

Rise and Fall of Species Occupancy in Cenozoic Fossil Mollusks

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appreciable component of plate boundary motion. The most compelling evidence connecting the megasplay to the recent tsunamigenic slip is the geographical coincidence with the updip termination of slip during the 1944 Tonankai event, as inferred from tsunami (17, 26) and seismic (27) waveform inversions and recent structural studies. These studies all suggest that the megasplay may have experienced coseismic slip, so our discovery of recent movement along a strand of the megasplay system is strong evidence that lends support to this interpretation.

Inversion of earthquake seismicity data shows that rupture in the Tonankai earthquake initiated near the downdip end of the slip area and propagated updip (23). Inversion of tsunami data (17) cannot adequately distinguish contributions to wave generation from interplate slip along the décollement or along the splay fault during the Tonankai earthquake, but results favor slip along the splay fault. Because of the modeling techniques employed, the vertical resolution of the updip extent of both coseismic slip and tsunami source area is relatively poor. The horizontal resolution is better, however, and the slip inversions suggest that rupture did not propagate to the trench but terminated close to where the megasplay intersects the surface (17, 23). As rupture approached the surface, it could have (i) continued along the basal décollement, dying out in soft sediments of the outer accretionary wedge, or (ii) propagated up the megasplay. Kame *et al.* (22) modeled this scenario using an elastodynamic fault formulation and concluded that coseismic slip on the megasplay branch is favored over the basal décollement and that simultaneous slip on both is unlikely. This mechanical argument, com-

bined with the tsunami source modeling and our current observations, suggests that the megasplay thrust system is presently a part of the “plate boundary fault,” as defined by megathrust earthquake rupture (Fig. 4C).

We have shown that the most active fault in the prism is the megasplay and that there is less activity on the frontal décollement. This splay fault represents one single fault that is continuous from the deep seismogenic zone up to the surface. This observation supports the suggestion by Wang and Hu (21) that the velocity-strengthening behavior of the frontal décollement causes the slip to concentrate along the megasplay during great earthquakes. As the mechanical boundary between the inner and outer accretionary wedge (21), the megasplay could thus be seen as producing a (deformable) backstop for the outer wedge. Major slip along a fault with the geometry of the megasplay during great earthquakes thus increases the potential for tsunamis and explains why this and some other margins foster tsunami generation whereas still others do not.

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Supporting Online Material

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Figs. S1 and S2
Table S1
Movie S1

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regularity to the waxing and waning of species, although a number of models, with varying predictions, have been proposed on the basis of limited available evidence [summarized in (1, 2)].

Within marine invertebrates over the Phanerozoic Eon, species richness, frequency of occurrence, and geographic range increase and decrease nearly symmetrically on average over the duration of a genus (3), although certain subsets of genera show asymmetrical patterns (3, 4). The pattern of regular increase in geographic range has also been demonstrated for Ordovician marine invertebrate genera (5). A survey of Late Cretaceous mollusks from the Gulf and Atlantic coasts of the United States found that geographic range and geologic longevity are correlated and that species originating

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Rise and Fall of Species Occupancy in Cenozoic Fossil Mollusks

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In the time between speciation and extinction, a species' ecological and biogeographic footprint—its occupancy—will vary in response to macroecological drivers and historical contingencies. Despite their importance for understanding macroecological processes, general patterns of long-term species occupancy remain largely unknown. We documented the occupancy histories of Cenozoic marine mollusks from New Zealand. For both genera and species, these show a distinct pattern of increase to relatively short-lived peak occupancy at mid-duration, followed by a decline toward extinction. Thus, species at greatest risk for extinction are those that have already been in decline for a substantial period of time. This pattern of protracted rise and fall stands in contrast to that of incumbency, insofar as species show no general tendency to stay near maximal occupancy once established.

Every biologic group, at species rank and higher, varies over time in the size of its footprint on Earth. For example, *Homo sapiens* has spread from a minor species occupying a spot on the globe to complete dominance in many environments, whereas the

phylum Brachiopoda has declined in species richness, numerical abundance, and range of occupied environments since the Paleozoic Era. Such observations are part of the basic narrative of the history of life. What is virtually unknown, however, is whether there is any overarching

shortly before the end-Cretaceous extinction had a statistical distribution of geographic ranges similar to that of species that had originated over a longer span of time leading up to the latest Cretaceous. These observations were used to infer that individual species tend to reach maximal geographic range early in their lifetimes (6). It is not known whether the difference between species and genera reflected in these studies holds in general. If so, it could come about because the rise and fall of a genus depends both on the pattern within constituent species and on temporal changes in the number of species within the genus (3, 5).

To examine the history of species and genera, we analyzed Cenozoic marine molluscan data within the Fossil Record File [FRED (www.fred.org.nz/)]. This comprehensive archive of the New Zealand fossil record provides a compilation of taxonomic lists from field-based collections tied to specific localities (7). One strength of the FRED data set is that the species in 81% of the collections were identified by just three paleontologists (A. G. Beu, C. A. Fleming, and J. Marwick), often working in collaboration; thus taxonomic consistency is high. The FRED data were downloaded in March 2007 and comprised 6885 collection lists [see supporting online material (SOM)]. From these we eliminated the following: (i) Taxonomic lists for which the identifier of taxa in the collection is unknown or of doubtful reliability. (ii) Collections that could not be assigned to a single New Zealand stage on the basis of their paleontologically or stratigraphically determined age. (iii) Collections from northernmost New Zealand that represent a biogeographically distinct warm-water fauna that is constrained by outcrop to just a brief interval of time (21.7 to 15.9 million years ago) (8). (iv) All but level-bottom benthonic taxa that are inferred to have been confined to, or to have ranged into, shelf water depths, because off-shelf environments are inconsistently and poorly sampled [fig. 2 of (7)]. Results are similar if the off-shelf and northern data are included (fig. S18). The resulting data were further edited with a variety of automated and manual procedures (9) (SOM). After these adjustments, our data set comprised 3974 collections containing 29,361 occurrence records of 2023 species and subspecies and 608 genera and subgenera. Of these species, we conservatively retained 140 extinct, well-sampled species that collectively span 17 stages and about 40 million years (My) (SOM).

Some previous work has found correlations among local abundance, total biogeographic range, and the proportion of that range actually occupied (3, 10–12); we therefore include all these concepts under the term “occupancy.” Lacking reliable data on numerical abundance, we operationally measured occupancy as the proportion of collections in a given time interval in which a given species occurs. This measure correlates well with geographic range in our data (figs. S5 and S6). Except for rare species in stages with

low numbers of collections, this measure, as a simple proportion, is essentially unbiased by the number of collections (figs. S15 and S16). In order to follow the full history of occupancy of each species, we considered only those species that are extinct (SOM). Given that over 98% (138 of 140) of the species we studied are endemic to New Zealand, we have documented nearly the entire history of this set of species.

Occupancy histories can be severely biased by sparsely occurring species, which perform best to be at or near maximum occupancy at

their times of first and last appearance, but near zero in between (3). For this reason, such species cannot yield meaningful occupancy histories. We therefore restricted the analysis to species with a high estimated sampling probability, namely those that occur at least once in every stage within their stratigraphic range, although less stringent culling yields similar results (fig. S10). Given this protocol, and the nature of the fossil record itself, our main analyses strictly apply to the best-sampled species, which are likely to be the most widespread and abundant species and

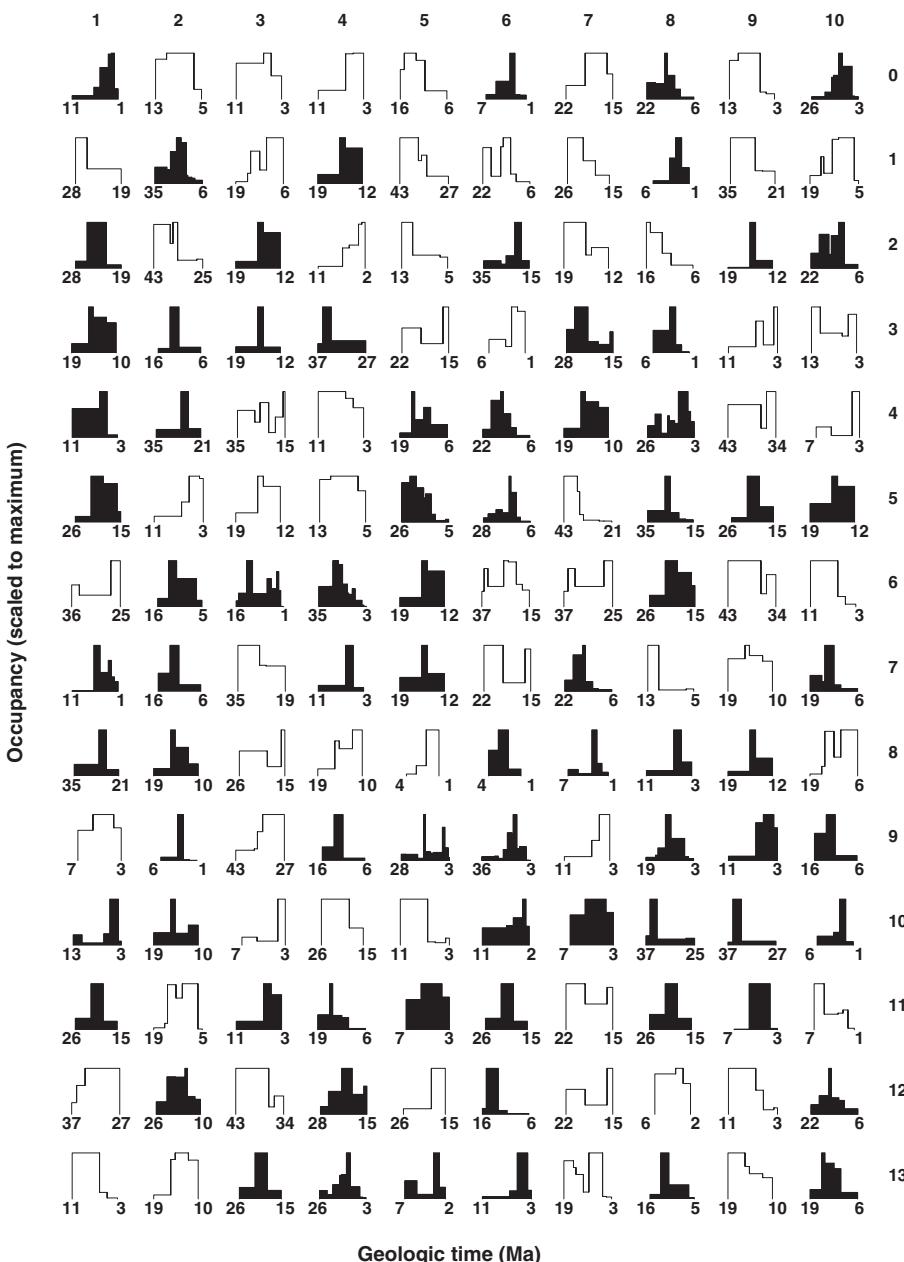


Fig. 1. Empirical occupancy histories of Cenozoic molluscan species of New Zealand. Species are keyed to table S1; for example, species number 16 in table S1 is in row 1, column 6 in this figure. Durations are scaled to unit length from the base of the stage of first appearance to the top of the stage of last appearance, with the given numerical ages in millions of years ago (Ma) based on (27). Each occupancy history is scaled to its maximum. Species showing a relatively short-lived peak in occupancy away from the endpoints of the stratigraphic range are shaded.

also the ecological dominants. Large-scale biogeographic patterns are apparently determined disproportionately by common species rather than rare ones (13), and we therefore expect our data to capture general trends. We find similar temporal patterns in occupancy and geographic range if we do not cull the data to remove the more sparsely occurring species (SOM).

Because the stratigraphic resolution in our data is at the stage level, no variance in occupancy within stages can be detected and little information on occupancy history can be gleaned from short-lived species. We therefore restricted our analysis to species with a range of three or more stages, although we find compatible results if we include all but single-stage taxa (SOM). In addition to documenting occupancy histories for individual species, we characterized the average occupancy of all species. To aggregate data on species with different durations, we rescaled the stratigraphic range of each species to unit length (3). We calculated the height of the average species occupancy history at each point in scaled time as the mean occupancy of all species at that time (SOM). We estimated the uncertainty about this average occupancy history by a bootstrap resampling procedure (SOM). We applied the same protocol to genera.

The occupancy histories for individual species exhibit a variety of shapes (Fig. 1). The most common tendency is for occupancy to increase from the time of first appearance, to attain a relatively short-lived maximum sometime between the stages of first and last appearance, and to decline from this maximum to the time of last appearance (14). Roughly 56% of species (78 of 140) exhibit this pattern, a high proportion given that there are several alternatives: 22 species (16%) peak in their stage of first appearance, 20 (14%) peak in their last stage, and 20 (14%) show equivocal patterns. The predominance of species showing the rise-and-fall pattern holds if we consider only those species in which the difference between minimum and maximum oc-

cupancy is statistically significant (fig. S11). Statistical analysis of times of peak occupancy shows that these are significantly concentrated toward the middle of species' durations (table S3). There are many individual exceptions and ambiguous cases, but the average species history (Fig. 2) shows that the tendency to reach a peak at mid-duration is a general feature of species-level occupancy. The average occupancy history of species deviates substantially from the relatively constant pattern that would be expected if occurrences within the history of individual species were distributed in proportion to the overall number of occurrences within each stage rather than the relative position of that stage within the species' history (fig. S12). It is possible in principle that the proportion of sites occupied by a species is constant while its local abundance, and therefore its probability of detection, varies over time in a regular way that parallels the occupancy histories we have documented. This would not be an artifact but rather would reflect biologically meaningful variation in an important aspect of occupancy.

Individual and average species occupancy histories in the New Zealand Cenozoic are similar to those for genera (Fig. 2 and fig. S4). Because genera consist of multiple species, the amplitude of the genus curve is higher than that for species. Genera show an earlier peak in average occupancy, but because the number of taxa suitable for our genus-level analysis is small (SOM) and the sampling variance consequently large, this difference in the location of the peak may not be biologically meaningful. Because species are shorter-lived than genera, they rise to maximum occupancy more rapidly in absolute terms, but this rise is nonetheless protracted over several million years (14). At their time of extinction, species, like genera, tend to have been in decline rather than being truncated by extinction events at or near their maximum occupancy. As expected given the correlation between occupancy and geographic

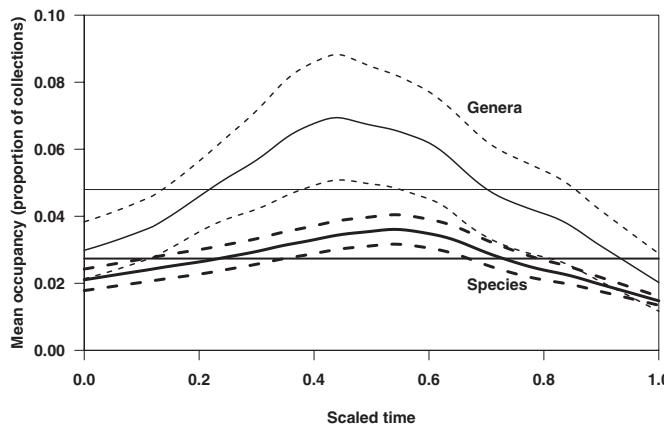
range (figs. S5 and S6), average histories of geographic range are similar to occupancy histories for New Zealand Cenozoic mollusks (figs. S7 and S8). Our results broadly agree with patterns seen in Cenozoic species of unicellular marine plankton (15), a few late Cenozoic mammal species from Italy (16), and a larger sample of European Neogene mammal genera (11), but they disagree with previous suggestions that species attain their maximal geographic ranges shortly after they originate (6).

Because taxa that become extinct at a given point in time are preferentially those that have declined in occupancy and geographic range relative to an earlier peak, our results imply that the prior history of a species is an important determinant of its risk of extinction, and they support the notion that presence over a greater geographic range helps to confer extinction resistance (17). Because species tend to take about as long to increase to peak occupancy as to decrease to extinction, our results also suggest that neither the first nor the last appearance can be assumed a priori to be a substantially better biostratigraphic datum in general (18).

Easy dispersal is a component of many ecological models that predict substantial shifts in geographic range over short time spans (19). In accord with this, rapid range expansions in the present day are well documented (2). The contrast with our results suggests that different processes may control occupancy and geographic range on ecological versus geological time scales. Perhaps factors such as dispersal and competitive ability enable species to rapidly fill the ecological and geographic space available to them at any moment, whereas this space in turn is strongly controlled by slowly varying geological processes such as marine transgression and regression (20, 21). It is also likely that many species' ranges are in flux today in response to more rapid anthropogenic forcings and to post-Pleistocene deglaciation and related changes (22, 23).

Finally, ecological incumbency, or the tendency of taxa that already occupy a niche or adaptive zone to resist displacement, is commonly invoked to explain the persistence of certain higher taxa over geological time, even in the face of apparently superior competitors (24–26). If incumbency were generally important at the species level, we would expect to see most species persisting for long times at or near maximal occupancy. Our findings do not bear this out.

Fig. 2. Average occupancy history of Cenozoic molluscan species (thick curves) and genera (thin curves) of New Zealand, with durations scaled to unit length from the base of the stage of first appearance to the top of the stage of last appearance (27). The solid curves are the smoothed averages of the level of occupancy of all taxa at 100 evenly spaced, interpolated points between the times of first and last appearance (SOM). Dashed curves show 1 SE on either side of the average, as estimated from a bootstrap resampling procedure (SOM). The horizontal lines show the overall mean occupancy of all taxa over time.



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14. The geological durations of species in our analysis, from the base of the stage of first appearance to the top of the stage of last appearance, vary from 2.0 to 32 My, with a median [± 1 SE (SOM)] of 8.7 ± 0.4 My (27). Median durations are 9.3 ± 0.4 My for the shaded species in Fig. 1, and 8.3 ± 0.4 for the remaining species. The median time taken to attain peak occupancy, measured from the base of the stage of first appearance to the midpoint of the peak stage, is 4.0 ± 0.5 My for all species, 3.9 ± 0.5 My for the shaded species in Fig. 1, and 4.6 ± 0.6 My for the remaining species. The median time between the midpoint of the peak stage and the top of the stage of last appearance is 4.5 ± 0.3 My for all species, 4.6 ± 0.4 My for the shaded species in Fig. 1, and 4.5 ± 0.6 My for the remaining species. The subsets of species are statistically indistinguishable from each other in median duration, time from first appearance to peak occupancy, and time from peak occupancy to last appearance (SOM). Nor are there any significant differences between the median time from first appearance to peak and the median time from peak to last appearance (SOM).
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Supporting Online Material

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Materials and Methods

SOM Text

Figs. S1 to S20

Tables S1 to S3

References

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Transgenerational Plasticity Is Adaptive in the Wild

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Plants exhibit adaptive responses to light, but it is not known whether parental plants transmit environmental cues that elicit adaptive responses in offspring. We show that offspring life history (annual versus biennial) is influenced by the maternal light environment (understory versus light gap). This transgenerational plasticity is adaptive when offspring are grown in their maternal light environment, where seeds typically disperse. Projections of population growth show that plants that are appropriately cued for their light environment through maternal effects have 3.4 times greater fitness than otherwise. Transgenerational plasticity has evolved in response to natural variation in light and provides a flexible mechanism by which sedentary organisms cope with heterogeneous environments.

All organisms experience environmental heterogeneity. Some move to cope with variable environments, but those that cannot move require other mechanisms to ensure success. Plants have little choice in their growth environment, and seed dispersal is often limited, with most seeds falling relatively close to the maternal plant (1, 2). Thus, a seedling's growth environment may frequently be similar to its mother's, especially where habitat patches are constant between generations and larger than the scale of seed dispersal. Under these conditions, adaptive maternal cues elicited by the local habitat may evolve if they increase offspring fitness (3). In a heterogeneous environment, flexible maternal effects will confer a greater fitness advantage than fixed genetic specialization to local habitats (4, 5), because gene movement between habitats through pollen may result in sampling different environments between generations.

Plants respond to heterogeneity in their immediate environment through plasticity. This plasticity may be adaptive, enhancing individual performance (6), or simply a passive consequence of resource limitation (7, 8). Plasticity may also occur between generations if the parental environment influences the expression of offspring

traits. Transgenerational plasticity in response to maternal environments is common in plants (9–12), and maternal effects may increase maternal fitness (10). There is little evidence that transgenerational plasticity enhances offspring fitness in plants, although conditions, such as sedentary growth form, spatially patchy habitats, and limited seed dispersal, favor its evolution (10, 13). The demonstration of adaptive maternal effects requires that (i) the maternal environment influences offspring trait expression, (ii) these maternal influences are genetically based, and (iii) maternal effects enhance offspring fitness.

Campanulastrum americanum is a monocarpic herb whose populations span distinct light environments and include annual and biennial life histories. Seeds that germinate in the fall are annuals, whereas those germinating in the spring are biennials and flower during their second summer. Annual and biennial plants co-occur, and an individual's seeds may germinate in either or both seasons. We hypothesized that adaptive maternal effects may influence the life-history schedule, because germination time de-

Table 1. Analysis with generalized linear models of the influence of offspring life history and of maternal and offspring light environment on fitness components in *C. americanum*. For seedling yield, life history indicates the probability of germination and early survival as annuals and biennials. Dashes indicate factors not included in the model. *, P < 0.10; †, P < 0.05; ‡, P < 0.01; §, P < 0.001.

	Seedling yield (χ^2)	Rosette survival (χ^2)	Adult survival (χ^2)	Fruit number (F)	Seeds per fruit (F)
Life history (LH)	13.14§	-	9.54‡	41.13§	14.55§
Offspring light (OL)	10.40‡	0.00	0.58	39.09§	16.89§
Maternal light (ML)	2.86*	0.00	0.07	0.41	0.31
OL × ML	8.86‡	1.98	0.00	0.23	0.06
OL × LH	947.80§	-	15.43§	0.16	0.78
ML × LH	7.61‡	-	0.29	0.63	0.40
OL × ML × LH	0.02	-	0.11	0.15	0.00
Block	845.26§	19.69	167.08§	2.50‡	1.70†
Herbivory	-	-	-	9.02§	0.80

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