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Research paper

Distinguishing relative specialist and generalist species in the fossil record

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ABSTRACT

The fundamental niche comprises the range of environmental variables under which a species can live. Specialist species have narrower fundamental niches than do generalists. Thus, specialists benefit from homogeneous environments while generalists can exploit heterogeneous ones. The challenge is distinguishing relative specialists from generalists in a sedimentary rock succession. This is overcome by taking replicate samples from several horizons in a heterogeneous formation and comparing species' mean percentage abundances using analysis of variance (ANOVA). The mean proportional abundances of specialists will differ between horizons in a heterogeneous succession, while those of generalists will not.

The *Globorotalia fohsi robusta* Zone Middle Miocene Cipero Formation of Trinidad, western central Atlantic Ocean, consists of alternating, diffuse layers of light to dark grey clays. Five replicates of 40 g each were taken from four horizons across a light- to dark-grey cycle. They were picked entirely clean of benthic foraminifera, of which they yielded 5186 specimens in 153 species. Total recovery was dominated by *Brizalina* cf. *tectiformis*, with lesser *Globocassidulina subglobosa*, *Pleurostomella alazanensis* and *Planulina wuellerstorfi*. ANOVA applied to each species in turn indicated three species groups: 64 accessory species (each represented by ≤3 specimens, ≤0.06% of total recovery); 21 specialist species, for which mean percentage abundance varied significantly between at least two horizons; and 68 generalist species, for which mean percentage abundances did not differ across the horizons. It might be thought that ANOVA would preferentially assign a specialist status to less abundant species. However, this did not happen; of the four most abundant species, *P. alazanensis* was a specialist, while *B.* cf. *tectiformis*, *G. subglobosa* and *P. wuellerstorfi* were generalists. The mean percentage abundance of the specialist species did not differ from that of the generalists.

Both specialist and generalist species have palaeoenvironmental applications. The generalist nature of *P. wuellerstorfi* shows that bottom current strength probably did not differ across the four horizons. The occurrence of the specialist and opportunistic *Epistominella exigua* in the lowest horizon indicates an interlude of seasonal phytodetrital flux, while sequential increases in the mean percentage abundance of the specialists *Oridorsalis umbonatus* and *Uvigerina auberiana* show that the organic carbon flux increased across the four horizons.

1. Introduction

Ever since Steno (1669) wrote that "When the lowest stratum was being formed, none of the upper strata existed" (see Scherz, 1969; Winter, 1916), the Law of Superposition, which states that, within a section of tectonically-undisturbed sedimentary rocks, the beds at the base are older than those at the top, has been an axiom of geology. That there is a biostratigraphic faunal and floral succession within such sedimentary sections has been known since the pioneering work of Smith (1816, 1817). Such was the early appeal of using fossils for primarily biostratigraphic (relative age assignment) purposes that Colbert (1947) admonished that during the early part of the 20th century many palaeontologists had been mere students of "the stratigraphic sequence of little objects that happen to be fossils." The work of these students had been based on the premise that, where a section spans sufficient time, the evolutionary appearance of some species and the extinction of others will force the fossil assemblages to form a succession through the sedimentary section, even if there were no change in palaeoenvironment (Patzkowsky and Holland, 2012). However, some palaeontologists (e.g., Ager, 1963) had by the middle of the 20th century become aware that, by comparing aspects of total fossil assemblages at different points (samples) through a stratigraphic section, it is possible not only to piece together a community's evolutionary development, but also the section's palaeoenvironmental history (Turner, 2011). Twenhofel (1934) had presaged this work, writing that it was "extremely

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important for stratigraphy, as organisms appear and disappear in the rocks of the geologic column without, as yet, adequate explanation as to what were the causative factors for such appearance and disappearance." Thus, macropalaeontologists in the mid-20th century began, for example, to consider the palaeoecological importance of the many oysters contained in a sample in addition to the biostratigraphic importance of the lone ammonite. Among foraminiferal micropalaeontologists it was realised that, while planktonic foraminifera are more useful than the smaller benthic foraminifera for biostratigraphy (Bolli, 1957), the latter play a greater role in determining palaeoenvironments (Bandy and Arnal, 1960). It was found that, in sections spanning only a short time interval, changes in non-living variables (in the marine environment these include temperature, salinity, organic carbon and dissolved oxygen), coupled with variations in the strength of interspecific interactions (competition, predation), led to changes in the palaeocommunity despite the apparent lack of impact from evolution. In this paper, we focus on the benthic foraminifera in one such short sedimentary succession.

Biological uniformitarianism states that, just as with modern species, each fossil species had a fundamental niche — a set of ranges in environmental variables within which it could exist (Mayr, 1982; Soberón and Peterson, 2005). As long as the set of variables in a palaeoenvironment lay within a species' fundamental niche, it had the potential to live within that palaeoenvironment, where it would form part of the community (see Malanson et al., 1992). The same argument can be made regarding interspecific interactions. For example, if a species found itself subject to overly strong biotic interactions (competition, predation), towards the top of a section, then it would become excluded from it (Olden et al., 2004).

The extent of fundamental niches differs between species, generalists having wider niches than do specialists (Devictor et al., 2008). Thus, a generalist can thrive across a range of environmental conditions and use an assortment of resources (as does, say, a heterotroph with a diverse diet). In contrast, a specialist can either thrive across only a limited range of environmental conditions, or it has a limited diet across a range of environmental conditions. There is, however, a continuum from narrowly specialist to broadly generalist species. In terms of food, for example, some highly specialised species, such as monophagous animals like the giant panda *Ailuropoda melanoleuca*, which eats only bamboo, can be readily assigned a specialist status (Broom, 1981). Those oligophagous species that eat a limited range of foods (such as the koala bear *Phascolarctos cinereus*, which eats the leaves of about five species of *Eucalyptus* trees, and the brent goose *Branta bernicla*, which rarely eats anything other than species of the eel grass *Zostera*), can likewise be readily recognised as having a relatively specialist role. Polyphagous species that consume a variety of foods may be rendered generalist or specialist because of some other limiting factor, whether living or non-living, in their fundamental niche. Regarding habitat, Lapiedra et al. (2013) examined behaviour among pigeons and doves. They termed 'terrestrial' those species that primarily obtain their food by searching on the ground and 'arboreal' those that primarily forage on fruits on trees, rarely descending to the ground. While almost all species examined could be easily classified as either terrestrial or arboreal, twelve had a mixed strategy and were classified as generalists. Thus, most species cannot be neatly assigned either specialist or generalist status without statistical analyses of occurrences (Chazdon et al., 2011). Here we use statistical analyses to distinguish relative generalist and specialist benthic foraminiferal species in a Miocene deep-sea section.

There have been several attempts to discern whether recent and fossil benthic foraminifera are or were generalists or specialists, but these have made limited use of statistical techniques. For example, van der Zwaan et al. (1999) suggested that, like most microbiota, foraminifera in general are not stenotopic to most environmental variables. However, not all benthic foraminifera are generalists. Kaiho (1994) distinguished oxic and dysoxic benthic foraminifera, while Sen Gupta and Machain-Castillo (1993) showed that some endobenthic foraminifera are conspicuously dominant in bathyal oxygen minimum zones. Matera and Lee (1972) compared epiphytic and sediment-dwelling foraminiferal communities around Long Island. Although the epiphytic foraminiferal community was patchily distributed, with 2.6% of samples containing 56.4% of epiphytal foraminifera, they concluded that *Elphidium incertum* (Williamson, 1858) and *Ammotium salsum* (Cushman and Brönnimann, 1948) are generalists, being common in both epiphytic and sediment communities. In contrast, Steineck and Bergstein (1979) suggested that modern *Ammobaculites exiguus* Cushman and Brönnimann, 1948 and *Ammonia beccarii* (Linnaeus, 1758) are opportunistic generalists, occupying a wider range of paralic environments than do other species. This generalist behaviour for *A. beccarii* may be more apparent than real, however, authors having applied this name to many disparate forms (Hayward et al., 2004). Langer (1993) showed that some epiphytal foraminifera in the Mediterranean region are specialists, the community on seagrass leaves differing markedly from that among adjacent leaf bosses. Gooday (1988) and Smart (2008) found bathyal and abyssal *Epistominella exigua* (Brady, 1884) and *Alabaminella weddellensis* (Earland, 1936) to be specialists that bloom opportunistically in the presence of marine phytodetritus and so can be used to distinguish areas with a seasonal phytodetritus rain.

Specialist species benefit from environments that are relatively homogeneous (whether geographically or temporally so), whereas generalists benefit from heterogeneous environments (Futuyma and Moreno, 1988). This is illustrated by marsh foraminifera. Kemp et al. (2011) examined the distributions of dead marsh foraminifera [*Miliammina fusca* (Brady, 1870), *Trochammina inflata* (Montagu, 1808), *Arenoparrella mexicana* (Kornfeld, 1931), *Tiphotrocha comprimata* (Cushman and Brönnimann, 1948), *Haplophragmoides wilberti* Andersen, 1953, *Jadammina macrescens* (Brady, 1870)] in replicate surface samples from low-, middle-, and high-marsh floral zones along a transect in North Carolina, USA. They investigated the influence of patchiness using unispecies ANOVA for six benthic foraminiferal species. Each had a significantly ($p < 0.05$) different abundance in the three floral zones, as would be expected from previous studies of marsh foraminifera (Horton and Edwards, 2006; Scott and Medioli, 1986). Within the low- and high-marsh floral zone there was no patchiness of any foraminiferal species. Kemp et al. (2011) concluded that "this result supported the validity of our initial assumption of environmental homogeneity in salt-marsh floral zones". Division by cluster analysis of the middle marsh floral zone into two foraminiferal assemblages showed, however, that, while *A. mexicana*, *T. comprimata*, *H. wilberti* and *J. macrescens* did not have patchy distributions in the middle marsh, *M. fusca* and *T. inflata* did. From this it follows that *A. mexicana*, *T. comprimata*, *H. wilberti* and *J. macrescens* are generalist species while *M. fusca* and *T. inflata* are specialists. The challenge for palaeontologists is distinguishing objectively the specialist and generalist species within a stratigraphic succession.

It follows from the foregoing that generalist species should range through a section with no significant difference in mean abundance between one horizon and the next despite changes in the palaeoevironment, while specialists will differ significantly in mean abundance between two or more horizons to reflect those changes. If changes in the environment are sufficiently large, generalist species will also change in abundance or entirely disappear. Such studies of modern dead assemblages as that by Kemp et al. (2011) are comparable to those of fossil communities, which likewise comprise dead specimens. This paper uses the General Linear Model approach to analysis of variance (ANOVA) to test this ontological assumption (sensu Wilson and Hayek, 2014) regarding relative specialist and generalist species. We present our technique for doing so using benthic foraminifera in a Middle Miocene section of the Cipero Formation of Trinidad, western central Atlantic Ocean (Fig. 1), which was the subject of a classic study by Cushman and Stainforth (1945). In contrast to Cushman