Online supplemental material

Description of paleontological sites.

Porcupine Cave is located at 2900 m in the Central Rocky Mountains of Colorado (UTM 426.9E 4283.7N) (1). Thousands of fossils were excavated from the Pit Locality of Porcupine Cave, which represents one of the largest middle Pleistocene vertebrate assemblages in the world. The fossils from the Pit were deposited primarily by wood rats (*Neotoma* spp.) and span at least three glacial-interglacial transitions. The oldest stratigraphic level is approximately 950,000 ybp; the youngest is 800,000 ybp. Many of the species are extinct; others are early forms of surviving taxa. Several species (14%) are the first occurrences of the modern North American mammalian community.

The Kennewick Road Cut exposure is located at 389 m in southeastern Washington in the Horse Heaven Hills (UTM 334.4E 5104.3N)(2). The deposit spans several glacial-interglacial cycles and is inferred to be from loess and soils that accumulated over faunal remains. The oldest age of this deposit is suggested to be middle Pleistocene, about 328,000 ybp, based on stratigraphic thickness and rates of calcrete horizon formation. The youngest stratigraphic level is middle Holocene, which is underlain by Mazama tephra dated at 6,600 ybp. The Kennewick deposit contains thousands of fossils, representing amphibians, reptiles, birds and mammals, some of which are extinct.

Baker Bluff Cave is located in Tennessee within the Ridge and Valley province of the Appalachian Mountains at an elevation of 450 m (UTM 367.9E 4027.8N)(3). The site is a fissure-fill wood rat midden and raptor roost containing thousands of specimens of plants, invertebrates, fish, amphibians, reptiles, birds and mammals. The oldest stratigraphic level from the site has been radiocarbon dated to 19,100 ± 850 ybp. This late Pleistocene age and the characteristics of the fauna suggest that the level was deposited during a full glacial period. The site was apparently continuously deposited through the late Pleistocene and Holocene, until at least 555 ± 185 ypb.

Lamar Cave is located in northwestern Wyoming within the Rocky Mountains at an elevation of 1835 m (UTM 555.3E 4974.0N)(4). This paleontological site spans the late Holocene from 3000 ybp to the present (5) and has been continuously accumulating faunal material throughout that time. Lamar Cave is a wood rat midden (*Neotoma cinerea*) and occasional carnivore den. The site contains thousands of fossil fish, reptiles, amphibians, birds and mammals.

Complete list of species and higher level taxa used

Taxon	Lamar Cave	Baker Bluff	Kennewick	Porcupine Cave
Sorex (Shrews)	Sorex palustris	Sorex arcticus	Sorex palustris	Sorex sp.
	Sorex hoyi	Sorex cinereus		
	Sorex merriami	Sorex dispar		
		Sorex fumeus		
		Sorex hoyi		
Ochotona (Pikas)	Ochotona princeps			Ochotona sp. (Trout Cave)
				Ochotona sp.
Leporidae (Rabbits &	Lepus americanus	Leporidae	Lepus sp.	Lepus sp.
	Lepus townsendii			Hypolagus sp.
	Sylvilagus audubonii		Sylvilagus idahoensis	Sylvilagus sp.
	Sylvilagus nuttalli		Sylvilagus nuttallii	Brachylagus coloradensis
				Aztlanolagus sp.
Tamias (Chipmunks)	Tamias minimus	Tamias minimus	Tamias sp.	Tamias sp.
	Tamias amoenus	Tamias striatus		
	Tamias umbrinus			
Marmota (Marmots)	Marmota flaviventris	Marmota monax		Marmota monax
Spermophilus (Ground	Spermophilus armatus	Spermophilus		Spermophilus lateralis
	Spermophilus lateralis			Spermophilus elegans
Tamiasciurus (Red	Tamiasciurus hudsonicus	Tamiascuirus hudsonicus		Tamiasciurus hudsonicus
Thomomys (Pocket	Thomomys talpoides		Thomomys talpoides	Thomomys talpoides
				Thomomys bottae
Peromyscus (Deer mice)	Peromyscus maniculatus	Peromyscus maniculatus	Peromyscus maniculatus	Peromyscus sp.
		Peromyscus leucopus		
Neotoma (Wood rats)	Neotoma cinerea	Neotoma floridana	Neotoma cinerea	Neotoma cinerea
			Neotoma lepida	Neotoma mexicana
				Neotoma floridana
				Neotoma micropus
				Neotoma stephensi
Clethrionomys (Bank	Clethrionomys gapperi	Clethrionomys gapperi		
Phenacomys (Heather	Phenacomys intermedius	Phenacomys intermedius	Phenacomys intermedius	Phenacomys gryci
				Phenacomys sp.
Ondatra (Muskrats)	Ondatra zibethicus	Ondatra zibethicus		Ondatra sp.
Microtus (Voles)	Microtus montanus	Microtus chrotorrhinus	Microtus meadensis	Allophaiomys pliocaenicus
	Microtus longicaudus	Microtus pennsylvanicus	Microtus sp.	Microtus meadensis
	Microtus ochrogaster	Microtus xanthognathus		Microtus paropaerarius
	Microtus pennsylvanicus	Microtus pinetorum		Microtus sp.
		Microtus ochrogaster		
Zapus (Jumping mice)	Zapus princeps	Zapus hudsonicus		
Mustela (Weasels etc)	Mustela frenata	Mustela nivalis		Mustela frenata
	Mustela erminea	Mustela frenata		Mustela eminea
				Mustela nigripes
				Mustela sp.

Table S- 2 The left-most column gives the 16 genera used in our analysis (Leporidae is actually a family). The four remaining columns show which species were found in this category in each site.

Regression details

	r	p	n	Distance (km)	ΔT(yrs)	Post hoc r
Lamar vs Baker	0.39	0.071	16	2,525	8,340	0.61*
Lamar vs Porcupine	0.70***	0.001	16	785	895,290	0.74**
Lamar vs Kennewick	0.70***	0.001	16	700	102,290	0.63**
Baker vs Porcupine	0.19	0.245	16	2,075	886,950	0.51*
Baker vs Kennewick	0.19	0.264	14	3,225	93,950	0.58*
Porcupine vs Kennewick	0.53*	0.026	14	1,365	793,000	0.51*

Table S- 3 Comparison between sites

The four sites produce six pairwise comparisons. The first column, r, gives the Pearson r correlation as described in the text and in the legend for Figure 2 in the main text, while p gives the two-tailed probability and n gives the number of taxa that had non-zero abundances at least one site. The distance in km and the time between average age of deposition for each comparison is given in the next two columns. Mantel tests show that similarity and distance are significantly related but similarity and time (and time and distance) are not. The final column shows the effect of a post hoc removal of three taxa as discussed in the text where * signifies $p<0.05$ and ** $p<0.01$.

Between sites (n=105)

	CII vs. time (/100,000yrs)				*CII vs. log(1+time)*				*CII vs. distance (/1000 km)*			
	Species	Genus	Family	Order	Species	Genus	Family	Order	Species	Genus	Family	Order
b	-0.044	-0.014	0.003	-0.012	-0.17	-0.058	0.0026	-0.039	-0.360	-0.200	-0.140	-0.001
b lo	-0.068	-0.027	-0.007	-0.018					-0.421	-0.230	-0.162	-0.022
b hi	-0.020	-0.002	0.013	-0.007					-0.301	-0.173	-0.114	0.021
p	0.0004	0.0279	**0.5576**	<0.0001	<0.0001	0.0032	**0.8606**	<0.0001	<0.0001	<0.0001	<0.0001	**0.9369**
# sig	69	40	42	41								

Within sites (n=25)

CII vs. time (/100,000 yrs)

Species	Genus	Family	Order
-0.360	-0.210	-0.150	0.040
-0.419	-0.282	-0.220	-0.016
-0.302	-0.146	-0.089	0.096
<0.0001	<0.0001	<0.0001	**0.1574**
24	24	24	10

Table S- 4 How CII varies with space and time

These two tables show the results of regressions on the data presented in Figure 2 in the main text. The first row gives the regression slope. So for example, CII decreases by 0.044 per 100,000 years at the species level when looking between sites. The second and third rows give the upper and lower bounds for 95% confidence intervals on the slope. The fifth row gives p-values for the regression. Non-significant p-values are bolded. The fifth and final row gives the number of individual data points (CII or r) that are significantly different from zero. The use of log(1+time) did not affect significance levels by much and the coefficients are much more difficult to interpret so log time is not used in further analyses although it continues to be used for display convenience on graphs. Note that the main text suggests that the most accurate estimates for CII vs. time are to be found in the second table (within sites).

Methods for neutral model simulations

We implemented computer simulations of the neutral theory of biogeography (6, 7). The computer code was based on code previously made publicly available (8) with one modification: Hubbell's birth-death equations and the algorithm in chapter 9 of his book model the dynamic equilibrium abundances of species in a metacommunity, but do not give a clear prediction for the 'drift' of individual species in the metacommunity on the same time scale as the drift in the local community. In short, the afore-mentioned algorithms assume a metacommunity of infinite size with no drift, which is unrealistic for the time scales we explore here. Therefore we implemented a spatial model containing multiple individual local communities. Whenever an open slot created by a death was to be filled by a migrant, the migrant was randomly selected from an individual in a different local community. This is similar to the approach of Hubbell in Chapter 6 (7) and Bell (6).

The parameters of the simulation are: $\boldsymbol{\theta}$, the fundamental biodiversity number which roughly correlates with species diversity; ***m***, the migration rate or probability that an individual is replaced from outside its local community, ***J***, the local population size; and ***C***, the number of local communities (giving a metacommunity of size $C*J$). We performed all runs at $\theta=6$ which produced about 70 species similar to the empirical data. Sensitivity analysis showed that theta had little effect on the final community inertia over the time scales we studied – this is presumably because the neutral communities were reduced to 3-5 species by about 10,000 years regardless of initial species diversity. We chose $J=10{,}000$ (although runs at $J=100{,}000$ were similar with drift just taking somewhat longer), and $C=20$. There is no data to suggest a correct value of C. We chose C=20 as a reasonably large number (metacommunity effective population sizes ranged up to 2,000,000 for our J=100,000 analyses) and with the idea that many of the communities at least at many points in their existence were isolated mountain top communities.

This would imply that 20 local communities would cover a very large geographic area. For example 19 mountaintop islands covers the entire Great Basin of the Western US (Hadly & Maurer 2001). We ran simulations for a wide range of values of m.

The neutral model measures time in number of death/replacement events, so one year in the neutral model occupies J/G time steps (death and replacements) where G is the average generation time of an individual (9). We took G to be one year for the small mammal communities we studied. Of course, some species and individuals live much longer, but on average we believe this to be a good approximation (Eisenberg 1981, *The mammalian radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior*, University of Chicago Press). Such a small value of G makes simulation of the spatial and temporal scales spanned by the empirical data challenging. For example, assuming a community of J=10,000 individuals and simulating T=100,000 years across C=20 sites required $J*T*C$=20 billion deaths and replacements. Thus, all time-sensitive code was written in C and carefully optimized for performance. We suggest that authors who have run simulations of Hubbell's neutral model and found a high degree of inertia may simply have not run the model for enough time steps to produce a realistic number of years for the taxa they study. We report results for the average of 20 replicates of the neutral model unless otherwise noted (where a replicate represents Monte Carlo runs of all 20 sites starting in each replicate with a different initial random seed).

The observed loss of species in neutral communities created some challenge for the calculation of CII for neutral communities over long time periods. Pearson correlation, r, was used for comparison, but |r| increases as the number of points decreases (with r always being ±1 for two points). This is evident in Figure 3 in the main text. To partially address this, we eliminated all comparisons that involved three or fewer extant species (since correlations with n

≤ 3 have 0 power), but this effect still introduces a bias conservatively in favor of the neutral model having a higher CII

Effects of various measures of community similarity (CII).

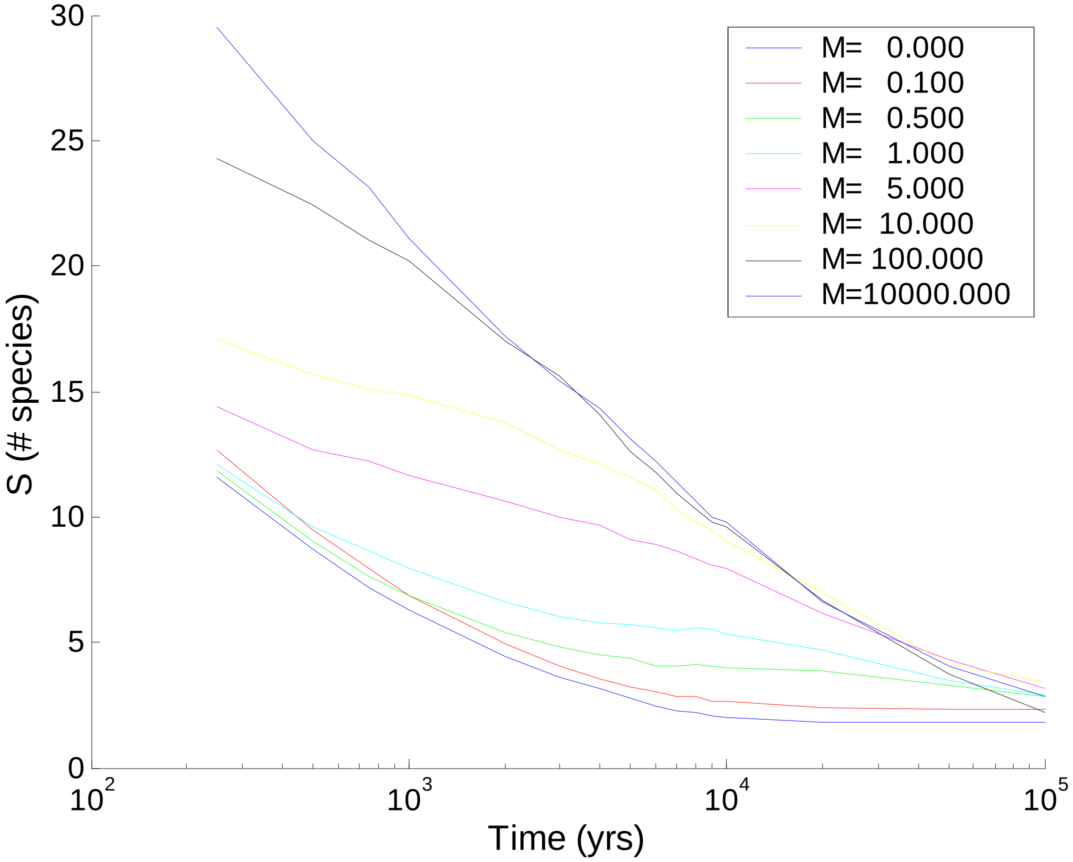
The main text used Pearson's r as a CII. We claimed that our results were robust to different measures of CII. Here we give detail for this claim. We examined four other measures of CII. We used the square-chord distance (SCD) and Jaccard described in the main text. We also used Whittaker's measure. See Legendre & Legendre for details. We also devised our own measure %swap which emphasizes the degree to which rare taxa become common and vice versa. See the legend for Table S- for details. Three of these measures (all except Jaccard) are actually measures of dissimilarity and hence to create a measure of similarity or CII, one must take 1-dissimilarity.

None of these four measures have simple tests of significance as for Pearson r, so the claims about significance vs. the null model of CII=0 are not applicable to these measures. However, the other claims are:

1. CII trends down with distance in time and space and is significant except for at the order level. Deviations from this claim include that the swap index is significant for order for time and space, the Whittaker index is significant for order for space, and the Jaccard index loses significance (p=0.06-p=0.24) for Species-Family level for time.
2. The ANCOVA suggests a significant interaction between time and taxon and space and taxon. The only exception is the Jaccard index for effect of time (p=0.12).

3. The aggregation to higher taxa is significantly different from random for between sites but not significantly different from random for within sites. The two exceptions are that the Jaccard is not significantly different from random for family (p=0.16) and that order becomes significantly different from random for order for the Whittaker index (p=0.003).
4. In the comparison of neutral vs. empirical CII, the empirical CII is higher than even the most favorable (m=1.0) neutral CII beyond several thousand years. With other indices of CII, three exceptions to this were found (Table S-)

In summary, these four indices produce similar results except that: 1) the Jaccard index sometimes loses significance (hardly surprising given that it uses only presence absence data instead of abundance and is therefore throwing out data and statistical power) and 2) The Whittaker index sometimes takes on significance at the order level



5.

Figure S- 5 – Species diversity decays with time in the neutral model

This graph plots the average species diversity at a local community (averaged across 20 sites and 20 Monte Carlo replicates) as it decreases over time. Note the semi-log scale, implying a nearly exponential rate of decay of species richness. Most species disappear in the first few hundred years.

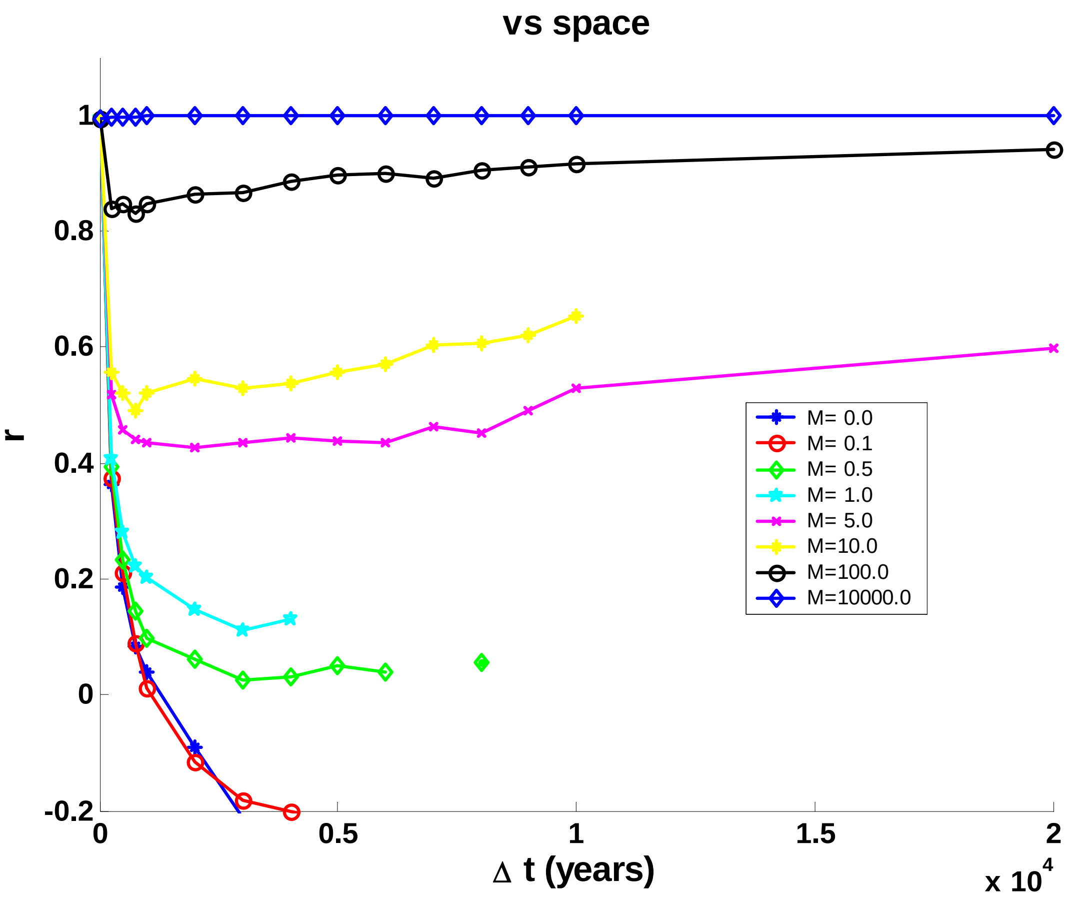


Figure S- 6 – Decay of community similarity between sites

Compare with the dashed lines Figure 4 main text (no analog to the empirical data presented as symbols in Figure 4 in the main text could be computed across space). This plot shows the average community similarity between each possible pairwise comparison of 20 sites, further averaged across 20 Monte Carlo replicates. This graph confirms neutral population genetic predictions that the effect of migration depends on M=m*J, with M>>4 behaving as a panmictic population, M << 4 rapidly losing similarity between sites, and M ≈ 4 being intermediate. The exact constant (e.g. 4 here) depends on the exact nature of the spatial model. The fact that the computer simulations match previously existing theory confirms the accuracy of the simulations. The lines do not always extend for the full time duration because we threw out calculations of similarity when only 1-3 species were in the community. These communities have no statistical power and have artificially inflated Pearson r values.

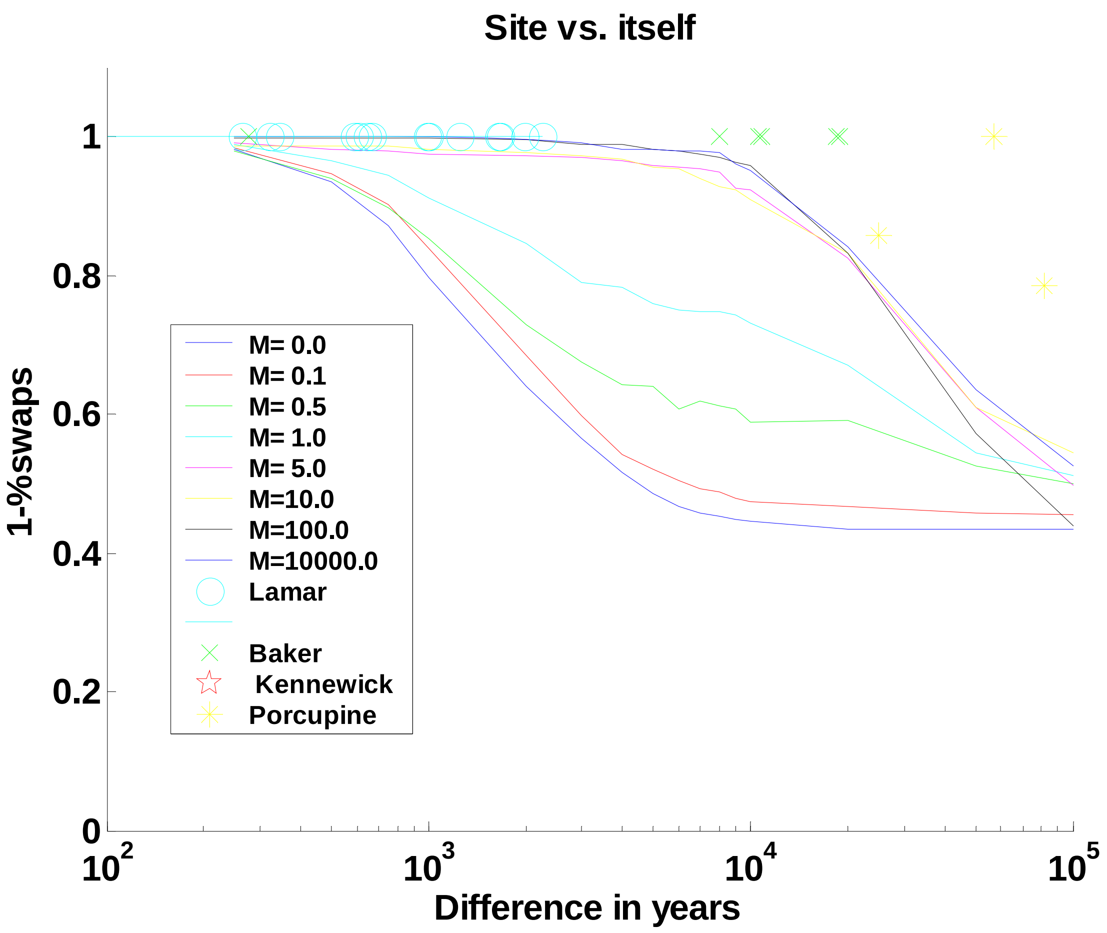


Figure S- 7– Site vs. itself over time – using different measure of similarity

This figure is similar to Figure 4 in the main text, but using a different measure of similarity. See the legend for Table S- for a definition of %swaps. This gives a robust, nonparametric measure of drift in a community. By plotting 1-**%swaps** as done here, we get a measure of similarity (inertia). Note that the empirical data is in all cases on or above the M=J (m=1.0) line. Although not plotted, Porcupine has a point at 190,000 years with a similarity by this measure of 87.5% also well above the neutral model.

	%swaps			SCD			Jaccard			Whittaker		
M	**1000 yrs**	**10,000**	**100,000**	**1000 yrs**	**10,000**	**100,000**	**1000 yrs**	**10000**	**100000**	**1000 yrs**	**10,000**	**100,000**
0	14.5%	55.3%	56.8%	0.38	1.05	1.11	0.354	0.138	0.124	0.38	0.73	0.76
0.1	13.4%	53.4%	54.0%	0.38	0.97	1.04	0.373	0.168	0.152	0.41	0.74	0.78
0.5	9.9%	38.2%	52.3%	0.35	0.72	0.81	0.398	0.258	0.193	0.37	0.6	0.61
1	9.7%	25.8%	49.2%	0.31	0.7	0.85	0.423	0.308	0.187	0.37	0.62	0.69
5	1.6%	11.7%	53.8%	0.23	0.39	0.74	0.567	0.430	0.203	0.31	0.41	0.58
10	1.2%	13.2%	48.7%	0.18	0.32	0.74	0.624	0.440	0.204	0.28	0.37	0.61
100	1.0%	9.5%	53.4%	0.05	0.28	1.03	0.742	0.474	0.147	0.15	0.34	0.74
10000	0.0%	2.2%	52.5%	0.03	0.23	0.91	0.762	0.487	0.170	0.1	0.27	0.68

Table S- 5– Community drift (1- community inertia) for alternative measures

This table shows four alternative measures of community inertia to the Pearson r used in the main text. Three measures, squared chord distance (SCD), Jaccard and Whittaker, are commonly used in the analysis of communities (See *Numerical Ecology, 2nd Ed* by Legendre and Legendre). The first measure, %swaps is our own as it clearly emphasize the degree to which rare species become common and common species become rare. We define %swaps = the % of all species that move from the top 1/3 of abundances (tertile) to the bottom 1/3 (tertile) and vice versa, not counting species that stay in the same tertile or move up or down just one tertile. By time t=100,000 years, it has stabilized to about 50% swaps for all values of M. All three measures except Jaccard are measures of community drift or distance. Community inertia can be approximated by 1-the reported values (i.e. lower values indicate greater inertia). We report values for three time durations and 8 values of M (# of individuals migrating).

Site	Time	%swaps	SCD	Jaccard	Whittaker
Lamar	0	0.0%	0.000	1.000	0.000
Lamar	263.5	0.0%	0.085	0.800	0.180
Lamar	321	0.0%	0.069	0.750	0.178
Lamar	343	0.0%	0.081	0.800	0.190
Lamar	584.5	0.0%	0.050	0.938	0.154
Lamar	606.5	0.0%	0.102	0.875	0.227
Lamar	646.5	0.0%	0.091	0.867	0.253
Lamar	668.5	0.0%	0.081	0.813	0.239
Lamar	989.5	0.0%	0.166	0.786	0.316
Lamar	1001.5	0.0%	0.051	0.786	0.122
Lamar	1253	0.0%	0.128	0.867	0.281
Lamar	1648	0.0%	0.058	0.800	0.175
Lamar	1670	0.0%	0.052	0.750	0.180
Lamar	1991	0.0%	0.125	0.714	0.249
Lamar	2254.5	0.0%	0.093	0.688	0.221
Baker	0	0.0%	0.000	1.000	0.000
Baker	277.5	0.0%	0.012	1.000	0.094
Baker	8000	0.0%	0.047	0.846	0.129
Baker	10545	0.0%	0.101	0.923	0.254*
Baker	10822.5	0.0%	0.125	0.923	0.309
Baker	18545	0.0%	0.133	0.923	0.298
Baker	18822.5	0.0%	0.146	0.923	0.333
Porcupine	0	0.0%	0.000	1.000	0.000
Porcupine	25000	14.3%	0.521*	0.500	0.457*
Porcupine	57000	0.0%	0.194	1.000	0.374
Porcupine	82000	21.4%	0.257	0.500	0.266
Kennewick	0	0.0%	0.000	1.000	0.000
Kennewick	190000	12.5%	0.643	0.750	0.600

Table S- 6 – other measures of community inertia empirical data

This table reports four alternative measures of community inertia (see Table S- for definitions) for the 25 “within site, between time” comparisons. Three of these are measures of distance, so 0 indicates an identical community, and in general lower values indicate more inertia. One (Jaccard) is a measure of similarity and hence inertia. When compared to Table S- , we can see that on all three measures, community drift is much lower (i.e. inertia is much higher) than in the neutral model after the first 3,000 years of transients. There are only three instances across all three measures (after 3,000 years of transients) where the empirical data has less inertia than the neutral model (and they are marked with an asterisk).

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