous-Permian transition interval. This coincides with an abrupt reduction in local plant richness that persists throughout the Permian. Time series regression analysis supports a negative relationship of plant richness with herbivore richness but a positive relationship of plant richness with minimum herbivore body size. This is consistent with studies of present-day ecosystems in which increased diversity of smaller, more selective herbivores places greater predation pressures on plants, while a prevalence of larger bodied, less selective herbivores reduces the dominance of a few highly tolerant plant species, thereby promoting greater local richness. The diversification of herbivores across the Carboniferous-Permian boundary, along with the appearance of smaller, more selective herbivores like bolosaurid parareptiles, constrained plant diversity throughout the Permian. These findings demonstrate that the establishment of widespread vertebrate herbivory has structured plant communities since the late Palaeozoic, as expected from examination of modern ecosystems, and illustrates the potential for fossil datasets in testing palaeoecological hypotheses.

Key Words: Paleozoic; Herbivore; Tetrapod; Plant; Diversity

## Introduction

Organisms within communities interact with each other, influencing survival and fitness, and therefore evolution and diversification [1]. Interactions between plants and animals have been a fundamental aspect of terrestrial ecosystems since these groups first moved onto land. Plants are primary producers, influencing the structure of higher trophic levels and architecturally defining the environment in which animals live, modifying moisture, light and space regimes [2]. However, plants are also influenced by interactions within these ecosystems, responding to the selection pressures placed on them by animals.

Terrestrial vegetative ecosystems were established at least by the beginning of the Silurian [3,4]. An architecturally modern terrestrial flora was established by the Middle Devonian, with large, lignified, tree-like plants, a shrubby understory, and herbaceous plants at ground level [5]. Alongside this, a fauna of arthropods, and later tetrapods, was being established. At first, this consisted only of carnivores and detritivores [6,7], with no animals feeding directly on living plants. The earliest evidence of arthropod herbivory occurs in the Devonian and indicates removal of spores from sporangia and piercing of stems [8]. Direct consumption of leaves, roots or seeds (high-fibre herbivory) did not appear until the late Carboniferous in either arthropods or tetrapods [2,7-10].

The earliest tetrapod herbivores appear in the fossil record in the Pennsylvanian, although the precise time of origin for this behaviour is uncertain due to the difficulty of assessing diet in extinct organisms. Potentially herbivorous taxa appear in the Bashkirian (earliest Pennsylvanian)-aged Joggins Formation: pantylid microsaur with robust palatal dentition, a possible adaptation for grinding plant material or crushing the thick exoskeletons of arthropods (or both) [11]. More probable herbivores are known from the Kasimovian stage later in the Pennsylvanian: specimens of the diadectid *Desmatodon* from the Conemaugh Group of Pennsylvania [12].

The potential impacts of herbivory on Paleozoic plant evolution have been discussed extensively. Much of this discussion concerns morphological innovations in plants, both to defend against herbivory and to encourage biotic dispersal of seeds [2,13-16]. However, most work on early plant-animal interactions has been focussed on arthropod herbivory [13-16], overlooking the potential importance of tetrapod herbivores in influencing plant evolution [17]. Moreover, thus far there has been little discussion on how the origin and early evolution of herbivory, either in arthropods or tetrapods, affected patterns of community richness in plants.

Here we examine how the origin and evolution of herbivorous tetrapods may have affected plant species richness in local communities, using sampling-corrected estimates of alpha diversity and estimates of body size in tetrapods.

## **Abbreviations**

AMNH – American Museum of Natural History; BP – Bernard Price Institute; FMNH – Field Museum of Natural History; PBDB – Paleobiology Database; SAM – South African Museum

## **Materials and Methods**

### *Diversity and size estimates of herbivorous tetrapods*

*Dataset* – A dataset of herbivorous tetrapod occurrences between the Carboniferous and early Triassic was derived from a review of the published literature, museum collections and the Paleobiology Database (PBDB), downloaded in March 2020. The herbivorous taxa were determined based on prevailing dietary opinions in the literature (Supplementary Data 1).

*Alpha diversity* – The impact of environmental and biotic drivers and processes is scale dependant, so the scale of the observations affects the inference of biological and ecological patterns [18-22]. Competitive interactions, such as herbivores feeding on plants, will have their effect at a local (community) scale [23], and so where possible are better tested by comparing the alpha diversities of herbivores and plants.

Here, geological formations were used to represent contemporaneous long-term communities of organisms (see supplementary text for discussion of this protocol). Where well-established biostratigraphic subdivisions existed within formations e.g. assemblage zones, these were used. To account for sampling heterogeneity, the species richness within each formation was estimated using shareholder quorum subsampling (SQS) [24], implemented in R 3.4.3 [25], using the *estimateD()* function in the package iNEXT. A coverage quorum of 0.9 was applied, following research suggesting that values lower than this produce imprecise results [26,27]. Formations containing only a single amniote taxon were removed prior to analysis, as were those from which fewer than five localities had been sampled. This left a dataset 164 herbivorous species and species of uncertain diet in 42 formations.

Species for which diet categorisation was uncertain were included or excluded at random before calculating the diversity within each formation. This was repeated 100 times, and the median of the diversities obtained from each formation was calculated.

*Size* – As cranial remains are the most commonly reported anatomical region for Paleozoic tetrapods, skull length is used as a proxy for body size (Supplementary Data 2). Cranial size is a relatively poor estimator of body mass, but this is the only widely-available index of size for Palaeozoic tetrapods [28] and we temper our interpretations with an understanding of the possible errors.

Skull lengths in the data set represent the largest known complete specimens for the 160 species for which they are available. Specimens were measured from the anterior tip of the snout to the junction between the skull roof and occipital plate along the cranial midline. The majority of measurements were taken from specimens photographs processed in ImageJ 1.52a [29] and checked against published measures and direct calliper measurements where possible. Scale bars in photographs were placed as closely as possible to the plane of the skull roof in a horizontal position to minimise the effects of parallax; comparison with direct calliper measures indicates measurement error associated with scale bar position is <2.0%. Other specimens were included based directly on measurements from the published literature or measured from images in the literature, again using ImageJ.

#### *Diversity estimates of plants*

*Dataset* – The plant data was downloaded from the PBDB in March 2020 (Supplementary Data 3). The dataset includes global plant fossil occurrences from the Carboniferous, Permian and Early Triassic. The plant data was assessed at the genus level, as species-level assignments are only very rarely reported in the PBDB data (PBDB plant data from this time is primarily derived from the Paleogeographic Atlas Project, compiled at the genus level).

*Alpha Diversity* – The same procedure as used in herbivorous tetrapods was used to calculate alpha diversity within each formation in plants. The same sampling criteria for inclusion of a formation were also applied, leaving a dataset of 124 formations containing 267 taxa. Sensitivity tests to assess the impact of various issues that may affect the reliability of diversity estimates of plants are presented in the Supplementary Text.



### *Multivariate Comparisons of Diversity*

The time bins used were informal substages, produced by splitting each stage in two (early and late) at the midpoint. To produce time series of alpha diversity, the median diversity of all formations whose range overlaps with each time bin was calculated; for herbivore size, the median, minimum, maximum and variance of skull lengths of the species present in each time bin was used. These time series were compared using generalised least squares regression (GLS). This method allows models comparing multiple independent variables to the dependant variable [30], enabling testing of hypotheses that may not be mutually exclusive, where otherwise apparently weak correlations between time series may simply be due to the tested variable representing a composite signal [31].

The GLS analyses were carried out in R using the function from the package nlme, using a first order autoregressive correlation structure in all cases to account for autocorrelation [30]. All comparisons cover the period of time from the Gzhelian until the Olenekian, the span for which there is data for all variables for all substages. Ten models were tested as explanations of the alpha diversity of plants: (1) a null model (random walk); (2) alpha diversity of herbivores only; (3-6) median, variance, maxima and minima of herbivore size respectively; (7-10) multivariate models comparing both herbivore diversity and, respectively, median, variance, maxima and minima of size respectively to plant diversity. Akaike weights [32] were used to determine the best fitting models; due to the shortness of the time-series (23 bins) these were based on the sample-size corrected Akaike information criterion (AICc). The relative importance of the independent variables was calculated by averaging  $R^2$  contributions over ordering of regressors [33], implemented in the R package relaimpo [34].

## **Results**

### *Alpha Diversity of Plants*

Median alpha diversity of plants is at its highest during the Carboniferous (Fig. 1). Across the Carboniferous/Permian boundary, the median diversity drops noticeably. None of the Permian plant-bearing formations contain species richness equal to the most diverse Carboniferous formations, and the median plant alpha diversity remains lower than that of the Carboniferous throughout the Permian, undergoing another abrupt decrease across the Permian/Triassic boundary.

### *Alpha diversity of Herbivores*

Alpha diversity of herbivores (Fig. 1) is low during the Gzhelian (the last stage of the Carboniferous)). Median alpha diversity increases rapidly across the Carboniferous/Permian boundary and remains at a similar level for the rest of the Permian. Diversity decreases across the Permian/Triassic boundary.

### *Herbivore size*

The earliest herbivores appear at relatively large sizes (median skull length of about 175mm). Maximum skull length increases slightly across the Carboniferous/Permian boundary, and larger sizes appear throughout the Permian (Fig. 2). However, the appearance of numerous small herbivore species in the earliest Permian causes both the median and minimum sizes to drop across the Carboniferous/Permian boundary, and the variance to increase. Large herbivores become extinct over the Permian/Triassic boundary and small herbivore species increase in richness, so that median herbivore size is lower in the Early Triassic than at any time in the Palaeozoic.

### *Generalised Least Squares*

The two best-fitting GLS models explaining alpha diversity of plants receive similar support based on Akaike weights. The best fit explains plant alpha diversity in terms of herbivore alpha diversity and minimum body size (AICc weight = 0.51;  $R^2 = 0.55$ ), whereas the second explains it in terms of herbivore diversity and size variance (AICc weight = 0.31;  $R^2 = 0.39$ ), both substantially higher than the other models, including the null (Table 1). In both cases, the alpha diversity of herbivores explains less variance than herbivore body size. The relationship of plant diversity with minimum herbivore size was positive, whereas that with between herbivore size variance and herbivore diversity was negative.

## Discussion

The presence, diversity (species richness), body size and dietary selectivity of herbivores influences plant diversity in modern-day ecosystems [23,35-37]. These effects depend on the environment under study and the spatial scale at which the system is examined and can include both increases and decreases in plant diversity (reviewed by Olf and Ritchie [23]). The Carboniferous–Permian transition documents the first evolutionary appearance of widespread vertebrate herbivory, leading us to ask: what was the effect of this on the species richness of plant communities?

Studies of invasive herbivores show that increased predation pressure from novel herbivore species can reduce plant diversity [38]. In contrast, increased predation pressure can also reduce the dominance of highly abundant plants leading to increased diversity, as shown by studies comparing grazed areas to areas from which herbivores are excluded [39-41]. This is particularly the case when herbivores are less selective.

Among modern-day herbivores, selectivity is more pronounced in insects and small-bodied tetrapods [36,41-48] although it is also seen in some large mammals [49-52]. Browsing herbivorous mammals tend to be more selective than grazers [53-55] and generally

larger species are less selective than smaller [36,56]. These two patterns are perhaps interrelated; larger herbivores can survive on plant matter of lower nutrient quality, due to lower energy requirements relative to their body size: the Jarman-Bell principle [53,55,57]. As such, a greater presence of large-bodied herbivores reduces the dominance of plant species and increases species richness [36,58], whereas an increased presence of smaller, more selective species leads to reduced species richness by targeting more palatable taxa, as demonstrated by selectively excluding herbivores of varying sizes from sites [36,48,56].

We find that the early Permian diversification of herbivorous tetrapods constrained the alpha diversity of plants for the rest of the Paleozoic. However, the variation in herbivore body size has a greater impact, and by itself is responsible for more than 30% of the variance in plant alpha diversity. Leaving aside the uncertain diet of the pantylid microsaurs, the Carboniferous tetrapod herbivores appear to have originated at, or rapidly evolved to, relatively large sizes [59,60]. The fall in plant diversity across the Carboniferous-Permian boundary, while mirroring the increase in herbivore diversity at this time, also coincides with the origin of smaller, presumably more selective herbivores such as the bolosaurids [61], and a lowering of minimum body size relative to the Carboniferous. The influence of herbivore body size variance on plant diversity found by the GLS analysis might simply reflect this same effect of the radiation of small herbivores. Alternatively, it may reflect the fact that size variance is an indicator for the diversity of functional groups [62,63]; the presence of a greater ecological diversity of herbivores places greater predation pressure on plants.

The impact of arthropod herbivory on plant diversity is difficult to ascertain. Patterns of terrestrial arthropod diversity, in particular of herbivorous arthropods, are uncertain, due in part to difficulty assessing the diet of extinct forms. The terrestrial arthropod record, particularly in the Permian, is heavily biased by the rock record and dominated by isolated wings [64,65]. Even in specimens preserving mouthparts, diet is not always clear [66].

Herbivorous arthropods underwent a decrease in diversity of functional feeding groups at the beginning of the Permian (assessed by types of damage to plant fossils [66]), potentially indicating a relaxation of predation pressure from arthropods on plants. Diversity of arthropod herbivory types similar to that of the Carboniferous is not again seen until the Middle Triassic [67].

The relative contributions of the origin of arthropod and vertebrate herbivores to plant evolution is clearly a complicated issue. It is possible that the origin of vertebrate herbivory had a greater impact on plant diversification than arthropod herbivory. Studies on modern patterns of herbivory suggest that vertebrates are responsible for most of the attacks on seedlings, at which stage the attack is more often fatal to the plant [68]. Arthropods cause more damage to adult plants, but these are using fewer resources for growth and more for defence and tolerance [68,69]. These inferences remain uncertain and require thorough reviews of the biases affecting preservation of feeding damage on plants.

Past studies of Palaeozoic plant diversity have attributed a drop in global (rather than local as tested here) species richness in the latest Carboniferous to the climatic changes occurring at this time [70-72], in particular a ‘rainforest collapse’: the shift from everwet ‘coal-swamp’ environments characteristic of the Carboniferous to the more open summerwet environments characteristic of the equatorial Permian. This climatic shift could account in part for the drop in plant alpha diversity observed here independently of the evolution of herbivorous tetrapods; while tetrapod evolution is found to be responsible for the majority of the observed variance in plant diversity, it does not explain all. However, this possibility is not consistent with timing of palaeofloral changes based on recent examinations of the transition, which appears to have been largely complete by the end of the Moscovian (307 mya, preceding the end of the Carboniferous by 7 Ma) [72]. Examinations of temperature and carbon dioxide levels suggest that these were relatively stable, with no substantial changes

from the end of the Mississippian until the late Sakmarian [73,74]. Although a shift in climate might have caused turnover of plant lineages, it cannot explain why plant diversity remained low throughout the Permian. In fact, particularly when considering diversity at small spatial scales, examinations of modern ecosystems suggest that summerwet biomes may have greater plants richness than everwet biomes [75,76]. Although these observations of the extant flora might not be directly applicable to the radically different floras of the Palaeozoic, it does make it less likely that the shift in environment was primarily responsible for the persistence of a low-diversity flora, rather than the radiation of smaller-bodied herbivores.

## **Conclusions**

The earliest diversification of vertebrate herbivores across the Carboniferous-Permian boundary coincides with a substantial drop in plant diversity. Although it is difficult to infer direct macroevolutionary interactions between clades, our findings suggest that plant richness was to some extent structured by vertebrate herbivory from its earliest origins more than 300 million years ago. Studies of modern ecosystems suggest that this should be the case, but this has generally been overlooked in previous examinations of plant diversity. This study provides an illustration of the potential for fossil data to test predictions of ecological interactions first observed in extant ecosystems.

## **Acknowledgements**

We thank Ricardo Pérez-de la Fuente, Hilary Maddin, David Ford and three anonymous reviewers for helpful comments and discussion. NB's research is funded by Deutsche Forschungsgemeinschaft grant number BR 5724/1-1. CFK's research is funded by Deutsche Forschungsgemeinschaft grant number KA 4133/1-1. This is Paleobiology Database Official Publication #369

## References

1. Thompson JN. 2005. *The Geographic Mosaic of Coevolution*. The University of Chicago Press, Chicago.
2. Tiffney BH. 1992. The role of vertebrate herbivory in the evolution of land plants. In *Essays in Evolutionary Plant Biology* (eds BS Venkatachala, DL Dilcher, HK Maheshwari), pp 87-97. Birbal Sahni Institute of Palaeobotany, Lucknow
3. Edwards D, Bassett MG, Rogerson ECW. 1979. The earliest vascular land plants: continuing the search for proof. *Lethaia* **12**, 313-324
4. Gray J, Laweson JD. 1985. The microfossil record of early land plants: advances in understanding of early terrestrialization, 1970-1984. *Phil. Trans. R. Soc. B* **309**, 167-195
5. Chaloner WG, Sheerin A. 1981. The evolution of reproductive strategies in early land plants. In *Evolution Today* (eds GGE Scudder, JL Reveal), pp. 93–100. Second International Congress of Systematics and Evolutionary Biology, Hunt Institute of Botanical Documentation. Pittsburgh: Carnegie–Mellon University.
6. Almond JE, Lawson JD. 1985. The Silurian-Devonian fossil record of the Myriapoda. *Phil. Trans. R. Soc. B* **309**, 227-237
7. Shear WA. 1991. The early development of terrestrial ecosystems. *Nature* **351**, 283-289
8. Labandeira C. 2007. The origin of herbivory on land: initial patterns of plant tissue consumption by arthropods. *Insect Sci.* **14**, 259-275
9. Behrensmeyer AK, DiMichele JE, Potts WA, Suess RH-D, Wing SI. 1992. *Terrestrial Ecosystems Through Time: Evolutionary Paleobiology of Terrestrial Plants and Animals*. University of Chicago Press, Chicago.

10. Sues H-D, Reisz RR. 1998. Origins and early evolution of herbivory in tetrapods.  
*Trends Ecol. Evol.* **13**, 141-145
11. Carroll RL, Gaskill P. 1978. *The Order Microsauria*. American Philosophical Society, Philadelphia
12. Kissel R. 2010. *Morphology, phylogeny, and evolution of Diadectidae (Cotylosauria: Diadectomorpha)*. University of Toronto, Toronto
13. Hughes NF, Smart J. 1967. Plant-insect relationships in Paleozoic and later time.  
*Geological Society of London, Special Publications* **2**, 107-117
14. Scott AC, Taylor TN. 1983. Plant/animal interactions during the upper Carboniferous.  
*Bot. Rev.* **49**, 259-307
15. Scott AC, Stephenson J, Chaloner WG. 1992. Interaction and coevolution of plants and arthropods during the Paleozoic and Mesozoic. *Phil. Trans. R. Soc. B* **335**, 129-165.
16. Tiffney, B. H. 2004. Vertebrate dispersal of seed plants through time. *Annu. Rev. Ecol. Evol. Syst.* **35**, 1-29
17. Zavada MS, Mentis MT. 1992. Plant-animal interaction: the effect of Permian megaherbivores on the glossopterid flora. *Am Midl. Nat.* **127**, 1-12
18. Brocklehurst N., Fröbisch J. 2018. The definition of bioregions in palaeontological studies of diversity and biogeography affects interpretations: Paleozoic tetrapods as a case study. *Front. Earth Sci.* **6**, 200
19. Palmer MW, White PS. 1994. Scale dependence and the species-area relationship.  
*Am. Nat.* **144**, 717-740
20. Rosenweig ML. 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.



21. Whittaker RJ, Willis KJ, Field R. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *J. Biogeogr.* **28**, 453-470
22. Field R, Hawkins BA, Cornell HV, Currie DJ, Diniz-Filho JAF, Guégan JF, Kaufman DM, Kerr JT, Mittelback GG, Oberdorff T, O'Brien EM. 2009. Spatial species-richness gradients across scales: a meta-analysis. *J. Biogeogr.* **36**, 132-147
23. Olf H, Ritchie ME. 1998. Effects of herbivores on grassland plant diversity. *Trends Ecol. Evol.* **13**, 261-265
24. Alroy J. 2010. Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology* **53**, 1211-1235
25. R Core Team. 2017. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
26. Close RA, Evers SW, Alroy J, Butler RJ. 2018. How should we estimate diversity in the fossil record? Testing richness estimators using sampling-standardised discovery curves. *Method Ecol. Evol.* **9**, 1386-1400
27. Brocklehurst N, Day MO, Fröbisch J. 2018. Accounting for differences in species frequency distributions when calculating beta diversity in the fossil record. *Method Ecol. Evol.* **9**, 1409-1420
28. Therrien F, Henderson DM. 2007. My theropod is bigger than yours... or not: estimating body size from skull length in theropods. *J. Vert. Paleontol.* **27**, 108-115.
29. Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**, 671-675.
30. Pinheiro J, Bates D, Debroy S, Sarkar D. 2013. Nlme: Nonlinear mixed-effects models. *R Package* **3**, 1
31. Benson RBJ, Mannion PD. 2011. Multi-variate models are essential for understanding vertebrate diversification in deep time. *Biol. Lett.* **8**, 127-130

32. Wagenmakers EJ, Farrell S. 2004. AIC model selection using Akaike weights.  
*Psychon. Bull. Rev.* **11**, 192-196.
33. Lindeman RH, Merenda PF, Gold RZ. 1980. *Introduction to Bivariate and Multivariate Analysis*. Scott, Foresman and Company, Glenview Illinois
34. Grömping U. 2006. Relative importance for linear regression in R: the package relaimpo. *J. Stat. Softw.* **17**, 1-27
35. Hawkins BA, Porter EE. 2003. Does herbivore diversity depend on plant diversity? The case of California butterflies. *Am. Nat.* **161**, 40-49
36. Bakker ES, Ritchie ME, Olff H, Milchunas DG, Knops JMH. 2006. Herbivore impact on grassland plant diversity on habitat productivity and herbivore size. *Ecol. Lett.* **9**, 780-788.
37. Maron JL, Agrawal AA, Schemske DW. 2019. Plant-herbivore coevolution and plant speciation. *Ecology*, **In Press**.
38. Wardle DA, Barker, GM, Yeates GW, Bonner KI, Ghani A. 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. *Ecol. Monogr.* **71**, 587-614
39. Huntly N, Reichman OJ. 1994. Effects of subterranean mammalian herbivores on vegetation. *J. Mammal.* **75**, 852-859
40. Jefferies RL, Klein DR, Shaver GR. 1994. Vertebrate herbivores and northern plant communities – reciprocal influences and response. *Oikos* **71**, 193-206
41. Gedan KB, Crain CM, Bertness MD. 2009. Small-mammal herbivore control of secondary succession in New England tidal marshes. *Ecology* **90**, 430-440
42. Milchunas, D.G. and Lauenroth, W.K. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, **63**, 327-366

43. Dethier VG. 1954. Evolution of feeding preferences in phytophagous insects. *Evolution*, **8**, 33-54
44. Jermy T. 1966. Feeding inhibitors and food preference in chewing phytophagous insects. *Entomol. Exp. Appl.* **9**, 1-12
45. Singer MC. 1971. Evolution of food-pant preferences in the butterfly *Euphydryas editha*. *Evolution* **25**, 383-389
46. Powell JA. 1980. Evolution of larval food preference in Microlepidoptera. *Annu. Rev. Entomol.* **25**, 133-159
47. Brown JH, Heske EJ. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* **250**, 1705-1707.
48. Edwards GR, Crawley MJ. 1999. Herbivores, seed banks and seedling recruitment in mesic grassland. *J. Ecol.* **87**, 423-435
49. Milton WEJ. 1940. The effect of manuring, grazing and liming on the yield, botanical and chemical composition of natural hill pastures. *J. Ecol.* **28**, 326-356
50. Bryant JP, Reichardt PB, Clausen TP. 1992. Chemically mediated interactions between woody plants and browsing mammals. *J. Range Manage.* **45**, 18-24.
51. Fahnestock JT, Kapp AK. 1994. Plant responses to selective grazing by bison: interactions between light, herbivory and water stress. *Vegetatio* **115**, 123-131
52. Van Soest PJ. 1996. Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review. *Zoo Biol.* **15**, 455-479
53. Bell RHV. 1971. A grazing ecosystem in the Serengeti. *Sci. Am.* **225**, 86-93.
54. Jarman PJ. 1974. The social organization of antelope in relation to their ecology. *Behaviour* **48**, 215-266.
55. Jannis CM, Ehrhardt D. 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zool. J. Linn. Soc.* **92**, 267-284.

56. Brown JH, Heske, EJ. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* **250**, 1705-1707.
57. Geist V. 1974. On the relationship of social evolution and ecology in ungulates. *Am. Zool.* **14**, 205-220.
58. Milchunas DG, Lauenroth WK. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol. Monogr.* **63**, 327-366.
59. Reisz RR, Fröbisch J. 2014. The oldest caseid synapsid from the Late Pennsylvanian of Kansas, and the evolution of herbivory in terrestrial vertebrates. *PLoS One* **9**, e94518.
60. Brocklehurst N, Brink KS. 2017. Selection towards larger body size in both herbivorous and carnivorous synapsids during the Carboniferous. *Facets* **2**, 68-84
61. Falconnet J. 2012. First evidence of a bolosaurid parareptile in France (latest Carboniferous-earliest Permian of the Autun basin) and the spatiotemporal distribution of the Bolosauridae. *Bull. Soc. Géol. Fr.* **183**, 495-508
62. Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, Warren PH. 2005. Body size in ecological networks. *Trend Ecol Evol* **20**
63. Rooney N, McCann KS. 2012. Integrating food web diversity, structure and stability. *Trend Ecol Evol* **27**, 40-46, 402-409
64. Karr JA, Clapham ME. 2015. Taphonomic biases in the insect fossil record: shifts in articulation over geologic time. *Paleobiology* **41**, 16-32
65. Schachat SR, Labandeira CC, Saltzman MR, Cramer BD, Payne JL, Boyce CK. 2018. Phanerozoic  $pO_2$  and the early evolution of terrestrial animals. *Proc. R. Soc. B* **285**, 20172631
66. Shear WA, Kukalová-Peck J. 1990. The ecology of Paleozoic terrestrial arthropods: the fossil evidence. *Can. J. Zool.* **68**, 1807-1834

67. Labandeira CC. 2013. Deep-time patterns of tissue consumption by terrestrial arthropods herbivores. *Naturwissenschaften* **100**, 355-364
68. Boege K, Barton KE, Dirzo R. 2011. Influence of tree ontogeny on plant-herbivore. In *Size and Age-Related Changes in Tree Structure and Function* (eds FC Meinzer, B Lachenbruch, T Dawson), pp. 193–214. Springer, Dordrecht
69. Boege K, Marquis RJ. 2005. Facing herbivory as you grow up: the ontogeny of resistance in plants. *Trends Ecol. Evol.* **20**, 441-447
70. Cascales-Miñana B, Cleal CJ. 2012. Plant fossil record and survival analyses. *Lethaia* **45**, 71-82
71. Cascales-Miñana B, Cleal CJ. 2012. The plant fossil record reflects just two great extinction events. *Terra Nova* **26**, 195-200
72. Cleal CJ, Opluštil S, Thomas BA, Tenchov Y. 2009. Late Moscovian terrestrial biotas and palaeoenvironments of Variscan Euramerica. *Neth. J. Geosci.* **88**, 181-278.
73. Hyde WT, Grossman EL, Crowley TJ, Pollard D, Scotese CR. 2006. Siberian glaciation as a constraint on Permian-Carboniferous CO<sub>2</sub> levels. *Geology* **34**, 421-424
74. Montañez IP, Tabor NJ, Niemeier D, DiMichele WA, Frank TD, Fielding CR, Isbell JL, Birgenheier LP, Rygel MC. 2007. CO<sub>2</sub>-forced climate and vegetation instability during late Paleozoic deglaciation. *Science* **315**, 87-91
75. Wilson JB, Peet RK, Dengler J, Pärtel M. 2012. Plant species richness: the world records. *J. Veg. Sci.* **23**, 796-802
76. Pennington RT, Lehmann CER, Rowland LM. 2018. Tropical savannas and dry forests. *Curr. Biol.* **28**, 541-545

## Figure Captions

Figure 1: Alpha diversity of plants (grey) and tetrapod herbivores (black), calculated by SQS. Each thin line represents the diversity in a fossil-bearing formation. The thick lines represent the median diversity of all formations in each time bin.

Figure 2: Size of Palaeozoic herbivorous tetrapods. Thin lines represent the log transformed skull length of each taxon; those in grey are those whose diet is uncertain. The thick black line represents the median size in each time bin, and the bars represent the standard error. A) *Diasparactus zenos* (FMNH UC 679), a diadectid; B) *Bolosaurus striatus* (AMNH FARB 4321), a bolosaurid; C) *Embrithosaurus schwarzi* (SAM PK 8034), a pareiasaur; D) *Casea broilii* (FMNH UC 656), a caseid; E) *Cistecephalus microrhinus* (BP/1/33), a dicynodont.

## Tables

Table 1: GLS models tested, their log likelihood (LnL), Akaike information criterion (AICc), Akaike weights, coefficients, and the proportion of variance explained by the variables. The two best-fitting models highlighted in grey

Model	LnL	AICc	Akaike weights	Coefficient of variable 1	Coefficient of variable 2	Variance explained by model
Plant alpha diversity ~ Null	-1.97	7.94	$9.3 \times 10^{-8}$	NA	NA	NA
Plant alpha diversity ~ Herbivore alpha diversity	11.90	-15.80	0.013	-0.09	NA	19.6%
Plant alpha diversity ~ Median herbivore size	12.69	-17.40	0.030	0.38	NA	20.2%
Plant alpha diversity ~ Herbivore size variance	14.06	-18.11	0.043	-0.25	NA	28.4%
Plant alpha diversity ~ Maximum herbivore size	11.84	-15.67	0.013	-0.22	NA	2.0%
Plant alpha diversity ~ Minimum herbivore size	14.62	-19.25	0.075	0.41	NA	29.6%
Plant alpha diversity ~ Herbivore alpha diversity + Median size	11.86	-13.72	0.0047	-0.14	0.37	7.44%
Plant alpha diversity ~ Herbivore alpha diversity + Size variance	1504	-22.09	0.31	-0.14	-0.44	39.8%
Plant alpha diversity ~ Herbivore alpha diversity + Maximum size	11.02	-12.05	0.0021	-0.24	-0.29	9.18%
Plant alpha diversity ~ Herbivore alpha diversity + Minimum size	15.54	-23.08	0.51	-0.15	0.58	55.34%

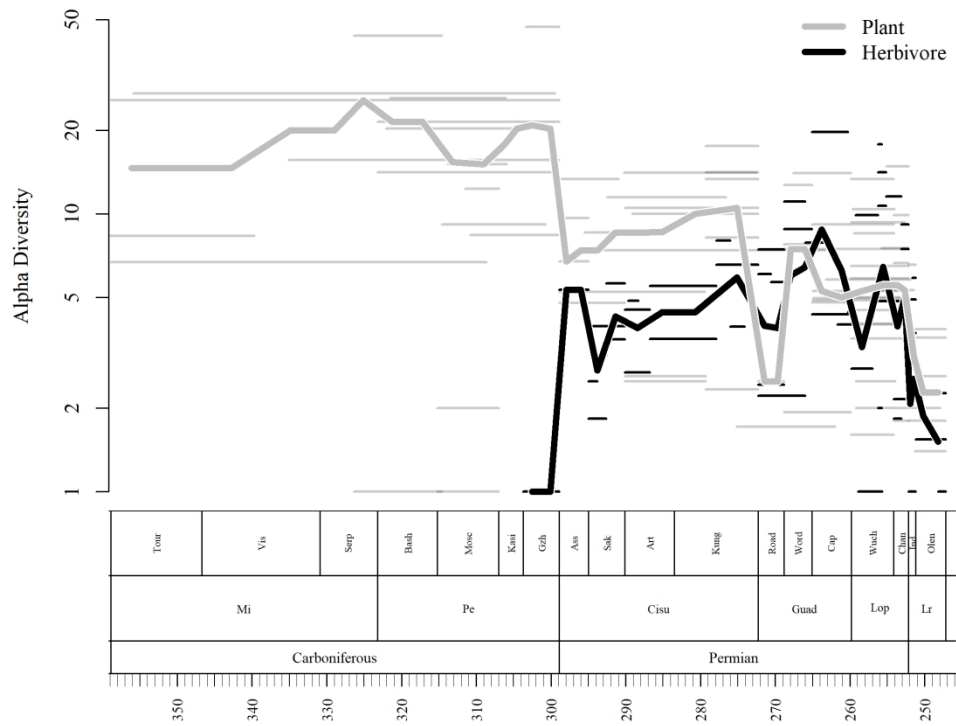


Figure 1: Alpha diversity of plants (grey) and tetrapod herbivores (black), calculated by SQS. Each thin line represents the diversity in a fossil-bearing formation. The thick lines represent the median diversity of all formations in each time bin.

199x159mm (300 x 300 DPI)



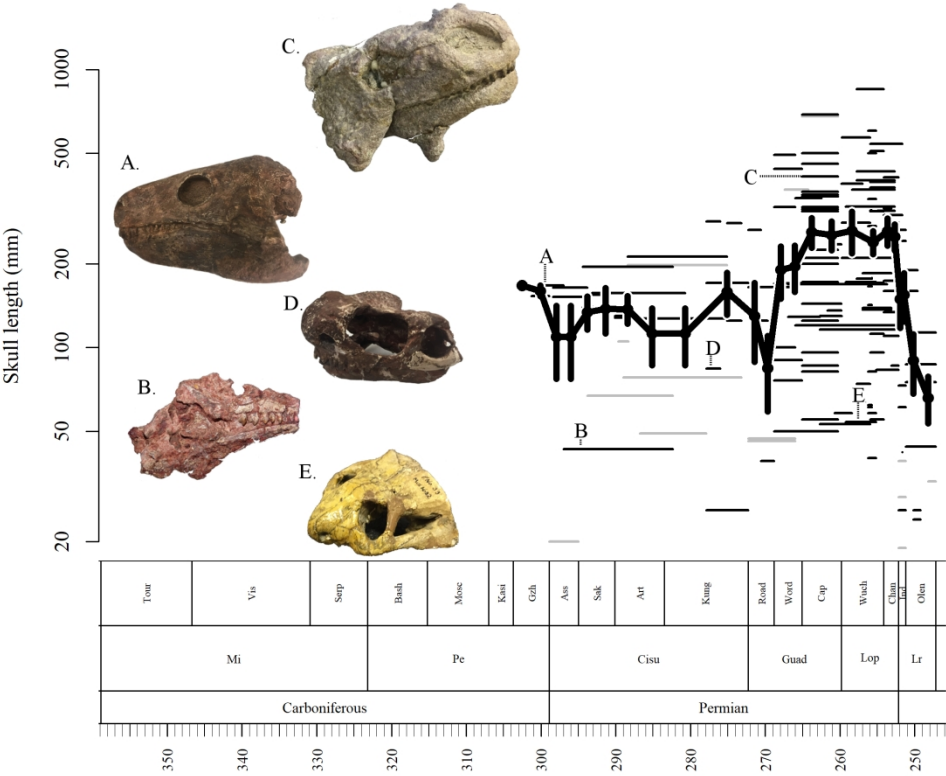


Figure 2: Size of Palaeozoic herbivorous tetrapods. Thin lines represent the log transformed skull length of each taxon; those in grey are those whose diet is uncertain. The thick black line represents the median size in each time bin, and the bars represent the standard error. A) *Diasparactus zenos* (FMNH UC 679), a diadectid; B) *Bolosaurus striatus* (AMNH FARB 4321), a bolosaurid; C) *Embrithosaurus schwarzi* (SAM PK 8034), a pareiasaur; D) *Casea broilii* (FMNH UC 656), a caseid; E) *Cistecephalus microrhinus* (BP/1/33), a dicynodont.

199x159mm (300 x 300 DPI)