Climate-Driven Range Extension of *Amphistegina* (Protista, Foraminiferida): Models of Current and Predicted Future Ranges

Martin R. Langer1*, Anna E. Weinmann1, Stefan Löters2, Joan M. Bernhard3, Dennis Rödda

1 Steinmann Institut für Geologie, Mineralogie und Paläontologie, Rheinische Friedrich-Wilhelms Universität, Bonn, Germany, 2 Biogeography Department, Universität Trier, Trier, Germany, 3 Department of Geology and Geophysics, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, United States of America, 4 Zoologisches Forschungsmuseum Alexander Koenig, Museum Koenig, Bonn, Germany

**Abstract**

Species-range expansions are a predicted and realized consequence of global climate change. Climate warming and the poleward widening of the tropical belt have induced range shifts in a variety of marine and terrestrial species. Range expansions may have broad implications on native biota and ecosystem functioning as shifting species may perturb recipient communities. Larger symbiont-bearing foraminifera constitute ubiquitous and prominent components of shallow water ecosystems, and range shifts of these important protists are likely to trigger changes in ecosystem functioning. We have used historical and newly acquired occurrence records to compute current range shifts of *Amphistegina* spp., a larger symbiont-bearing foraminifera, along the eastern coastline of Africa and compare them to analogous range shifts currently observed in the Mediterranean Sea. The study provides new evidence that amphisteginid foraminifera are rapidly progressing southwestward, closely approaching Port Edward (South Africa) at 31°S. To project future species distributions, we applied a species distribution model (SDM) based on ecological niche constraints of current distribution ranges. Our model indicates that further warming is likely to cause a continued range extension, and predicts dispersal along nearly the entire southeastern coast of Africa. The average rates of amphisteginid range shift were computed between 8 and 2.7 km year

---

**Introduction**

Sea surface temperature is a key environmental predictor that affects the biogeographic distribution of many organisms. Global climate change is likely to alter the range of areas potentially suitable for habitation [1–4]. Among the predicted effects of rising temperature is the range expansion of species into areas where they previously did not exist [5–8]. The expansion of species ranges along their cooler boundaries appears to be a prominent consequence of the global warming trend [7,9]. A rapidly increasing number of studies have shown “fingerprints” of recent climate-driven changes in various biological systems. This includes range shifts of species towards higher latitudes, higher elevation and earlier springtime phenologies [9–12]. To date, however, only a limited number of studies have addressed rates of range shifts in marine biotas [13].

Our studies concern the distribution and biogeographic range expansion of unicellular, larger symbiont-bearing foraminifera in modern oceans [4,14]. Larger symbiont-bearing foraminifera have a circum-tropical distribution and are indicative of warm tropical and subtropical waters [14,15]. Temperature has long been considered as the primary factor regulating their latitudinal distribution [14]. For the majority of these foraminifera, the lower temperature limit is 18 to 20°C [14]. Relatively low temperatures are tolerated by species of the genus *Amphistegina* and their distributional range is currently delimited by the 13.8° winter isotherm [4,16,17]. Among the larger symbiont-bearing foraminifera, amphisteginids are of particular interest because they display the widest latitudinal ranges in all oceans [14]. Today, amphisteginids have been found as far as 40° North and 31° South [14,18]. They are among the most conspicuous and ubiquitous foraminifera on coral reefs and tropical carbonate shelves [14], where they often have been referred to as living sands [19]. As key carbonate producers [20–22], amphisteginids contribute significantly to carbonate substrate stability, growth of reefal structures, and habitat formation [20–24]. Recent studies have shown a widening of the tropical belts with far-reaching changes for oceans, ecosystems, and the biosphere [25–27]. A distributional range expansion of amphisteginid foraminifera due to global warming could trigger substantial changes in ecosystem functioning (e.g. changes in species diversity, carbonate production, impact on native biota [4]).

---

**Citation:** Langer MR, Weinmann AE, Löters S, Bernhard JM, Rödder D (2013) Climate-Driven Range Extension of *Amphistegina* (Protista, Foraminiferida): Models of Current and Predicted Future Ranges. PLoS ONE 8(2): e54443. doi:10.1371/journal.pone.0054443

**Editor:** Purificación López-García, Université Paris Sud, France

**Received** September 24, 2012; **Accepted** December 11, 2012; **Published** February 6, 2013

**Copyright:** © 2013 Langer et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Funding:** This work was supported by grants from the German Science Foundation (DFG; www.dfg.de) to ML and SL (LA 884/10-1, LA 884/5-1). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing Interests:** The authors have declared that no competing interests exist.

* E-mail: martin.langer@uni-bonn.de
Recently, amphisteginid foraminifera were shown to expand their biogeographic range in the Mediterranean where a rapid progression northwesterns now shows them closely approaching the Adriatic and Tyrrenhian seas [4,18,28,29]. In addition, their increasing abundance and rapid proliferation of invasive amphisteginids were shown to impair the dynamic equilibrium of established foraminiferal biotas, ultimately replacing diverse assemblages by rapidly spreading monocultures [4].

To date, the overwhelming majority of studies on organismal range shifts in response to climate change focus on terrestrial species [30]. In contrast, comparatively few studies have addressed range shifts in marine systems [31–35] although the impact of climate-driven range expansion is considered the “next frontier” in climate change research [36]. Understanding, monitoring, and predicting range expansions are, therefore, vital for effective management and conservation [37,38]. Consequently, there is a pressing need to improve our ability to predict these phenomena. This requires the deployment of modeling approaches that can be successfully utilized at a range of spatial scales. Here we apply a species-distribution model (SDM) to assess potential range expansions of Amphistegina spp. under current and future climate conditions (for the years 2050, 2100) along the eastern coast of southern Africa. The coastline from equatorial Somalia along Kenya, Tanzania, and Mozambique to Cape Town, in South Africa, displays a distinct latitudinal sea-surface temperature gradient that is ideally suited to apply SDM and to project range shifts in the future. In addition, the Indian Ocean has been undergoing a pronounced multidecadal warming trend [39] that is likely to affect the biogeographic ranges of species living along the eastern coastline of Africa.

Species distribution models have been applied previously to project range expansions of amphisteginids in the northern hemisphere including the Mediterranean Sea [4]. In this study, we provide the first modeling approach for foraminifera from localities of the southern hemisphere to assess the rates of range expansions under rapid environmental change. The model uses an environmental envelope of information from localities where amphisteginids are currently known to occur. The physical niche constraints were compiled from all presently available data containing the environmental conditions for population dynamics. The environmental variables that define the current niche of east African amphisteginids then were used to develop correlative models to extrapolate potential occurrences at sites where the environmental constraints are projected to match physiological constraints under current and future conditions. We also calculated the rate of amphisteginid range expansion along latitude based on historical and recent occurrence records, and compared them to rates currently observed for amphisteginids in the Mediterranean. Rates of latitudinal range expansion in Amphistegina were then compared with rates recorded in recent reviews on the expansion of terrestrial and marine taxa [10,13,40,41]. Using this modeling approach, we project the result on climate scenarios for the years 2050 and 2100, and compute the extent of potential range expansion and the probable speed of future range shifts.

Materials and Methods

Species Records and Environmental Data

The species distribution modeling and range expansion analyses of Amphistegina is based on an extensive sample set that was collected recently (2004–2012) between equatorial sites of Somalia/Kenya, and Cape Town, in South Africa (no specific permits were required for the described field studies). We compiled all amphisteginid species occurrences and collected additional citations from primary literature and review papers. The biogeographic survey covers a latitudinal range between 1.2° S at Somalia and 34° S at Cape Town (Figure 1A). Literature occurrences were extracted from historical and recent studies [42–67]. Occurrences of amphisteginid foraminifera were recorded from a total of 118 sites, and include 82 sites from our own sampling and 36 literature records. Our own samples were taken by scuba-diving or by a Van Veen grab at depths between 0 and 200 m, and include both live and dead foraminifera. Occurrence records of dead individuals were only included when the test(s) did not show any signs of transport. All records are situated within unique grid cells derived from DIVA-GIS [68].

Environmental data were obtained from the BIO-ORACLE dataset designed for species distribution modeling [69]. The data package contains a global set of 23 variables obtained through remotely sensed and in situ measured data. Raster grid-cells of BIO-ORACLE have a resolution of 5 arcmin or 9.2 km. We used the mean sea surface temperature (°C), diffuse attenuation (an indicator of water turbidity, m−1), the minimum chlorophyll a content (mg/m³), the annual sea surface temperature range (difference between maximum and minimum, °C) and the maximum photosynthetically active radiation (Einstein m⁻² day) as biologically relevant predictor sets for SDM modeling.

The SDM scenarios for range expansion of Amphistegina for the years 2050 and 2100 are based on predictions provided by the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [70]. We used the response of the 30-year average SST between 2070–2099 and 1961–1990 as an approximation for the rise in ocean temperature until 2100. For the model for 2050, we adopt a 50% decrease of the 2100 temperature approximation. The winter prediction was presumed to conform to SSTmin, and the summer prediction was used for SSTmax. The projected climate change datasets then were applied to our georeferenced grid-cell format.

Computation of the SDM

We used Maxent 3.3.3 k for SDM modeling and projections onto future climate conditions [71,72]. The program uses a grid-based, machine-learning algorithm following the principles of maximum entropy [73]. It is a presence-only method, generating pseudo-absences from a defined background, ideally covering areas potentially colonizable for the taxon [74]. The Maxent modeling begins with a uniform distribution and successively fits the distribution to the data (occurrence records and environmental variables). By iteratively permuting and varying the input variables, Maxent repeatedly tests the predictive capability and improves the model. This is measured as log likelihood or “model gain” that records increasing distances from the uniform distribution. A full description and details of the procedure can be found in Elith et al. [75].

To predict the potential and future amphisteginid distribution, a total of 10,055 random background points were automatically selected by Maxent from the biogeographic range of Amphistegina spp. along the eastern coast of Africa. Maxent then predicts the suitability of a habitat, representing the potential distribution of the taxon. For clarity, the logistic output format with suitability values ranging from 0 (unsuitable) to 1 (optimal) was used [76]. The probability of the taxon’s presence at sites with “typical” environmental conditions is set to 0.5 by default [75]. The modeling process was performed with 30 replicates and the average predictions across all replicates were used for further processing.
Model Evaluation

The quality of the SDM provided by Maxent can be tested by calculating the Area Under the Curve (AUC) and refers to the Receiver Operation Characteristic curve [72]. The AUC reassesses the ability of the model to distinguish presence from (pseudo-) absences. Occurrence records were randomly split into training (70%) and test samples (30%). This non-parametric method is recommended for ecological applications [77,78]. Values of AUC range from 0.5 for models with no better than random predictability to 1.0 for models supplying perfect SDM prediction. According to the classification of Swets [79], AUC values >0.9 describe “very good”, >0.8–0.9 “good”, and >0.7–0.8 “useful” discrimination ability. The continuous probability surfaces of the SDMs were subsequently converted into presence/absence maps using the “Equal training sensitivity and specificity logistic threshold” as recommended by Liu et al. [80]. The impact of individual environmental predictors for the resulting model is specified as the percent contribution of every variable. Additional evaluations are provided by the permutation importance, which displays the drop in AUC values (normalized to percentages) when the values of every variable on training presence and background data are randomly permuted. Furthermore, a jackknife test is implemented in Maxent, which allows the analysis of the predictability potential of individual variables. The model is repeatedly created by using variables in isolation to examine how well the results fit the known model gain (both on training and test data) and the AUC values. To assess the importance of individual predictors, each variable then is omitted, and model gain and AUC value are evaluated. A decrease in model gain results in an approximation of the model to the uniform distribution.

Results

Computed data provide “very good” AUC values (AUC_{train-ing}: 0.9703; AUC_{test}: 0.9513) for our SDM. The lowest Maxent value obtained at the training records is 0.0239. Analysis of the relative contributions of environmental variables reveals the following hierarchy in descending order of explanatory power (Table 1): Mean sea-surface temperature (SST_{mean}) has the highest explanatory power with 41.78%, followed by mean diffuse attenuation (DA, 25.11%), minimum chlorophyll (CHLO, 23.07%), sea-surface temperature range (SST_{range}, 6.99%), and maximum photosynthetically available radiation (PAR, 3.04%). The permutation importance of individual variables reveals a similar picture (Table 1). The jackknife tests show that omitting SST_{mean} from the model results in the sharpest drop in model gain and AUC values, followed by DA, CHLO, SST_{range}, and PAR (Table 2). When used in isolation, DA and SST_{mean} provided the best results (Table 2).

All amphisteginid occurrence records modeled in the area are displayed in Figure 1A. The current biogeographic range covers the area from tropical sites at the equator off Somalia (1°N at Somalia) southwest along the coastlines of Kenya, Tanzania, Mozambique, and south to Shelley Beach in South Africa at 31°S. The distance from the equator at Somalia to the southernmost occurrence record covers ~3410 km (1°N = 110 km). Offshore island occurrence records of amphisteginid foraminifera from the southwestern Indian Ocean include sites off Madagascar, Reunion, Mauritius, Rodrigues, the Seychelles [54], Glorioso Islands [46], and Mayotte [45].

Figure 1B displays the potential distribution for amphisteginid foraminifera as computed from SDM under current climate conditions. The potential distribution of the genus correlates well with the actual biogeographic range. The distribution model reveals, however, that amphisteginid foraminifera may potentially expand their coastal range occurrences further south to Port Edward (31°S), which is located 18.34 km south from the southernmost record at Shelley Beach (30.84°S). The potential distribution thus exceeds the known realized distribution by only a few kilometers. The model also shows that the areas of highest suitability comprise the coastal regions between 1°N (Mogadishu) and 17°S (Quelimane). Lower habitat suitability values are indicated for the areas between the Zambezi River Delta (18.1°S), Beira (20°S), and the Save River Delta (21°S).

The SDM computed under climate conditions projected for the year 2050 projects a substantial southward shift of habitat suitability for amphisteginid foraminifera (Figure 2A). The model projects a coastal range expansion south to Kosi Mouth, located at 32.65°S. The prognosticated range extension to Kosi Mouth is an additional 1.641° (=182.68 km) south of the potential range of Amphistegina at Port Edwards, and 201.12 km south of the current southernmost occurrence record at Shelley Beach. Climate conditions projected for the year 2050 indicate that SST increases from 23.26°C to 24.51°C for the Shelley Beach location. In the 2050 model, the areas of highest suitability comprise the coastal regions between 1°N (Mogadishu) and 17°S (Quelimane), and 29°S (Muzinzi) and 31.4°S (Port St. Johns). Areas of low suitability values continue to be between the Zambezi River Delta (17.5°S), Beira, and the Save River mouth (21°S).

The SDM computed under climate conditions projected for the year 2100 predicts a temperature rise of 2.5°C and an additional range expansion of amphisteginid foraminifera (Figure 2B). The model indicates a southerly expansion along the coast of South Africa down to Kayeris Beach, located at 33.22°S. The modeled range expansion to Kayeris Beach marks an additional latitude extension of 0.5754° (=64.05 km), compared to the potential range of Amphistegina for the year 2050. The model computed for climate conditions for the year 2100 indicates a total southward range expansion of 265.07 km (=2.4°), when compared to the current distribution limit of amphisteginid foraminifera.

In the model for the year 2100, highest suitability areas for amphisteginid foraminifera are between the equatorial coastal regions off Somalia (Mogadishu at 1°N) and Quelimane near the northernmost end of the Zambezi Delta (18°S). Low habitat suitability values were computed for coastal areas between major rivers, Zambezi and the Save (18°S–21°S), and around the Maputo Harbor area (26°S).
Biogeographic Range Expansions

Occurrence records of amphistegnid foraminifera indicate that the current biogeographic range covers the coastal area from the equator at Somalia 1°N to Shelley Beach (31°S) in South Africa, and a multitude of offshore islands in the Indian Ocean (Figure 1A). The biogeographic range of east African amphistegnid foraminifera attests that species of this genus have a tropical to subtropical distribution delimited by the 14°C winter isotherm [14].

East African amphistegnid foraminifera were reported first by d’Orbingy [81], Wright [82,83], and Möbius [42] from tropical locations off Madagascar, Mauritius, and the Seychelles. Later, Heron-Allen & Earland [45] recorded three species of Amphistegina from the nearshore Kerimba Archipelago between 11.5°S and 13°S. Records of amphistegnid foraminifera previously were not reported even though extensive sampling was undertaken [44,62,63,85–87]. Belderson’s report [88] of amphistegnid foraminifera from Durban Bay could not be verified by Albani [85], but suggests that this taxon has repeatedly tried to colonize habitable environments along the coast. Recent and extensive sampling campaigns (2004–2005) conducted by this working group reveal numerous new amphistegnid occurrences as far south as Shelley Beach (30.84°S). This indicates a southward biogeographic range extension over ~1.3° latitude (= 145 km, from the Mgeni

Table 1. Variable contribution and permutation importance for predictors used during model training.

| Contribution (%) | Permutation importance [%] |
|------------------|---------------------------|
| Mean sea-surface temperature | 41.78 | 47.19 |
| Mean diffuse attenuation | 25.11 | 30.97 |
| Minimum chlorophyll a | 23.07 | 16.26 |
| Maximum photosynthetically available radiation | 3.04 | 1.39 |
| Sea-surface temperature range | 6.99 | 4.18 |

Note high values for mean sea surface temperature, mean diffuse attenuation, and minimum chlorophyll indicating their importance as prime factors regulating the distribution and habitat suitability of amphistegnid foraminifera.

Model iterations using the maximum winter surface temperatures show an increasing range expansion, but not to the extent of the model presented here. Mean SST accounts for nearly 42% of the modeled effect, while SST range contributes only 7% to the variation. Hence the model presented exhibits the maximum range extension that can be predicted but it is realized that amphistegnid species may not fully occupy this potential niche in the future as they do today.

Pilot studies involving the present range prediction of amphistegnids along the African coast using minimum chlorophyll a values parallel the empirical biogeographical distribution. This parameter was retained in the SDM with the understanding that maximum chlorophyll a values would impact the foraminiferal ranges.

doi:10.1371/journal.pone.0054443.t001

Table 2 Results of the Jackknife test for training and test data.

| Species distribution model for Amphistegina spp. | Training gain | Test gain | AUC values |
|-----------------------------------------------|---------------|-----------|------------|
| Model without variable:                       |               |           |            |
| Mean sea-surface temperature                   | 1.4824        | 1.3361    | 0.8897     |
| Mean diffuse attenuation                       | 2.1529        | 2.1274    | 0.9509     |
| Minimum chlorophyll a                          | 2.1804        | 2.148     | 0.9505     |
| Maximum photosynthetically available radiation | 2.1852        | 2.1442    | 0.951      |
| Sea-surface temperature range                  | 2.0586        | 2.038     | 0.9459     |
| Model with variable in isolation:              |               |           |            |
| Mean sea-surface temperature                   | 0.5427        | 0.6459    | 0.8018     |
| Mean diffuse attenuation                       | 0.6616        | 0.5953    | 0.7959     |
| Minimum chlorophyll a                          | 0.6413        | 0.5856    | 0.7923     |
| Maximum photosynthetically available radiation | 0.3108        | 0.2944    | 0.6908     |
| Sea-surface temperature range                  | 0.2637        | 0.3123    | 0.7012     |

Note strong decrease in gain and AUC values for mean sea-surface temperature, sea-surface temperature range, and mean diffuse attenuation when omitted from the SDM for Amphistegina. When variables are used in isolation the values are most similar to the original gain and AUC for mean sea surface temperature, mean diffuse attenuation, and minimum chlorophyll. This indicates their important role in regulating the biogeographic distribution of amphistegnid foraminifera.

doi:10.1371/journal.pone.0054443.t002
Estuaries [60] to Shelley Beach [Langer, unpubl. data]) between 1987 and 2005, equivalent to a range extension of ~8 km year⁻¹.

The range expansion projected by the SDM under climate conditions of the year 2050 (Figure 2A) prognosticates the occurrence of amphisteginid foraminifera south to Kei Mouth (located at 32.65°S). The predicted range extension to Kei Mouth is an additional 301.12 km south of the current southernmost occurrence record at Shelley Beach (30.84°S). This would constitute an average range shift of ~5.29 km year⁻¹ if the range shift is realized in the year 2050. The model for 2050 also projects a general increase in habitat suitability for amphisteginid foraminifera along the east coast of Africa (Figure 2A). Suitability is particularly increased from the equator at Somalia, along the coast of Kenya and Tanzania, down to Angoche in Mozambique (16.2°S). The SDM also shows an increase in habitat suitability from Richards Bay (28.4°S) to Port Edward (31.0°S) in South Africa.

For climate conditions predicted for the year 2100 (Figure 2B), the species distribution model suggests a total range expansion over 2.38° latitude southwards to Kayseris Beach at 33.22°S (~242 km). If realized in 2100 and referenced to the current southernmost occurrence record at Shelley Beach, the marine range expansion of amphisteginids would occur at an average rate of ~2.75 km year⁻¹. The Amphistegina SDM generated for climate conditions in the year 2100 shows increasing habitat suitability over large stretches of coastline from the equator at Somalia to Kayseris Beach at 33.22°S in South Africa. Areas of lower habitat suitability are indicated for the regions around the major river mouth off the Rufiji, Rovuma, Lurio, Zambezi, Save, and Limpopo rivers. Low values of habitat suitability are also displayed around Beira, and between Maputo in Mozambique and Richards Bay in South Africa.

Discussion

Average global temperature has increased over the past century (0.74±0.18°C) and overall global warming is predicted to continue to rise between 2.0 and 4.5°C over the next 100 years [89]. Global warming and the extension of climate belts are likely to allow substantial range expansion for species with tropical or subtropical origins. This study reports the first SDM approach to project potential range expansion of foraminifera under current and future climate conditions. The computed SDM values affecting the biogeographic range reveal that sea surface temperature had the highest explanatory power among individual variable contributions (51%), followed by mean diffuse attenuation (25%) and minimum chlorophyll (23%). This agrees well with 1.) observations in the Mediterranean Sea where temperature has been identified as the key agent governing the range expansion of amphisteginid foraminifera [4] and 2.) with recent findings that temperature alone can readily predict the large scale geographic structure of shallow biogeographic schemes with 53–99% accuracy [90]. The Mediterranean range shift of amphisteginid foraminifera is attributed to the ongoing warming trend in the northern hemisphere. Research conducted on foraminifera from the east coast of Africa provides a baseline chronology illustrating an analogous spread of amphisteginids towards higher latitudes in the southern hemisphere.

Based on historical occurrence records, the range shift of coastal amphisteginid foraminifera was calculated to occur at an average rate of ~8 km year⁻¹ between 1987 and 2012. The average rate prognosticated under climate conditions for the year 2050 and 2100 was computed to continue at an average rate of ~5.29 km year⁻¹ for the year 2050 and at ~2.75 km year⁻¹ until the year 2100. However, it needs to be noted that the actual rate of marine range expansions in our case is likely to be higher. This is because the latitudinal calculations underestimate the true distances along east-westward oriented coastlines. In addition, the southward-flowing, warm Agulhas Current is deflected away from the coast by the cold Benguela Current, diverting potentially suitable habitats from coastal regions into open ocean territory.

The calculated range-expansion rates for Amphistegina from the east coast of Africa are at the lower end of average range shifts currently known for marine plankton, invertebrates, and vertebrates [13]. Sorte et al. [13] have calculated that the average rate shift in marine organisms occurs at 19.0 km year⁻¹. They also noted that the vast majority of range shifts in marine species were in poleward direction, consistent with global climate change scenarios. Rate shifts computed for amphisteginid range expansion in the northern hemisphere (Mediterranean Sea) were found to occur at an average rate of 12.5 km year⁻¹, concordant with expansion rates of other Lessepsian migrants in the Mediterranean [91]. Higher range-expansion rates computed for the Mediterranean Sea, however, appear not to be related to sea surface current velocities when compared to the southwestward flowing Agulhas current along the coast of east Africa, which is among the fastest flowing ocean currents (peaks speed up to 2 m/s). The computed range-expansion rates for amphisteginid foraminifera are up to an order of magnitude faster than rates for terrestrial range shifts (0.61±0.24 km year⁻¹) [13]. This observation commonly is attributed to the more open nature of marine versus terrestrial populations [13,92]. Because of their abundance and high reproductive rates [93,94], foraminifera are generally expected to adapt fast to warming climates. The comparatively low rates of range expansion recorded in this study highlight the importance of incorporating additional information about range-limiting factors in native communities, environmental tolerances, and species interactions.

Water temperature previously has been invoked as the major factor controlling the latitudinal extension of amphisteginid foraminifera [4,14,16]. In particular, Langer & Hottinger [14] have demonstrated that the ranges of larger symbiont-bearing foraminifera are limited by the minimum winter temperature extremes. Indeed, sea surface temperature data compiled from the Indian Ocean Thermal Archive (IOTA) show a significant late 20th Century Indian Ocean warming (0.5–1.0°C) [39,95].
Although warming has affected all oceans [96,97], rising temperatures are more pronounced in the Indian Ocean and recently reached their highest values in 120,000 years [98,99]. The observed southward directed range expansion of thermophilic amphisteginids along the eastern coast of Africa makes the ongoing warming trend the most likely agent facilitating the taxon’s current range expansion.

Paleontological evidence indicates that amphisteginid and other larger foraminifera cope particularly well with rising water temperatures and widening of the tropical/subtropical climate belt [100–107]. Miocene specimens are reported from Poland and the Vienna Basin at paleolatitudes between 48°–50°N [101]. Cretaceous and Eocene records [101] of larger symbiont-bearing foraminifera show a range extension from the equator to almost 50°N and 40°S [101,106]. In contrast, larger symbiont-bearing foraminifera from modern oceans are mostly limited between 40° North and 30° South, or the 20°C surface-water isotherms during the summer. The latitudinal range extensions during the Miocene, Eocene, and Cretaceous were attributed to higher surface-water temperatures during warmer climates similar to those affecting the poleward extension of current regimes [101,106]. The range extensions and mass abundances of larger foraminifera during climate periods with increased atmospheric CO2 [108–110] suggest that foraminifera are, potentially, beneficiaries of climate-driven temperature changes (e.g., nummulit, orbitolinid or alveolinid mass deposits, see also [22,111,112]). Global changes are not solely restricted to temperature increases. In addition to warming, the pH in oceans is currently decreasing due to the increased load of atmospheric carbon dioxide compared to pre-warming, the pH in oceans is currently decreasing due to the ongoing warming trend. Thus, while warming may permit significantly affect organisms that secrete calcium carbonate hard parts (skeletons, shells, tests). This, while warming may permit poleward expansion of habitat for some species, OA may cause this expansion to be more challenging than if warming alone were occurring. In the case of *Amphistegina gibbosa*, laboratory experiments indicate that the survival of this species is not negatively impacted after 6-week incubation in 1000 or 2000 ppm pCO2 compared to ambient control incubations [113]. Additionally, some specimens also reproduced in the enriched CO2 incubations, suggesting that amphisteginid dispersal, fitness, and range changes may not be significantly hampered by OA. Similar findings were obtained from experiments on *Amphistegina radula* [114].

The SDM computed under current climate conditions is closely congruent with the occurrence records of modern amphisteginids indicating that a few easily acquired oceanographic parameters are sufficient to predict the taxon’s biogeographic range. This robust, first-order link between the environmental parameters and biogeographic ranges indicate that model-based predictions may be applied to project large-scale system-level changes. Our analyses also suggest that the exceptionally detailed and well-preserved fossil record of foraminifera may be used to reconstruct the general paleoceanographic structure of ancient shallow seas. Such an application permits the use of fossil data in projected model scenarios of shelf and coastal ecosystems in a warm future.

**Effects on Ecosystems**

As noted, amphisteginid foraminifera are among the most prominent foraminiferal species and contribute significantly to the stabilization of reefal frameworks worldwide [20–22]. They are prominent producers of calcium carbonate within the world’s oceans where they often add more than 1 kg of CaCO3/m²/year to reef carbonate sediments [20–22]. In some of the east African reefs, amphisteginid foraminifers frequently represent up to 50% or more of the foraminiferal fauna (Langer, unpubl. data), implying that they play a prominent role in reef ecosystems.

The range expansion of amphisteginid foraminifers in the Mediterranean Sea was shown to lead to a drastic reduction of foraminiferal species diversity, increased carbonate production, substrate modifications and, at some sites, to the establishment of amphisteginid monocultures [4,115]. Because of their abundance, ubiquity and appearance in monocultures and as prominent carbonate producers with substrate modifying capabilities, amphisteginid foraminifera can be considered ecosystem engineers in the sense of Jones et al. [116,117]. While the immediate impact of such changes appears to be obvious, the resilience of ecosystems to the disruptive forces of key invaders remains to be determined. Given their prominent environmental role, rapid biogeographic range expansion, and impact on native ecosystems, amphisteginid range expansion and invasion into new territory are likely to trigger changes in ecosystem functioning [4]. With predicted environmental suitability increasing southward, further studies monitoring environmental changes and modification in community structure along the eastern coast of southern Africa are required.

In conclusion, the Indian Ocean is undergoing a warming trend that affects the biogeographic range of the native biota and ecosystem functioning. Amphisteginid foraminifera are among the key species that currently are expanding their range and rapidly progress southwestwards, closely approaching the coastline of Port Edwards in South Africa. Temperature has been identified as the most important physical oceanographic variable controlling their spatial distribution, congruent with analogous observations in Mediterranean amphisteginids [4] and numerous other marine ectotherms [3,13,90,118,119].

The computed rates of range shifts (between 2.75 and 8.0 km year–1) are at the lower end of average marine range-expansion spectrum and project a total range shift of 2.4° latitude for the year 2100. Examination of the rates of range shift and modeling potential range shift under future climate conditions provides a first approximation that helps to identify sites and magnitudes of potential impact. This, in turn, is vital to assess climate-change impact on coastal marine biotas and will be of use in directing monitoring efforts. It is anticipated that climate warming and the widening of the tropical/subtropical belt will foster the poleward migration of amphisteginid and other larger symbiont-bearing foraminifera. Modern and paleontological evidence of foraminiferal range expansions indicate that some species of symbiont-bearing foraminifera benefit from rising temperatures and become predominant producers of calcium carbonate under conditions of global climate warming.

**Acknowledgments**

The authors gratefully acknowledge Robert Gastaldo for productive comments on an earlier version of this manuscript, and Jan Bartholomé for field and laboratory assistance. We also thank Lopo de Vasconcelos (Maputo) for logistical support and assistance in Mozambique. We are grateful to the three referees and the associate editor for their constructive comments and suggestions.

**Author Contributions**

Sample Collection: MRL, AEW. Performed the experiments: MRL, AEW. Analyzed the data: MRL, AEW DR SL. Contributed reagents/materials/analysis tools: AEW DR SL. Wrote the paper: MRL, AEW JMB.
References

1. Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world’s marine ecosystems. Science 328: 1523–1528.
2. Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, et al. (2010) Global patterns and predictors of marine biodiversity across taxa. Nature 466: 1090–1101.
3. Yamano H, Sugihara K, Nomura K (2011) Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. Geophys Res Lett 38: L10601, doi:10.1029/2010GL044674.
4. Langer MR, Weinmann AE, Lotters S, Ro¨dder D (2012) “Strangers” in Paradise: Modeling the biogeographic range expansion of the foraminifera Amphistegina in the Mediterranean Sea. J Foramin Res 42: 234–248.
5. Simberloff D (2000) Introduced species: the threat to biodiversity and what can be done. American Institute of Biological Sciences. Available: http://www. aibs.org/biodiv/simberloff.html via the Internet. Accessed: 21MAR 2006.
6. Dale VH, Joyce LA, McNulty S (2001) Climate change and forest disturbances. BioScience 51: 725–734.
7. Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Ann Rev Ecol Ecol Syst 37: 637–669.
8. LeRoux PG, McGeoch MA (2008) Rapid range expansion and community reorganization in response to warming. Glob Chang Biol 14: 2950–2962.
9. Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, et al. (2003) Predicting the impact of global warming on the timing of spring flowering. Int J Climatol, 23: 1599–1613.
10. Cudmore TJ, Bjorklund N, Carroll AL, Lindgren BS (2010) Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in native host tree populations. J Appl Ecol, 47: 1056–1014.
11. Sorte CJB, Williams SL, Carlton JT (2010) Marine range shifts and species introductions: comparative spreading rates and community impacts. Glob Ecol Biogeograph 19: 303–316.
12. Langer MR, Hottinger L (2000) Biogeography of selected “larger” foraminifera in the Mediterranean Sea. J Foramin Res 42: 234–248.
13. Larsen AR (1976) Studies of recent Amphistegina. Arctic and Antarctic Research 33: 1–9.
14. Southward AJ, Hawkins SJ, Burrows MT (1995) Seventy years’ observations of Amphistegina in Mediterranean reefs. J Foramin Res 11: 40–46.
15. Pascoe JD, Gosling KV, Caddy JR (1990) Foraminifera of the Kenya coastline. J Foramin Res 11: 1–74.
16. Monier C (1973) Note préliminaire sur les foraminifères benthiques du platier de l’île de Bourbon (Mascareignes). Cahiers du Office de la Recherche Scientifique et Technique Outre-mer 11: 181–201.
17. Moura AR (1965) Foraminíferos da Ilha da Inhaca. Revista dos Estudos gerais do Instituto de Zoologia “Dr. Augusto Nobre” Faculdade de ciências do Porto 77: 21–80.
18. Ingle JA (1999) Foraminifera. In: Grosholz ED, editor. The impacts of exotic species on the biota of the Mediterranean. Sinauer Associates. 381–419.
19. Hawkins SJ, Southward AJ, Burrows MT (1995) Observations on the life cycle of the symbiont-bearing foraminifer Amphistegina lessoni Lin. J Foramin Res 11: 191–202.
20. Alory G, Wijffels S, Meyers G (2007) Observed temperature trends in the Indian Ocean over 1960–1999 and associated mechanisms. Geophys Res Lett 34: L20606, doi:10.1029/2007GL030944.
21. Grosbol ED (1996) Contrasting rates of spread for introduced species in terrestrial and marine systems. Ecology 77: 1060–1066.
22. Kinlan BP, Hastings A (2005) Rates of population spread and geographic expansion. What exotic species tell us. In: Sut DF, Stachowicz JJ, Gaines SD, editors. Species Invasions: Insights into Ecology, Evolution and Biogeography. Sunderland, Massachusetts: Sinauer & Associates. 381–419.
23. McKee KA (1880) Foraminiferae of Mauritius. In: McKee KA, Richters F, Martin E, editors. Beiträge zur Meeresfauna der Insel Mauritius und der Seychelen. Berlin: Gutmann. 658 p.
24. Heip RH (1884) Report on the foraminifera dredged by H.M.S. Challenger, during the years 1873–1876. Reports on the Scientific Results of the Voyage of the H.M.S. Challenger during the years 1873–1876. Zoology 9: 1–814.
25. Emery KJ (1895) Foraminifera of Neotropical forests. Google Books. 410 p.
26. Simberloff D (2000) Introduced species: the threat to biodiversity and what can be done. American Institute of Biological Sciences. Available: http://www. aibs.org/biodiv/simberloff.html via the Internet. Accessed: 21MAR 2006.
27. Lee JJ (1995) Living sands. BioScience 45: 252–261.
28. Murray JW (1973) Distribution and ecology of living benthic foraminifera. London: Heinemann Educational Books. p. 244.
29. Zmiri A, Kahan D, Hochstein S, Reiss Z (1975) Phototaxis and thermotaxis in some species of Amphistegina. (Foraminifera). Micropaleontology 21: 153–158.
30. Larsen AR (1976) Studies of recent Amphistegina. Taxonomy and some ecological aspects. Israel J Earth Sci 23: 1–26.
31. Sorte CJ, Williams SL, Carlton JT (2010) Marine range shifts and species introductions: comparative spreading rates and community impacts. Glob Ecol Biogeograph 19: 303–316.
32. Murray JW (1973) Distribution and ecology of living benthic foraminifera. London: Heinemann Educational Books. p. 244.
33. Zmiri A, Kahan D, Hochstein S, Reiss Z (1975) Phototaxis and thermotaxis in some species of Amphistegina. (Foraminifera). Micropaleontology 21: 153–158.
34. Larsen AR (1976) Studies of recent Amphistegina. Taxonomy and some ecological aspects. Israel J Earth Sci 23: 1–26.
35. Robinson LM, Elith J, Hobday AJ, Pearson RG, Kendall BE, et al. (2011) Pushing the limits of change and ecological community distribution modelling: lessons from the land present changes and opportunities. Glob Ecol Biogeograph 20: 709–712.
36. Kintisch E (2008) Impacts research seen as next climate frontier. Science 322: 102–103.
37. Hannah L, Midgley GF, Millar D (2002) Climate change integrative conservation strategies. Glob Ecol Biogeograph 11: 485–495.
38. Saikkonen K, Taulavuori K, Hyvönen T, Gundel PE, Hamilton CE, et al. (2012) Climate change-driven species’ range shifts filtered by photoperiodism. Science 335: 131–134.
39. Aron G, Wijffels S, Meyers G (2007) Observed temperature trends in the Indian Ocean over 1960–1999 and associated mechanisms. Geophys Res Lett 34: L20606, doi:10.1029/2007GL030944.
40. Grosbol ED (1996) Contrasting rates of spread for introduced species in terrestrial and marine systems. Ecology 77: 1060–1066.
41. Kinlan BP, Hastings A (2005) Rates of population spread and geographic expansion. What exotic species tell us. In: Sut DF, Stachowicz JJ, Gaines SD, editors. Species Invasions: Insights into Ecology, Evolution and Biogeography. Sunderland, Massachusetts: Sinauer & Associates. 381–419.
42. McKee KA (1880) Foraminiferae of Mauritius. In: McKee KA, Richters F, Martin E, editors. Beiträge zur Meeresfauna der Insel Mauritius und der Seychelen. Berlin: Gutmann. 658 p.
43. Heip RH (1884) Report on the foraminifera dredged by H.M.S. Challenger, during the years 1873–1876. Reports on the Scientific Results of the Voyage of the H.M.S. Challenger during the years 1873–1876. Zoology 9: 1–814.
44. Emery KJ (1895) Foraminifera of Neotropical forests. Google Books. 410 p.
45. Simberloff D (2000) Introduced species: the threat to biodiversity and what can be done. American Institute of Biological Sciences. Available: http://www. aibs.org/biodiv/simberloff.html via the Internet. Accessed: 21MAR 2006.

71. Phillips SJ, Dudík M, Shapire RE (2004) A maximum entropy approach to
70. Christensen JH, Hewitson B, Busuioc A, Chen X, Gao I, et al. (2007) Regional
68. Hijmans RJ, Guarino L, Rojas E (2001) DIVA-GIS. A geographic information
67. Pignatti J, Frezza V, Benedetti A, Carbone F, Accordi G, Matteucci R (2012)
75. Elith J, Phillips SJ, Hastie T, Dudík M, En Che Y, et al. (2011) A statistical
91. Hiddink JG
90. Belanger CL, Jablonski D, Roy K, Berke SK, Krug AZ, et al. (2012) Global
89. IPCC (2007b) Climate change 2007: the physical science basis. Contribution of
88. Belderson RH (1961) The size distribution characteristics of the Recent shallow
87. Toefy R, Gibbons MJ, McMillan IK (2005) The foraminifera associated with
81. d’Orbigny A (1826) Tableau me´thodique de la classe des Ce´phalopodes. Ann
79. Swets JA (1988) Measuring the accuracy of diagnostic systems. Science 240:
83. Wright EP (1877) Notes on Foraminifera (from the Seychelles and from
84. Banner FT, Pereira C (1981) A temporal and spatial analysis of foraminiferal
82. Ingold CK (1969) Foraminifera. In: Demchuk T, Gary AC, editors. Geological Problem Solving in Marine Geology. Pub- lishers 72: 149–171.
80. Ingold CK (1967) The foraminifera of the small dredged from the vicinity of Sydney Island, D’Urville Bay, South Africa. Antarct Sci 9: 307–316.
86. McMillan IK (1974) Recent and relic foraminifera from Agulhas Bank, South
85. Welsh CA (1987) Long-term stability of foraminifera in the late Pleistocene. Geol Soc Amer Bull 98: 275–302.
89. IPCC (2007b) Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge and New York: Cambridge University Press, 847–940.
78. Phillips SJ, Dudík M, Shapire RE (2004) A maximum entropy approach to species distribution modeling. Proceedings of the 21st International Conference on Machine Learning: 655–662.
77. Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Modell 200: 231–259.
76. Phillips SJ, Dudík M, Shapire RE (2004) Maximum entropy approach to species distribution modeling. Glob Ecol Biogeogr 21: 272–291.
75. Elith J, Phillips SJ, Hastie T, Dudík M, En Che Y, et al. (2011) A statistical
74. Zijlstra HJ, van Boom K (1981) In: Sen Gupta BK, editor. Modern Foraminifera. Dordrecht: Kluwer Academic Publishing. 37–56.
73. Janssen RP (1972) New data on the occurrence of foraminifera in the Seychelles. Proc R Ir Acad 29: 506–508.
72. Wright EP (1877) Notes on foraminifera from the Seychelles and from Cagha- lari, J Nat Hist Serie 4 19: 40–44.
71. Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, et al. (2009) Sample selection bias and presence-only distribution modeling: implications for background and pseudo-abundance data. Ecol Appl 19: 181–197.
70. Christensen JH, Hewitson B, Busuioc A, Chen X, Gao I, et al. (2007) Regional climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, et al., editors. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge and New York: Cambridge University Press. 847–940.
69. Hijmans RJ, Guarino L, Rojas E (2001) DIVA-GIS. A geographic information system for the analysis of biodiversity data. Manual: International Potato Center, Lima.
68. Hijmans RJ, Guarino L, Rojas E (2001) DIVA-GIS. A geographic information system for the analysis of biodiversity data. Manual: International Potato Center, Lima.
67. Pignatti J, Frezza V, Benedetti A, Carbone F, Accordi G, Matteucci R (2012)
64. Banner FT, Pereira C (1981) A temporal and spatial analysis of foraminiferal
diversity from the fringing reefs of Mombasa, East Africa. In: Neale JW, Brasier MJ (eds) Foraminiferal Ecology 1: 29–68.
63. Dale DC, McMillan IK (1999) On the Beach: A Field Guide to the Late Cenozoic Micropalaeontological History, Saldanha Region, South Africa. Cape Town: De Beers Marine. 127 p.
62. Perry CT (2003) Coral reefs in a high-latitude, siliciclastic barrier island setting: reef framework and sediment production at Inhaca Island, southern Mozambique. Coral Reefs 22: 485–497.
61. Perry CT, Beavington-Penney SJ (2005) Epiphytic calcium carbonate production and fishes development within sub-tropical seagrass beds, Inhaca Island, Mozambique. Sediment Geol 174: 161–176.
60. Langer MR, Schmidt-Sinats J (2006) Biogeography of modern benthic foraminifera from South Africa, Namibia and Mozambique. Ann Inst Geosci Paris 60: 689–687.
59. Pignatti J, Frezza V, Benedetti A, Carbone F, Accordi G, Matteucci R (2012)
58. Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, et al. (2009) Sample selection bias and presence-only distribution modeling: implications for background and pseudo-abundance data. Ecol Appl 19: 181–197.
57. Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, et al. (2009) Sample selection bias and presence-only distribution modeling: implications for background and pseudo-abundance data. Ecol Appl 19: 181–197.
56. Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, et al. (2009) Sample selection bias and presence-only distribution modeling: implications for background and pseudo-abundance data. Ecol Appl 19: 181–197.
55. Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, et al. (2009) Sample selection bias and presence-only distribution modeling: implications for background and pseudo-abundance data. Ecol Appl 19: 181–197.
54. Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, et al. (2009) Sample selection bias and presence-only distribution modeling: implications for background and pseudo-abundance data. Ecol Appl 19: 181–197.
53. Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, et al. (2009) Sample selection bias and presence-only distribution modeling: implications for background and pseudo-abundance data. Ecol Appl 19: 181–197.