A geographic test of species selection using planktonic foraminifera during the Cretaceous/Paleogene mass extinction

Matthew G. Powell and Johnryan MacGregor

Abstract.—Species selection has received a great deal of theoretical attention but it has rarely been empirically tested. It is important to determine the level of selection that operated during a particular extinction event because it can help distinguish between traits that were actually responsible for extinction and those that were merely correlated with it. Here, we present a test that can help distinguish between organismal and species-level selection, which we demonstrate using the high-resolution fossil record of planktonic foraminifera species recorded in deep-sea sediment cores. Our test examines the fate of survivors and victims during the Cretaceous/Paleogene (K/Pg) mass extinction within single geographic regions, where all individuals experience the same selection pressures. Selection at the organismal level implies that individual members of surviving species are more fit than those of victimized species, and therefore should be more likely to survive in affected areas; conversely, selection at the species level implies individuals will suffer equally within an affected area. We find that survivors of the mass extinction suffered very high extirpation rates in cores where the overall extinction rate was high, indicating that individual members of the surviving species were generally no more fit than individual members of extinct species. Rather, these species were able to survive because they possessed advantageous species-level traits, such as larger geographic ranges and greater abundances than victimized species. This geographic pattern of extirpation suggests that selection operated at the species, rather than organismal, level during the K/Pg mass extinction of planktonic foraminifera.

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Accepted: 17 January 2011

Introduction

Studies of extinction selectivity are among the most powerful means of identifying extinction mechanisms (McKinney 1997; Bambach 2006; Foote and Miller 2007). Selectivity is usually assessed either by identifying traits that differed between survivors and victims of a crisis, or by determining whether extinction rates differed between species grouped by shared morphological or ecological traits. The results of such assessments are commonly taken to implicate specific kill mechanisms. For example, echinoid species that were equipped to feed on fine detritus were more likely to survive the Cretaceous/Paleogene (K/Pg) mass extinction than those that were restricted to coarse detritus, implying that nutrient limitation may have been an important kill mechanism for this event (Smith and Jeffrey 1998). The end-Permian mass extinction has been attributed to hypercapnia due to elevated pCO2 because heavy calcifiers suffered the highest extinction rates (Knoll et al. 1996, 2007). Studies of extinction selectivity have also been used to understand the mechanisms of minor extinction events and the composition of the modern fauna, which has been shaped by past environmental changes (Johnson et al. 1995; Smith and Roy 2006).

Such studies are complicated by the fact that traits are often intercorrelated (Hunt et al. 2005; Jablonski 2005; Jablonski and Hunt 2006; Finarelli 2008; Roy et al. 2009). This intercorrelation may result in a spurious selectivity pattern that does not reflect the actual kill mechanism at the time of the extinction. For example, if species that were adapted to warm temperatures were selected against during an episode of global cooling, and if adaptation to warm temperatures also caused species to be restricted to a small geographic area, then both temperature adaptation and geographic range will show significant selectivity. It is possible for a trait to be indirectly selected against if it produces another trait
that is the true target of selection (a phenomenon that has been termed “screening off” [Jablonski and Hunt 2006; Jablonski 2008]). It is also possible for a trait to show significant selectivity even if it is not a target of selection at all, either directly or indirectly, but merely associated with another trait that is. The consequence of this fundamental problem of intercorrelation is that observed patterns of selectivity may not imply a particular mechanism of extinction.

The ability to pinpoint the true target of selection during an extinction event is fundamentally tied to questions about the level of selection that operated during a particular event. Traits may be expressed at either of two hierarchical levels. Organismal traits are those that all individuals of a species possess and which therefore serve to distinguish them from individuals of another species. By contrast, a species may also possess traits because it has measurable quantities that individuals cannot possess, such as population size and density, geographic range, intraspecific variation in fitness, or sex ratio, among others (Stanley 1975; Gould 2002; Jablonski 1987, 2000, 2008; Pigliucci 2009). In its strict sense, species selection says that differential evolutionary success is due to traits that are the exclusive properties of species (emergent traits), and not merely properties of their constituent individual organisms scaled up to species level (aggregate traits) (Stanley 1975; Jablonski 2008: his tables 1 and 2 contain many specific examples of emergent and aggregate traits).

There is evidence that traits at both levels of selection have operated in the past. Most studies of extinction selectivity have focused on morphological or ecological traits that enabled members of a species to survive a time of crisis, thereby ensuring the continuation of the species as a whole. As a result, many organismal traits have been identified as associated with extinction (e.g., Chatterton and Speyer 1989; Johnson et al. 1995; Banerjee and Boyajian 1996; Levinton 1996; Smith and Jeffery 1998; Lockwood 2004; Smith and Roy 2006; Rivadeneira and Marquet 2007; Clapham et al. 2009). However, species-level traits also appear to have played an important role during extinctions, the most prominent of which are geographic range and population size. Geographic range size is a consistent predictor of survival at all magnitudes of extinction (Payne and Finnegan 2007; Powell 2007), perhaps because a wide geographic range increases the likelihood that a species will live outside the crisis zone or survive in refugia. Species with larger population sizes are further from extinction to begin with, thus conferring a survival advantage (Stanley 1986). Population size has been important for the survival of Neogene bivalves (Stanley 1986; Simpson and Harnik 2009) and planktonic foraminifera (Stanley et al. 1988; Buzas and Culver 1989), in some cases overwhelming the influence of geographic range size.

A Geographic Test of Species Selection.— Resolving the level of selection is important because much of our understanding of the mechanisms of extinction and the nature of biotic replacements is based on accurately identifying the true target of selection. Unfortunately, empirical studies of species selection have lagged behind its theoretical development (Jablonski 2008; Pigliucci 2009). Indeed, Pigliucci (2009) characterized species selection as the only component of the Modern Synthesis that was conceptually mature but empirically poorly tested. Here, we present a method that can help determine the level of selection that operated during an extinction event. This simple test examines the geographic pattern of extirpation (local disappearance from a particular geographic region) of surviving species (Fig. 1). If selection was against organismal-level traits, then it follows that individual members of some species will have been better adapted than the individual members of other species, depending on whether they possessed such a trait. Consequently, in a single geographic location—where all individuals experience the same selection pressures—fit individuals should be more likely to survive than unfit individuals. In contrast, if selection was against species-level traits, then it follows that no individual was better adapted than any other individual, because the unit of selection lies above the individual level. Consequently, individual members of a fit species will die at the same
rate as individual members of the unfit species, although the fit species as a whole will survive because of its advantageous species-level traits. In this model of extinction, species survive crises not by being composed of superior individuals but by winning a war of attrition. That is, survival is a pyrrhic victory, because the survivors suffer devastating losses of individuals despite ultimately surviving as a species.

Other approaches to the problem of intercorrelated traits can rule out specific traits, but they cannot provide a general test of organismal versus species-level selection. These approaches typically attempt to identify which trait was causally associated with extinction by controlling for other variables. This can be done either by statistical techniques (e.g., Jablonski and Hunt 2006; Payne and Finnegan 2007; Finnegan et al. 2008) or by restricting the data to hold one trait constant before testing for differences between victims and survivors in another trait (e.g., Banerjee and Boyajian 1996). Such approaches are limited because they can only control for variables included in the model. For example, Jablonski and Hunt (2006) assessed the contributions of larval mode and geographic range, which covary, to the durations of late Cretaceous mollusk species. After statistically accounting for geographic range size, they found that larval mode had little independent effect on duration. Although this provides strong evidence against larval mode as a causal determinant of species duration, it cannot provide evidence in favor of geographic range, because a different, unmeasured variable that is also correlated with geographic range may be the causal factor. This issue is present in any statistical analysis that attempts to determine causality; however, the problem of intercorrelated traits is particularly acute when using fossil species because much of their original phenotype is irrevocably lost during fossilization. The suite of testable variables is limited because details of soft-part anatomy and behavior, which are just as likely to influence survival as skeletal anatomy is, are available only in unusual circumstances. The geographic test proposed here can help distinguish organismal from species-level selection without requiring all traits to be measured. The test cannot, however, identify specific traits that were selected against during a crisis, and thus

![Figure 1](image-url)

**Figure 1.** Conceptual model of the geographic test of species selection. This simple example uses two species that differ in organismal (color = black or white) and species-level (geographic range = one or two regions) traits, and which experience an environmental crisis in region 1 during time 2 (shaded area). If selection is against organismal traits only (A), then in areas where two species co-occur the species that possesses the advantageous trait will survive whereas the other will not. In contrast, if selection is against species-level traits only (B), then in areas where the two species co-occur, both species will die out because no individual was more fit than the other. The black species survived by being present outside the crisis zone. Note that selectivity appears to be against color and geographic range in both cases, but the true unit of selection can be distinguished because selection at different hierarchical levels predicts different patterns of regional extirpation.
serves as an explicit test of species selection rather than a test to determine the actual target of selection (which would require further statistical tests of various traits).

In this study we demonstrate the geographic test of species selection by using planktonic foraminifera species through the K/Pg mass extinction. Planktonic foraminifera are ideal for this test because a high-resolution, geographically explicit fossil record is available from deep-sea sediment cores. The K/Pg extinction event has been well characterized for planktonic foraminifera (Berggren 1969; Cifelli 1969; Lipps 1970; Keller 1989; Norris 1992; Keller et al. 2002).

**Methods**

We downloaded raw data from the Janus database (www-odp.tamu.edu/database), which contains Integrated Ocean Drilling Program (IODP) and most Ocean Drilling Program (ODP) core data, and from the National Geophysical Data Center (www.ngdc.noaa.gov/mgg/geology/drill.html), which contains Deep Sea Drilling Project (DSDP) and pre-Janus ODP core data. Nineteen cores in the Janus database included sediments that bracket the K/Pg boundary and contain planktonic foraminifera (Fig. 2).

Species from this data set were categorized into three groups based on their local and global stratigraphic ranges in relation to the K/Pg extinction boundary (Fig. 3): (1) extinct species, which became globally extinct during the K/Pg event; (2) extirpated species, which survived globally but were locally extirpated in a particular core; and (3) persistent species, which survived both globally and locally. In total, the 19 cores contained occurrences of 192 species. Species that became extinct before the K/Pg boundary or originated after the extinction event were excluded from analyses, resulting in a total of 86 species whose stratigraphic ranges crossed or ended at the K/Pg boundary. We classified survivors as extirpated or persistent in each core by assessing whether their stratigraphic range endpoint crossed the K/Pg boundary, which we determined from the biostratigraphic ages provided in the Janus data. Rather than using youngest occurrences, we calculated stratigraphic range endpoints for each species as the endpoint of the 50% confidence interval on their stratigraphic range (Marshall 1994). This approach mitigates bias caused by incomplete sampling, which may make species apparently disappear prior to their true last occurrence (Signor and Lipps 1982). Analyses were repeated using uncorrected stratigraphic ranges in
each core, and no result depended on whether uncorrected or sampling-corrected ranges were used. Note that survivors may also include those that tracked a favored habitat away from a region of crisis only to recolonize it later, just as many living species have adjusted their ranges in response to climate warming. Therefore, the measured extirpation rate, which only includes species that do not recolonize a particular region, is actually a conservative measure of the true extirpation rate.

Global stratigraphic ranges were obtained from the Neptune database (services.chronos.org/databases/neptune/index.html; Spencer-Cervato 1999). Species were categorized as extinct if their last appearance was between 66 and 65 Ma, which brackets the K/Pg boundary at 65.5 Ma (Fig. 4). Some workers have argued that many occurrences of Maastrichtian species above the K/Pg boundary are due to reworking (Olsson and Liu 1993; Huber 1996; Kaiho and Lamolda 1999; Huber et al. 2002; Molina et al. 2004). Therefore, we also used an expanded definition of the K/Pg boundary that counted species as extinct if their last global appearance was between 66 and 63 Ma, which in the raw data includes a secondary peak of extinctions that likely represents reworked specimens (Fig. 4). We have reported the results for both extinction intervals, which differ in some details. Nevertheless, the central conclusions of this study do not depend on the precise boundary of the K/Pg mass extinction. The extinction rate within each core was calculated as the number of species that became globally extinct divided by the total number of species in the core at the time of extinction; the extirpation rate was calculated as the number of species that disappeared from the core within the extinction window, but whose global stratigraphic ranges indicated they survived, divided by the total number of species in the core at the time of extinction.

Because species are expected to survive in areas that were unaffected by a crisis (regardless of the level of selection), the geographic test of species selection explicitly compares the fate of victims and survivors in regions of crisis. We define these regions as those that experienced high extinction rates. Although extinction rates are presumably an outcome of both the severity of the crisis and the susceptibility of the fauna, Wang and Bush (2008) recently teased these variables apart and found that extinction magnitude is a good proxy for overall extinction intensity, independent of the susceptibility of the fauna.

Geographic ranges and the abundance of each species were calculated directly from the raw occurrence data. We calculated the geographic range of each species as the maximum great-circle distance from the northeastern-most occurrence to the southwestern-most occurrence after rotating geographic coordinates to their paleopositions using PointTracker (C. Scotese, PALEOMAP Project). Because the presence of continents may cause the great-circle method to overestimate the range size of marine organisms, we also repeated analyses using latitudinal range. Results were not dependent on the choice of metric. Relative abundance data are available directly from the ODP data, and are recorded semiquantitatively (generally as “abundant,” “common,” “few,” and “rare”). We acquired data on organismal traits from morphological data in the Mesozoic Planktonic Foraminiferal Taxonomic Dictionary (Mesozoic Planktonic Foraminiferal Working Group 2006), which contains data for 20
organismal traits, with two to 13 character states per trait. This data set also includes a qualitative measure of geographic range size, which records distribution as either “cosmopolitan” or “low-to-mid latitude.” All data used for the following analyses are available online at Dryad: http://dx.doi.org/10.5061/dryad.8481.

Results

Selectivity at the Organismal and Species Levels.—Extinction rates differed significantly between groups defined by spiral suture type ($\chi^2$ test, $p = 0.04$) and aperture position ($p = 0.05$), and nearly significantly by shell porosity ($p = 0.07$) and accessory aperture type ($p = 0.07$) during the 66–65 Ma interval (Table 1). When the extinction boundary is expanded to include the interval 66–63 Ma, extinction rates differed significantly between groups defined by umbilicus structure, umbilical suture type, aperture type, aperture border, accessory aperture type, umbilical chamber shape, and spiral chamber shape ($\chi^2$ test, $p < 0.05$ for each trait). In addition, victims were significantly larger than survivors for both boundary definitions (t-test: 66–65 Ma, $p = 0.004$; 66–63 Ma, $p = 0.02$).

Victims and survivors of the 66–65 Ma extinction interval also differed in geographic range size, whether measured as maximum great-circle distance (t-test: $p = 0.02$; the mean maximum great-circle distance for survivors was 11,062 km versus 7982 km for victims) or as latitudinal range ($p = 0.002$; the mean latitudinal range of survivors was 55.8° versus 31.5° for victims), or assessed as the difference in extinction rates between cosmopolitan and low-latitude species as defined by the Mesozoic Planktonic Foraminiferal Taxonomic Dictionary ($\chi^2$ test, $p = 0.04$). Victims and survivors of the expanded 66–63 Ma extinction interval did not differ significantly in geographic range size when that was calculated directly from the Janus data ($p > 0.10$ for both maximum great-circle distance and latitudinal range). Extinction rates did, however, differ significantly between cosmopolitan species and those restricted to low-to-mid latitudes, using the data from the Mesozoic Planktonic Foraminiferal Taxonomic Dictionary ($p = 0.04$). For the 66–63 Ma interval, surviving species were slightly more abundant prior to the K/Pg boundary than victims ($\chi^2$ test, $p = 0.06$), with survivors having a modal abundance of “frequent” and victims a modal abundance of “rare,” but differences in abundance were not significant for the more restricted 66–65 Ma interval ($p > 0.10$). In summary, the 66–65 Ma interval indicates greater differences in geographic range size whereas the 66–63 Ma interval indicates greater differences in abundance. In either case, there was significant extinction selectivity by both organismal and species-level traits.

As expected, several organismal and species-level traits were correlated with one another. Species with strongly depressed spiral sutures had the largest mean latitudinal ranges (73°) and the largest mean maximum great-circle distances (12,959 km), and suffered no extinction during the 66–65 Ma interval. By contrast, species with other spiral suture types had smaller average ranges and higher extinction rates. In addition, species with an equatorial aperture had the largest

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*** = $p < 0.01$, ** = $p < 0.05$, * = $p < 0.10$.  

Table 1. Organismal and species traits significantly associated with the K/Pg mass extinction of planktonic foraminifera. Note that many of these comparisons would not be significant if corrected for multiple comparisons; here, the point is simply to demonstrate that many traits, at both the organism and species levels, may potentially be associated with extinction. In total, 23 traits were assessed for selectivity. GRS, geographic range size; MPFTD, Mesozoic Planktonic Foraminiferal Taxonomic Dictionary.
range sizes (63° or 10,788 km) and the lowest extinction rates (13%) compared to species with other aperture positions. For species classified using the 66–63 Ma interval, geographic range differed significantly between groups defined by umbilicus structure (ANOVA: latitudinal range, \( p = 0.02 \); great-circle distance, \( p = 0.009 \)), with species with a narrow umbilicus having the smallest ranges and the highest extinction rates, and by the type of accessory aperture (latitudinal range, \( p = 0.02 \); great-circle distance, \( p = 0.005 \)), with species with umbilical accessory apertures having the smallest ranges and the highest extinction rates. Overall, geographic range size and test width were weakly negatively correlated (latitudinal range: \( r = -0.14, p = 0.09 \); maximum great-circle distance: \( r = -0.16, p = 0.06 \)).

**Extinction and Extirpation Rates.**—Species extinction rates were strongly correlated with paleolatitude (Fig. 5; 66–65 Ma interval: \( r = 0.74, p < 0.001 \); 66–63 Ma interval: \( r = 0.84, p < 0.001 \), with the lowest extinction rates in cores recovered from high southern paleolatitudes (no cores that include the K/Pg boundary are available above 31°N paleolatitude for comparison). Extinction rates were also correlated with distance from the Chicxulub impact crater (~26°N) for the 66–63 Ma interval (\( r = -0.46, p = 0.05 \), but not for the 66–65 Ma interval (\( r = -0.31, p > 0.10 \)). Extirpation rates

**Figure 5.** Extinction and extirpation rates versus distance from the Chicxulub crater. Rates were calculated for the extinction interval spanning 66–65 Ma, and the more inclusive 66–63 Ma interval. Extirpation rates are reported for raw and sampling-corrected stratigraphic ranges.
of survivors showed a similar pattern, with significantly higher rates experienced at low paleolatitudes (66–65 Ma interval: $r = 0.67$, $p = 0.002$; 66–63 Ma interval: $r = 0.71$, $p < 0.001$), and nearer the Chicxulub crater (66–65 Ma interval: $r = -0.53$, $p = 0.02$; 66–63 Ma interval: $r = -0.57$, $p = 0.01$). Overall, there was a significant correlation between the extirpation rate of survivors and the overall extinction rate per core (Fig. 6; 66–65 Ma event: $r = 0.41$, $p = 0.08$; 66–63 Ma event: $r = 0.41$, $p = 0.004$). In general, survivors suffered comparable or even higher rates of extirpation than the overall extinction rate in a region, suggesting that no species was intrinsically superior to any other in hard-hit areas. In fact, only six species in the data set survived without having been extirpated from any sampled region.

Extinction rates within each core correlate strongly and negatively with mean latitudinal range size (Fig. 7; 66–65 Ma event: $r = -0.81$, $p < 0.001$; 66–63 Ma event: $r = -0.79$, $p < 0.001$) and maximum great-circle distance (66–65 Ma event: $r = -0.60$, $p = 0.007$; 66–63 Ma event: $r = -0.47$, $p = 0.04$). In contrast, extirpation rates with each core were not significantly correlated, or only weakly correlated, with mean latitudinal range size (66–65 Ma event: $r = -0.41$, $p = 0.08$; 66–63 Ma event: $r = -0.44$, $p = 0.06$) and maximum great-circle distance (66–65 Ma event: $r = -0.06$, $p = 0.8$; 66–63 Ma event: $r = -0.11$, $p = 0.7$). Although geographic range size was a highly significant determinant of extinction,

**Figure 6.** Extirpation rate of survivors versus extinction rate for each core. Many survivors suffered heavy losses in high-extinction regions, supporting the pyrrhic extinction model.

**Figure 7.** Extinction and extirpation rates versus mean latitudinal range size within each core. For simplicity, only results from the extinction interval spanning 66–65 Ma are shown; full statistical results are reported in the text.
the probability that a species would become locally exterminated was unrelated or only weakly related to the geographic range size of the species.

Relative Abundances.—The geographic test of species selection does not require that survivors be completely exterminated from a region, but predicts only that survivors should be reduced in abundance to the same degree as victims. Too few surviving species have abundance data available after the K/Pg extinction to rigorously assess abundance changes across the extinction boundary. Of the eight species for which Cenozoic abundance data exists, one increases in relative abundance, three show no change, and four decrease in relative abundance. Evidence for a decrease in foraminiferal abundance across the K/Pg boundary has been recorded in other sections by other workers (e.g., Coccioni and Luciani 2006; MacLeod et al. 2007).

Discussion

These results suggest that survival of planktonic foraminifera through the K/Pg event was primarily due not to properties of individuals but rather to those of species. When subjected to the same selective pressures, individuals of both surviving species and victimized species generally suffered the same fate. The key difference was that survivors were able to persist because they must have possessed advantageous species-level traits, most likely larger geographic ranges or higher initial abundances, which buffered them from extinction. Extirpation as a response to environmental crisis is not unexpected for either fossil or living taxa, but its significance for species selection has not been heretofore explored.

The geographic test is most useful when a variety of assumptions are met. First, using the correlation between extinction rate and extirpation rate as a test of species selection requires that species differ in both organismal and species-level traits. Generally, we can assume that species will have different organismal traits, or they would not have been defined as separate species. However, if all species shared a species-level trait, for example by occupying the same geographic range, then the extinction rate may be the same in all areas while extirpation rate may vary. Second, note that the geographic test does not rule out the possibility that individuals of different species were of different fitness, even under the condition of strict species selection. Extinction may be due to fitness differences at the species level despite the presence of individual-level fitness differences, or due to individual-level fitness differences despite the presence of species-level differences. Third, the correlation will accurately identify species selection only if extinction rate is an adequate proxy for the level of disturbance. For our data, it appears that this assumption is true because high extinction rates are associated with nearness to the impact crater, where the greatest disturbance presumably occurred. Finally, the geographic test cannot distinguish the level of selection when the cause of extinction differs from region to region (e.g., if anoxia was the agent of extinction in one region but temperature change was the agent of extinction in another). Complex scenarios such as this will produce more complicated patterns of survival than depicted in Figure 1. The geographic test should always be considered in conjunction with other available evidence to arrive at a conclusion regarding the level of selection that operated during a mass extinction event.

The geographic test also assumes that fitness differences between species were larger than fitness differences between individuals within a species. Geographic variation of fitness within a species (e.g., a latitudinal cline of body size) may lead a species to be extirpated in some regions but not in others because of differences in organism-level fitness. This could produce a geographic pattern of extirpation similar to that expected for species selection (Fig. 1B). However, the geographic test is probably robust to intraspecific variation in organismal traits, because species tend to differ more from other species than individuals within a species tend to differ from each other. Although there are cases where this is not true (e.g., cryptic species), species will tend to diverge from one another to minimize com-
petition, thus reducing phenotypic overlap. Even if this were not true, some authors have considered the degree of intraspecific variation to be a species-level trait (Jablonski 2008); if a highly variable species was more likely to survive because of different organismal-level responses in different regions, then it would still be considered species selection and have been accurately identified as such by the geographic test.

The importance of species selection during the K/Pg mass extinction of planktonic foraminifera does not imply that possessing particular organismal traits did not affect survival. Organismal traits were important for survival if they produced advantageous species-level traits (e.g., if small test size promoted larger geographic ranges). Indirect selectivity suggests that species with different organismal-level traits may be equally likely to survive an extinction event if those different traits produce the same advantageous species-level trait. For example, brachiopods with widespread geographic ranges were able to achieve long durations during the late Paleozoic ice age regardless of whether those ranges were achieved by broad climate tolerances or the ability to disperse widely (Powell 2007). Secondly, organismal traits may be important even during strong species selection if both organismal and species-level traits contributed to survival, as was apparently the case for Gulf Coastal Plain neogastropods (Hansen 1980). The overwhelming decimation of planktonic foraminifera survivors in crisis regions argues strongly in favor of species selection as the dominant (but not necessarily only) mode of selection during the K/Pg mass extinction.

The major limitation to extending the geographic test proposed here to other taxa is that it requires a relatively high-resolution, species-level, geographic data set. Planktonic foraminifera and other microfossil groups are adequate for this task, but at present such databases are scarce for metazoan taxa. The geographic test may be applied in a limited way to single regions that contain both victims and survivors, because significant extirpation rates of survivors (i.e., as high as or higher than the extinction rate) would suggest that species selection had operated during that crisis. It would be more difficult to demonstrate that survivors and victims differed in species-level traits with a more limited data set, however. The ubiquity of selectivity by geographic range size (Jablonski 1986, 2005; Kiessling and Aberhan 2007; Payne and Finneegan 2007; Powell 2007) suggests that species selection may be a general feature of mass extinctions, but this possibility remains untested.

Distinguishing organismal from species selection is increasingly important as biologists and paleontologists attempt to understand and mitigate the modern biodiversity crisis, because it allows them to distinguish between traits that cause extinction from those that are merely correlated with it. Wider application of the geographic test of species selection may substantially improve not only our understanding of past extinctions, but also our predictions of which modern species are at the greatest risk of extinction (e.g., Russell et al. 1997; Thuiller et al. 2005), and thereby aid modern conservation efforts.

Acknowledgments

J. MacGregor was supported by the Goodman Fund for Undergraduate Research at Juniata College. The authors thank J. Payne and C. Simpson for their helpful reviews.

Literature Cited


