

Assembly and persistence of foraminifera in introduced mangroves on Moorea, French Polynesia

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ABSTRACT: Foraminifera inhabiting the muddy substrata within the coastal mangrove forests (*Rhizophora stylosa* Griff.) on Moorea, French Polynesia, are distinct from other near shore foraminiferal assemblages around the island. Yet the mangroves were introduced from New Caledonia only in 1937 at Vaianahe Bay; they have since spread to many other sites around Moorea. They invade and occupy mud substrata below *Paspalum* marshes, the marshes themselves and mud under overhanging *Hibiscus* stands. The mangrove foraminifera cluster uniquely among themselves when compared to other lagoonal habitats, including those invaded by the mangroves. Thus, the introduction of mangroves has apparently allowed the development of a new community or assemblage of foraminifera.

Mangrove foraminifera include *Ammonia* *salsa*, *Ammonia* *tepida*, *Paratrochammina* *stoeni*, *Reophax* cf. *R. bacillaris*, *Trichohyalus* *aguayoi*, *Trochammina* *inflata*, and other subsidiary species of *Ammonia*, *Elphidium*, *Quinqueloculina*, *Cornuspira*, and *Rosalina*. *Arenoparrella mexicana*, a characteristic species in mangroves elsewhere, is absent from Moorea, perhaps because it was never there like the mangroves themselves. The mangrove species cluster midway between those of shallow-water lagoonal mud, salt grass *Paspalum* marshes, and the muddy habitats below *Hibiscus* trees, even when they occur at similar elevations above or below sea level.

The foraminifera in the unique cluster in the mangroves were not introduced with the initial mangrove trees, as the trees were established from propagules carried to the site by humans. The cluster is also found in other newer stands on the island that were colonized by floating propagules. The foraminiferal mangrove assemblage at Moorea is a more recent amalgamation of taxa recruited from the species pools in the associated salt grass *Paspalum*, *Hibiscus* and shallow-water lagoonal mud habitats. This recruitment happened quickly, most likely as soon as the mangroves grew to sufficient size to trap fine sediment and organic material, as these species are constantly transported about the lagoon chiefly by birds, rafts of algae or foam, and turbidity created by winds and storms. Some but not all foraminiferal species from these environments were able to occupy the new mangrove habitat. This indicates that the unique clusters of foraminifera have no biologic unity, but are simply associations of species that tolerate slightly different but similar environments at different elevations and with increased organic content, and with decreased wave action caused by mangrove roots. Previous studies of foraminiferal and other associations also indicate that in many situations marine organisms are not necessarily dependent on other specific species. Even in seemingly structured reef and rocky-shore communities with geologic histories of similar communities over thousands of years, the rapidity with which dispersal of larvae, eggs, or adult organisms takes place, and similar environmental conditions maintain this similarity of community, not principally any biologic dependence of species upon one another.

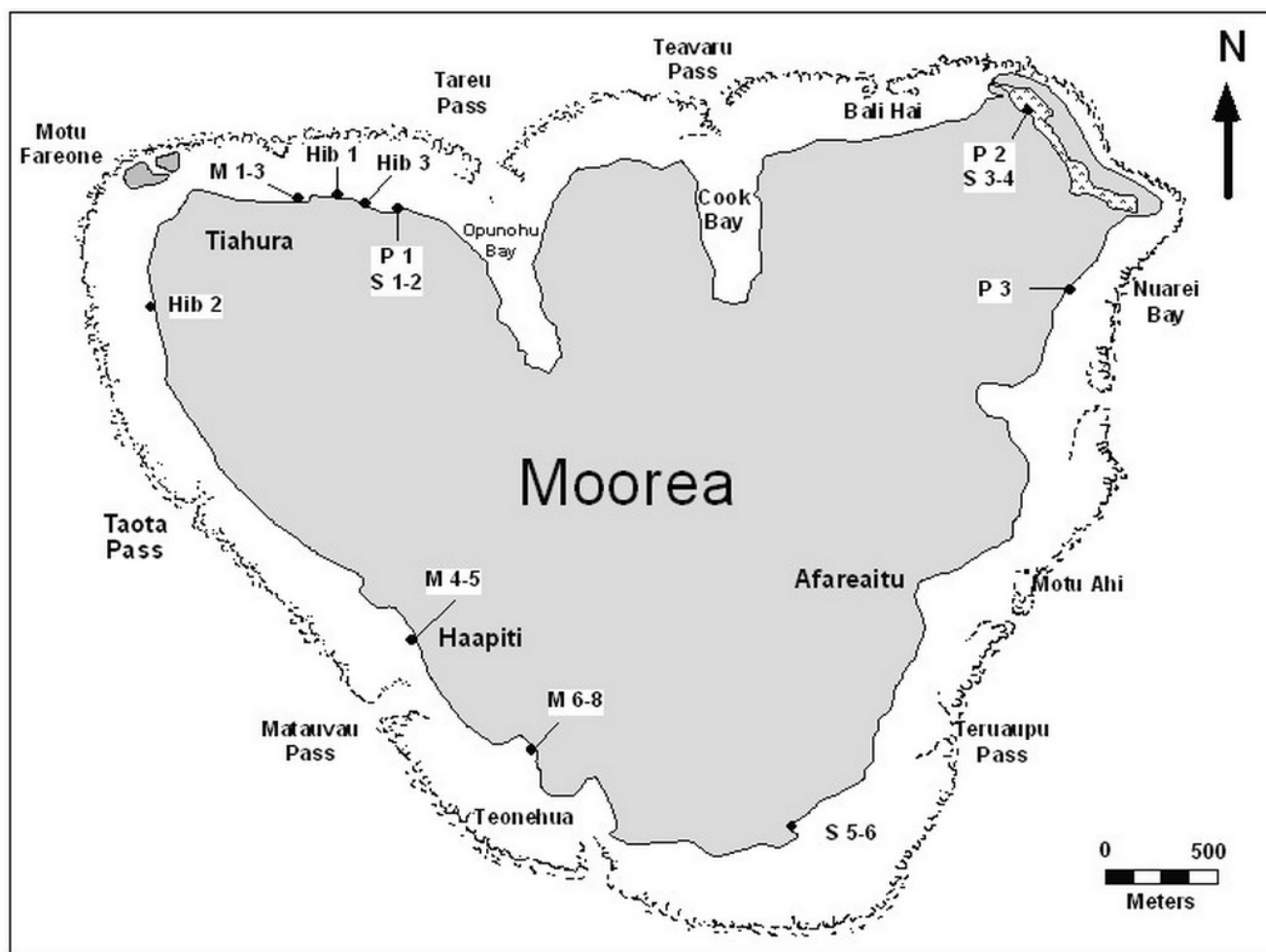
INTRODUCTION

Co-occurring fossil and recent foraminiferal species have long been referred to as communities, more or less in a descriptive sense, but also commonly with the inference that they represent some kind of persistent structural unit. Such species are well known to group together in various cluster analyses, and these clusters are used to define communities, assemblages or associations. The clusters of species seem to be consistent, at least within geographical areas at particular times. Among foraminifera on a geological time scale, the constituent species at any particular time and place in Eocene to Pliocene formations on the Atlantic and Gulf Coast of North America enter into new species associations independently of other species, indicating that biologically-structured communities do not exist among these foraminifera (Buzas and Culver 1994, 1998).

Whether or not species of particular organisms living together are somehow largely structured biologically, as Elton (1933) long ago suggested, or are simply a group of species with similar individual ecologic requirements or environmental tolerances, as Gleason (1926) thought, is not always clear. Recent

discussions and evidence favor the hypothesis that groups of co-occurring species, including foraminifera, exist together because they have similar requirements and/or tolerances (Bambach and Bennington 1996; Buzas and Culver 1994, 1998; Jackson 1994; Jackson et al. 1996), although this may well be a matter of temporal and spatial scale. These communities are not static entities, but come together over some time from a larger regional pool of species from a range of environments (Ricklefs 1987; Ricklefs and Schluter 1993). This is difficult to demonstrate in nature probably because communities are dynamic assemblages of species that are always changing locally to one extent or another. Theoretical models indicate that the nature of the regional species pool strongly influences the composition of the local community (Morton and Law 1997).

Herein we explore aspects of short-term community assembly of shallow-water, tropical foraminifera in an introduced (in 1937) but well-established mangrove (*Rhizophora stylosa* Griff.) habitat on the island of Moorea, French Polynesia (text-figs. 1, 2). In that habitat, we found a unique assemblage of foraminiferal species. The species composition and prove-



TEXT-FIGURE 1
Map of the Island of Moorea (French Polynesia, SW-Pacific) showing sampling sites and reefs, reef passes and bays.

nance of these associations in the introduced trees are of interest in understanding how they originated and how they have developed over short times. Short-term assembly and reassembly of communities may play an important role in community composition over geologic times. We compare benthic foraminifera from introduced mangrove habitats with those found in native salt grass (*Paspalum vaginatum* Sw.) marshes, mud below overhanging *Hibiscus tiliaceus* L. trees, and shallow-water mud habitats in the lagoon at Moorea. The comparison allows us to assess whether the introduction of mangroves has created a unique foraminiferal community or just allowed the assembly of an association of species utilizing them, and to what degree foraminifera have been assembled from nearby habitats. Our aim is to document this long-term natural experiment as a test of the concept of community unity, a still controversial issue among ecologists (see Jackson, 1994, for a clear statement of the problem), and assembly. We do not intend to document extensively the foraminiferal faunas of these habitats everywhere on Moorea, as that is not necessary to test this model.

NEARSHORE HABITATS OF MOOREA

The island of Moorea is located in the South Pacific (17°30'S, 149°50'W) just 18 km west of Tahiti, and both are part of the

Society Islands, French Polynesia. A wide variety of shallow-marine environments exist in this high island-barrier reef-lagoon system. The shoreline habitats at Moorea are distributed along the shallow lagoon, which is slightly less than 45 km in circumference around the island. These habitats are predominantly muds and roots in *Rhizophora stylosa* mangrove forests, shore sands and muds under overhanging *Hibiscus tiliaceus*, *Paspalum vaginatum* salt grass marshes, and mud and rocks without significant vegetation associated with them, with some sand and rare beach rock. Each habitat is distinct in most characteristics, and foraminifera are common in all of them.

Mangrove trees are significant constituents of tropical ecosystems worldwide that have developed a number of special characteristics (pneumatophores, breathing roots, viviparous seeding habitats) to thrive under conditions of poor nutrient availability, low oxygen, wide salinity variations, and substrate mobility. They occupy an area of about 20 million hectares worldwide and fringe more than 50 percent of the world's tropical and subtropical coastlines (Ellison 1994; Adams et al. 1990). Mangroves, however, were largely absent in most of the eastern Central Pacific including Polynesia (Woodruff 1987). In 1937, the mangrove *Rhizophora stylosa* was introduced to Moorea (Mueller-Dombois and Fosberg, 1998) from New Cal-



TEXT-FIGURE 2

Hibiscus and the mangrove *Rhizophora stylosa* on Moorea, French Polynesia. A. *Hibiscus* growing over the lagoon waters but rooted on land on the west side of Cook's Bay. B. *R. stylosa* invading the mud and low marsh of *Paspalum* on the coast, just south of Taota Pass. C. *R. stylosa* invading the high *Paspalum* marsh on the northwest coast of Moorea (site M 1-3; see text-fig. 1). D. A full stand of *R. stylosa*, viewed from the lagoon, just north of Haapiti, Moorea (site M 4-5; see text-fig. 1). All images by J. H. Lipps 2000-2003.

edonia with the intention of cultivating oysters on the extensive prop roots (Taylor 1979; Cavaloc 1988). The introductions consisted of a small number of propagules (germinated seeds with a spike-like root that develop while still on the trees) carried to Moorea. Although the oyster project did not succeed, the mangroves thrived and have since spread to many other nearshore sites on Moorea, Tahiti, Raiatea, Tahaa (Mueller-Dombois and Fosberg, 1998), and some other nearby islands.

Foraminifera were unlikely to have been introduced with the mangrove transplants since the propagules were taken from the trees before they fell into the water. Furthermore, the mangroves spread on Moorea by floating propagules and foraminifera are unlikely to have been transported from one site to another. After falling from the tree propagules ordinarily land in the water, and either stick in the mud below the trees where they grow or land in the water and float away.

The introduction and proliferation of mangroves around Moorea has been well documented (Cavaloc 1988), allowing

alterations in native communities to be monitored. Although mangrove forestry and aquaculture are now recognized as important economic resources in some areas (Christensen 1983) and as a way to ameliorate the impact of tsunamis (Kathiresan and Rajendran 2005), consequences of their introduction are poorly understood. On Moorea, they are sometimes allowed to proliferate while at other times they have been cut down, plowed up, and otherwise destroyed by individual landowners. Yet large stands have existed since their introduction on the SW and more recently on the NW sides of the island (text-figs. 1, 2).

When we observed the mangroves in 1992, 1994, 1995, and 1998 through 2003, they flourished at several shoreline sites around Moorea where they typically formed the transition from land to lagoon. Their arching roots anchor in dark, fine-grained muddy to silty sediment (text-fig. 2) which is rich in particulate organic matter, commonly oxygen depleted, and subject to tidal and salinity variations. Only a few species of woody plants thrive under such physiologically-adverse conditions and thus mangrove habitats typically exhibit a low floristic diversity.

The anthropogenic introduction of the mangroves to French Polynesia has affected original coastline habitats by growing in front of *Hibiscus*, invading grass marshes, trapping organic-rich sediments in the dense network of the prop roots, and by promoting the seaward progradation of coastal margins. The dense prop roots of mangroves retain moisture and entrap sediments rich in organic matter thereby creating a reducing environment that is commonly oxygen-depleted at depths greater than 0.5 cm (see also Boltovskoy 1984). Modifications of ecological constraints also affect processes of population dynamics and community assembly (Jackson 1994). As a result of this alteration in habitat, mangroves may support organisms that did not previously exist in these areas (e.g. Begon et al. 1986). They may function as important nurseries for a variety of commercially important fish, crabs, shrimp and other crustaceans (Christensen 1983).

Hibiscus tiliaceus shrubs and trees grow from the shore (text-fig. 2) to the high slopes on Moorea. Whether or not they are native to French Polynesia is uncertain, but they were certainly present when Lieutenant James Cook arrived at Tahiti in 1768, for they were illustrated by his artist Sydney Parkinson (Carr 1983). Polynesians may have carried *Hibiscus* with them when they occupied the islands, as they did with many other plants. The plant is also dispersed by floating seeds, hence always may have been part of the native vegetation. In any case, the trees have been a part of the strand vegetation for two thousand years, and relative to the mangroves can be considered a native tree for our purposes. When *Hibiscus tiliaceus* grows along the shore, the trees root in the sandy shore areas (as opposed to in the water) or on embankments, and commonly lean over the lagoon waters. The sedimentary substrate in the water under the *Hibiscus* is medium- to fine-grained sand or mud with a low organic content. However, a dark, low oxygen layer exists 1.5 cm beneath the surface of the substrate.

The salt grass *Paspalum vaginatum* grows throughout French Polynesia and was present along the coast of Tahiti when Cook first arrived in 1768 (D. Stoddart, pers. communication, 1996). While *Paspalum* was also possibly carried to French Polynesia by Polynesian voyagers, it has a wide distribution throughout the Pacific. It too has been a long-time resident of Moorea. The sedimentary substrate of the salt grass is also mud and closely resembles that under the mangroves. However, the soil is much denser due to the extensive root network of the plants. Mangrove trees commonly invade the salt grass habitat and locally tend to replace it or grow into the water in front of it (text-fig. 2). Solitary mangrove trees growing in and near the salt grass somehow maintain a well-marked clear area free of any grass around them (text-fig. 2). Clearly, they alter the environment of the marsh and the grass is eventually restricted to areas free of the trees.

Muddy habitats without vegetation occur at various places along the island's shores, but not on the barrier reef or even in the lagoon. These are dark, fine-grained silts composed chiefly of basaltic clasts and containing a high organic content. Again, the subsurface muds tend to be anoxic. Along certain coasts, basalt boulders occur as well, and these have coverings of filamentous algae below the water.

Temperature, salinity and tides of these environments are generally stable throughout the year. Seasonal variations are low, and river runoff is minor except in the watersheds of Cook's and Opunohu Bays, areas not considered in this report. Lagoon

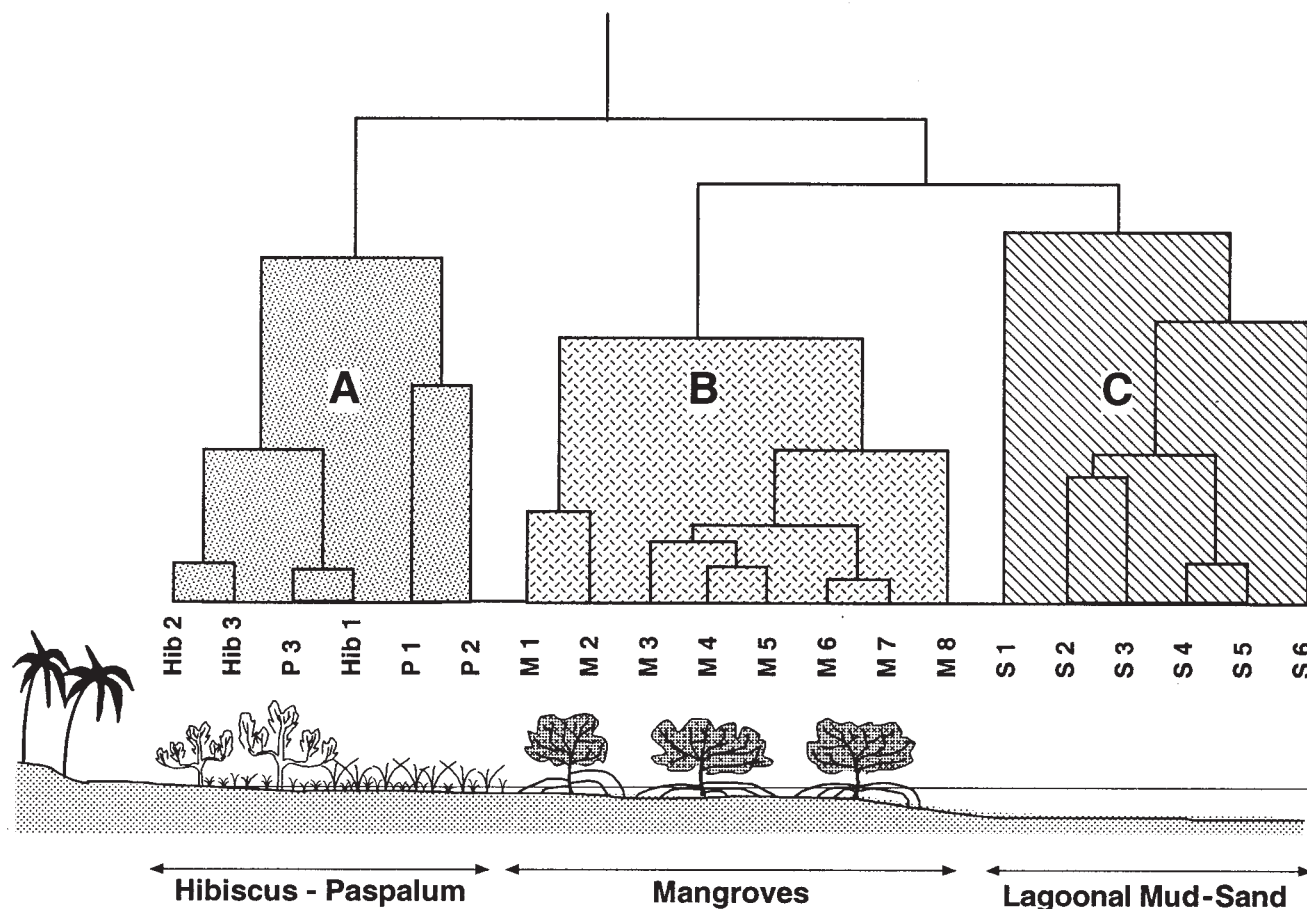
temperatures range throughout the year between 23° and 26°C. Salinity may vary if heavy rainfall and a low tide correspond, but only in the upper part of the rather negligible tidal range. Salinities thus remain near 33‰, the salinity of the lagoon and open ocean. Tidal range is less than .33m because Moorea lies near the amphidrome point for tides in the South Pacific. As a result, no expanses of mudflats, marshes or mangroves exist on the Society Islands. On rare occasion when prevailing winds push sea water into the lagoon through passes or over the reef, the lagoon level may rise significantly (we measured it once at 1.0 — 1.5 m in the mangroves at Haapiti). The effect of these floods is geographically minor because the mangroves and marshes grow closely to the base of the mountains and no extensive flat areas within that range are usually present. These are rare events that seem to have little or no permanent biotic effect.

MATERIAL AND METHODS

A total of 20 sediment samples were collected in October and November 1992 and in September 1994 at selected sites around the island (text-fig. 1). Four primary shallow-water habitats were selected and sampled to examine distributional patterns of foraminifera (text-figs. 1, 2): 1. established *Rhizophora stylosa* mangrove stands off Tiahura, Haapiti, and Teonehua (samples M1 through M8); 2. *Paspalum vaginatum* salt grass habitats off Papetoai and Teavaro and east of Teaharoa (samples P1 through P3); 3. *Hibiscus tiliaceus* tree habitats northwest of Papetoai and west of Tiahura (samples Hib1 through Hib3); and 4. shallow water lagoonal mud environments north of Papetoai, at the mouth of the Mahaerua River at Maatea, and north of Temae (samples S1 through S6). This strategy was designed to sample the fine-grained habitats and those associated with mangroves in the lagoon; it was not intended to document comprehensively these environments at Moorea.

Sediment surface samples (top two centimeters) were collected at the base of the mangrove trees (text-figs. 1, 2; M1-M8). They also included detritus from the prop roots. The *Hibiscus tiliaceus* groves sampled are located along the shore where the branches and leaves overhang the water and contribute debris to the sediment surface below. Unlike both mangrove and *Hibiscus* stands, the *Paspalum vaginatum* salt grass beds sampled were located at a variety of distances from the shoreline. Sample P1 was taken from a bed adjacent to the lagoon, sample P2 was located in a swamp area at Temae (approximately 200 meters from the shore), and sample P3 was collected from a bed located at the edge of an estuary near Teavaro (text-fig. 1). Careful sampling of the salt grass, as far removed from the mangrove trees as possible, was therefore done to justify habitat separation of the faunas from both environments. The lagoonal mud-sand samples (samples S1 through S6) comprised sandy mud and algae and scrapings from rocks. All sediment samples were collected at low tide and included sediment from the top two centimeters. Sampling was carried out using a plastic corer with a diameter of 6.5 cm. The corer was pressed into the substrate and the top 2 centimeters of the sample was removed and stored in plastic bags.

All samples were washed before drying over 63µm mesh sieves, the residues were dried and the foraminifera picked from each. We combined both living and dead tests to provide a time-averaged sample and to avoid known problems with detection of live foraminifera (Bernhard 2000). More than 10,000 foraminifera were obtained, identified to species whenever possible and counted.



TEXT-FIGURE 3

Q-mode cluster dendrogram showing correlation of assemblage clusters and habitat: A: *Hibiscus-Paspalum*-assemblage (samples Hib 1-3 and P 1-3); B: Mangrove-assemblage (samples M 1-8); C: Lagoonal sand and mud assemblage (samples S 1-6).

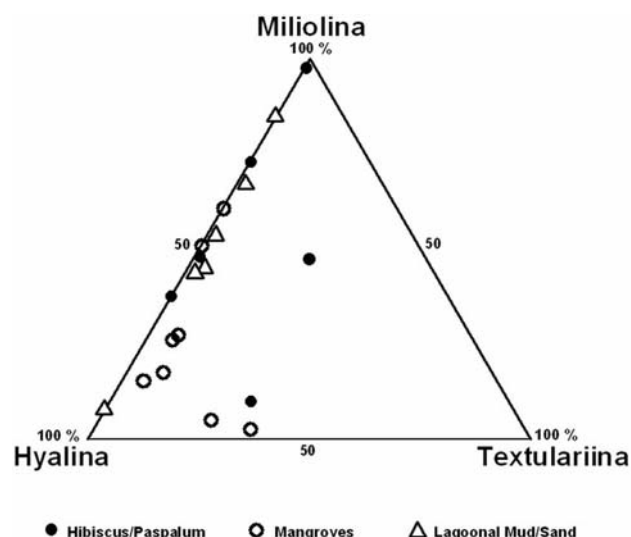
To determine structure in the foraminiferal data an A1-Pearson correlation coefficient Q-mode cluster analysis (complete linkage method, farthest neighbor) was used to analyze the relationship between the twenty samples taken from the four different habitats (text-fig. 3). This technique is used commonly in “community” studies because it objectively and repeatedly groups together in the same way samples with similar faunal assemblages. While foraminiferal assemblages may seem obvious from species lists, cluster analysis reduces misinterpretation and confusion in how samples are related to one another. Species diversity (simple diversity) was determined for each sample to establish diversity patterns within the four habitats (text-fig. 5). Agglutinated, miliolid and hyaline specimens were counted separately and plotted into triangular diagrams (text-fig. 4; Murray 1973). Foraminiferal diversity was also determined by plotting the total number of individuals against the total number of species in a Fisher α base-graph (text-fig. 6; Fisher et al. 1943). All statistical analyses were carried out with Systat 5.2 computer software.

RESULTS

A total of 10,044 benthic foraminifera, including agglutinated, perforate-hyaline and imperforate-porcellaneous taxa (table 1) belonging to 96 species (Appendix 1) were recovered from the

20 samples collected at Moorea. The foraminiferal fauna present comprises mostly common tropical to subtropical shallow-water benthic species previously recorded from Moorea (Vénec-Peyré 1991) and from other intertidal, mangrove or associated habitats. The fauna reliably represents the habitats where they were collected. The most commonly occurring species are *Ammonia tepida*, *A. convexa* and *Trochammina inflata* followed by *Elphidium craticulum*, *Spirolina arietina*, *Trichohyalus aguayoi*, *Reophax* cf. *R. bacillaris*, and *Quinqueloculina latidentella*. *Ammonia tepida* was also one of the most abundant species recorded in Puerto Rican (Culver 1990), South American (Debeney, et. al. 2002) and Australian (Horton, et al 1998) mangrove and mud habitats; the others occur commonly to rarely in mangrove and associated habitats around the world (see below). Significantly, two of the most common and abundant species in mangrove and marsh assemblages elsewhere, *Miliammina fusca* and *Arenoparrella mexicana*, were not found in our samples.

Three sample clusters were defined in the Q-mode cluster analysis from the data set recorded (text-fig. 3). The cluster assemblages, designated A-C, consist of samples that distinctly reflect three environmental habitats: *Hibiscus-Paspalum*, mangrove, and lagoonal habitats. Samples collected from *Hibiscus* and



TEXT-FIGURE 4

Triangular diagram showing percentage ratios of agglutinated (Textulariina), porcellaneous (Miliolina) and perforate (Hyalina) foraminifera. Note that mangrove foraminiferal assemblages (open circles) generally contain higher ratios of perforate taxa than the associated habitats.

Paspalum habitats exhibit similar faunal compositions and cluster together in cluster A. The largest cluster (Cluster B) exclusively contains samples that were collected in the mangrove habitat. The foraminiferal assemblage of cluster B is transitional between the two assemblages of Cluster A and Cluster C. The foraminiferal assemblages from shallow-water lagoonal sand and mud habitats adjacent to the mangrove environment represent Cluster C which contains 6 samples.

Samples of *Hibiscus* and *Paspalum* (Cluster A) are characterized by low diversity (6-12 species) and a commonly high percentage of miliolid taxa (table 1; text-fig. 4). Agglutinated species are absent in all *Hibiscus* samples but do appear in the *Paspalum* habitat (*Paratrochammina stoeni*, *Trochammina amnicola* and *Rheophax* cf. *R. bacillaris*). *Ammonia* cf. *A. tepida*, *Triloculina subgranulata* and *Paratrochammina stoeni* dominate the assemblages of cluster A, with frequencies of 35%, 95%, and 24% respectively (table 1). Only a single species, *Anomalinoidea* sp. 1, occurs exclusively in cluster A. It is, however, represented by only two individuals that limit its usage as an indicator taxon. Chloroplast-bearing elphidiids appear in all *Hibiscus* and *Paspalum* samples but other larger symbiont-bearing species (*Spirolina arietina*, *Sorites orbiculus*) are absent from assemblages of cluster A.

The mangrove assemblages (Cluster B) are characterized by moderate species diversity (15-48) and a high percentage of hyaline-perforate species (51-92%). The percentage of agglutinated foraminifera ranges between 0 and 35 % of which *Rheophax* cf. *R. bacillaris* and *Paratrochammina stoeni* are dominant while *Ammonoastuta salsa*, *Ammotium* sp. and *Textularia* sp. occur sporadically. Some mangrove sediment samples also contained significant numbers of *Trichohyalus aguayoi*. This species has been commonly recorded in mangrove habitats (Javaux and Scott 2003) and appears to be particularly well adapted (Lipps and Langer, 1999; Steinker and Butcher 1981, identified as *Discorinopsis aguayoi*). Despite the high organic

content of mangrove sediments, symbiont-bearing larger foraminifera (*Spirolina arietina*, *Amphistegina lessoni*) and numerous elphidiids are common constituents of Cluster B. Four species occur exclusively in the mangrove habitat: *Cibicides pseudolobatus*, *Elphidium* cf. *E. articulatum*, *Miliolinella* sp. B, and *Spirillina* cf. *S. sigilata*. Because some of these species have commonly been recorded from other environments (e. g. Loeblich and Tappan 1994; Vénec-Peyré 1991; Murray, 1991) and because of their low abundances, none of them are considered indicative of mangrove habitats.

The nearshore lagoonal environment (Cluster C) contains some of the most diverse foraminiferal faunal assemblages (e.g. sample S1 with 64 species). The samples from this cluster are characterized by a commonly high percentage of miliolids (45-84 %) and hyaline taxa (16-55 %). Agglutinated foraminifera are rare and never constitute more than 3 percent of the total lagoonal assemblage. Larger foraminifera are common and constitute some of the most frequently recorded taxa in the nearshore lagoonal habitat at Moorea (i.e. *Spirolina arietina*).

Among all foraminiferal taxa present, 19 species (19.7 % of all species) are distributed throughout the four primary habitats, either continuously or discontinuously (table 1). Twenty-three species (= 23.9 %) are confined to the shallow-water lagoonal mud habitat. Four taxa (= 5.2 %) are restricted to the mangrove environment and only one species (*Anomalinoidea* sp.) occurs exclusively in the *Hibiscus/Paspalum* assemblage. The majority of species (88 taxa = 91.6 %) have representatives dwelling in the lagoon. Only eight species (8.3 %) are confined to the *Hibiscus/Paspalum* and the mangrove environment of which *Quinqueloculina* cf. *Q. incisa* is considered to be characteristic. Among the species that appear to be particularly well adapted to the mangrove habitat, only *Reophax* cf. *R. bacillaris* is present in sufficiently high numbers to be considered a semi-true mangrove indicator taxon at Moorea. However, six individuals of this species were also recorded from within the salt grass *Paspalum* at site P1 (text-fig. 1).

Examination of foraminiferal diversity within these three cluster groups reveals that the number of species increases from intertidal *Hibiscus* and *Paspalum* habitats towards the mangrove and the lagoonal environments (text-fig. 5). Samples collected in the *Hibiscus* and *Paspalum* environments show the least diverse fauna with Fisher α values <3 (text-fig. 6). Mangrove habitats exhibit a moderate foraminiferal faunal diversity (15-48 species; average = 29.5 species) intermediate between lagoonal (average = 37.3 species) and *Hibiscus/Paspalum* environments (average = 9.5 species). Fisher α values typically recorded from mangrove habitats at Moorea are between 2.8 and 7.8. Diversity is highest in the lagoonal mud and sand samples (Cluster C) but also show the highest degree of variation (9-64 species). Fisher α values typically recorded from lagoonal samples range between 3 and 19.4.

Agglutinated foraminiferal species diversity in general is low but some mangrove samples have particularly large numbers of *Reophax* cf. *R. bacillaris*, and *Paratrochammina stoeni* besides *Ammonoastuta salsa*, *Ammotium* sp. and *Textularia* sp. Only some of the *Paspalum* samples contained a significant number of agglutinated species (*Paratrochammina stoeni* and *Reophax* cf. *R. bacillaris*), although the general diversity of agglutinated species in the *Hibiscus* and *Paspalum* habitats is low.

When plotted on standard triangular diagrams (text-fig. 4), all samples, with a few exceptions and transitions, fall broadly into

TABLE 1

Distribution and abundance of foraminifera in *Hibiscus* (Hib), marsh (P), lagoon (S), and mangrove (M) samples taken at Moorea, French Polynesia, for this study.

Species \ Sample Number	Hib1	Hib2	Hib3	P1	P2	P3	M1	M2	M3	M4	M5	M6	M7	M8	S1	S2	S3	S4	S5	S6
Water Depths (cm)	0	0	0	0	0	0	10	10	30	20	10	30	20	30	0	10	40	20	30	40
<i>Allasoida virgula</i> *	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
<i>Ammonia salsa</i> †	-	-	-	-	-	-	5	-	4	-	-	-	-	-	-	1	-	-	1	-
<i>Ammonia cf. A. tepida</i> *	21	2	6	35	13	28	3	1	3	6	22	5	10	-	-	3	-	3	-	-
<i>Ammonia convexa</i> *	-	-	-	-	-	6	17	3	12	74	10	29	17	40	30	118	11	310	160	9
<i>Ammonia tepida</i> *	-	-	-	-	-	450	210	377	321	300	280	192	73	9	114	-	-	32	76	-
<i>Ammonium sp. †</i>	-	-	-	-	-	-	2	17	-	6	2	-	-	-	1	-	-	-	-	-
<i>Amphistegina sp.*</i>	-	-	-	-	-	-	2	-	-	4	-	-	-	-	-	-	-	1	-	1
<i>Anomalina rostrata</i> *	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
<i>Anomalinoidea sp.*</i>	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Articulina alticostata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-	-	-	-	-	-
<i>Brizalina cf. B. subspatulata</i> *	-	-	-	-	1	-	-	-	-	2	-	-	-	2	1	-	-	2	1	-
<i>Brizalina sp.*</i>	-	-	-	-	-	-	-	-	-	4	-	2	2	-	-	-	-	-	2	-
<i>Brizalina striatula</i> *	-	-	-	-	-	3	-	55	4	-	16	7	9	3	13	-	-	1	11	-
<i>Cibicides pseudobabulatus</i> *	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
<i>Cibicides sp.*</i>	-	-	-	-	-	-	-	-	-	-	2	-	-	1	1	-	-	-	-	-
<i>Clavulinoides sp.†</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
<i>Cornuspira planorbis</i>	-	-	-	-	-	-	3	51	-	3	10	10	20	13	12	-	-	7	3	-
<i>Cyclorforina cf. C. carinata</i>	2	1	1	-	-	1	2	16	26	2	7	3	11	3	1	-	-	6	8	-
<i>Cyclorforina cf. C. granulocostata</i>	-	-	1	-	-	-	-	-	1	-	1	-	3	12	1	-	-	3	12	-
<i>Cymbaloporella bermudezi</i> †	2	-	-	-	-	3	-	4	7	8	6	3	5	2	17	-	-	9	12	1
<i>Cymbaloporella sp.*</i>	2	-	11	-	1	1	-	17	4	-	12	17	21	5	9	-	-	7	19	-
<i>Discorbinella sp.*</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-
<i>Discorbis cf. D. mira</i> *	-	-	-	-	-	-	-	-	-	-	-	-	2	12	-	-	-	-	-	1
<i>Edentostomina cultrata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	17	-	-	-	-	-	-
<i>Elphidium cf. E. articulatum</i> *	-	-	-	-	-	-	-	-	3	-	2	-	-	-	-	-	-	-	-	-
<i>Elphidium craticulatum</i> *	8	-	-	-	-	4	32	-	130	55	61	50	36	10	35	-	-	36	59	-
<i>Elphidium williamsoni</i> *	6	1	5	7	18	9	2	-	52	34	6	43	15	34	47	7	-	18	18	-
<i>Eponides repandus</i> *	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
<i>Fissurina sp.*</i>	-	-	-	-	-	-	-	-	4	-	-	1	-	1	2	-	-	-	1	-
<i>Fursenkoina sp.*</i>	-	-	-	-	-	-	-	10	-	-	-	-	-	1	3	1	-	1	3	-
<i>Globocassidulina sp.*</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	1	-
<i>Gypsina vesicularis</i> *	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
<i>Hauerina pacifica</i>	-	-	-	-	-	-	-	-	-	7	3	28	39	23	1	113	-	47	-	-
<i>Heterostegina sp.*</i>	-	-	-	-	-	-	-	1	-	1	-	-	-	2	3	-	-	2	-	4
<i>Lachlanella barnardi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	2	1	-
<i>Lachlanella corrugata</i>	-	-	-	-	-	-	-	-	-	4	-	1	-	9	-	-	-	8	7	1
<i>Litotubus minutus</i> †	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	7	-
<i>Litotubus sp.†</i>	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	6	-
<i>Loxostomina cf. L. africana</i> *	-	-	-	-	-	-	-	-	-	1	-	-	-	3	-	-	-	1	-	-
<i>Miliolinella cf. M. oceanica</i>	-	-	-	-	-	-	-	-	-	-	2	1	-	-	2	-	-	1	5	1
<i>Miliolinella heligmatera</i>	-	-	-	-	-	-	-	-	4	5	-	-	2	1	6	-	-	5	11	-
<i>Miliolinella sp. A</i>	2	1	9	-	-	4	-	-	1	-	2	3	1	8	6	-	-	4	6	-
<i>Miliolinella sp. B</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
<i>Miliolinella sp. C</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
<i>Milletiana milleti</i> *	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
<i>Neonorbina albida</i> *	-	-	-	-	-	-	-	-	-	-	2	-	-	6	-	-	-	-	5	-
<i>Nonion sp. A*</i>	-	-	-	-	-	-	-	1	-	1	2	-	-	2	-	-	-	-	-	-
<i>Nonion sp. B*</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
<i>Paratrochammina simplissima</i> †	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	1	-	-
<i>Paratrochammina stoeni</i> †	-	-	-	21	31	-	64	91	6	25	20	21	-	6	1	-	-	-	-	-
<i>Parrelina milleti</i> *	-	1	-	-	1	1	11	1	147	2	1	-	-	1	1	3	-	-	-	-
<i>Pitella haigi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	54	-	-	-	-	-
<i>Pitella transversariata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-
<i>Planogypsina acervalis</i> *	-	-	-	-	-	-	-	-	-	1	-	-	6	2	-	-	-	-	-	-
<i>Poreponoides lateralis</i> *	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	1	-	-
<i>Pseudomassilina sp.</i>	-	-	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-	-	-	-
<i>Pyrgo oblonga</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
<i>Pyrgo sp. A</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>Pyrgo striolata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-
<i>Quinqueloculina bicarinata</i>	1	-	-	-	-	-	-	-	1	-	3	2	-	4	-	-	-	8	-	-
<i>Quinqueloculina cf. Q. incisa</i>	1	-	4	-	41	1	-	-	-	-	-	-	4	-	-	-	-	-	-	-
<i>Quinqueloculina latidentella</i>	-	-	-	-	-	50	20	50	-	60	100	56	50	10	-	-	-	101	100	5
<i>Quinqueloculina sp.</i>	-	-	-	-	1	1	-	-	-	-	-	-	-	21	4	-	-	-	-	-
<i>Rectoglandulina sp.*</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
<i>Reophax cf. R. bacillaris</i> †	-	-	-	6	-	383	13	12	-	1	16	4	-	-	-	-	-	-	-	-
<i>Rosalina bradyi</i> *	-	-	-	-	-	8	9	14	6	19	54	24	9	1	28	-	14	-	-	-
<i>Rosalina sp. A*</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
<i>Sigmohauerina bradyi</i>	-	-	-	-	-	-	-	4	-	3	-	-	-	4	4	-	4	5	-	-
<i>Siphonoperina sp. A*</i>	-	-	-	-	-	-	-	-	-	3	-	-	-	8	1	-	4	2	-	-
<i>Siphonaperta cf. S. pittensis</i>	-	-	-	-	-	1	-	5	-	12	12	11	6	5	10	1	48	35	37	-
<i>Siphonaperta wiesneri</i>	-	-	1	-	-	-	-	2	-	3	-	-	-	21	1	-	21	14	-	-
<i>Sorites orbiculus</i>	-	-	-	-	-	1	-	2	-	3	1	2	13	5	-	-	6	12	6	-
<i>Spirulina cf. S. sigillata</i> *	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
<i>Spirulina sp. A*</i>	-	-	-	-	-	-	-	-	-	-	1	-	-	2	6	-	-	-	-	-
<i>Spirolina arietina</i>	-	-	-	-	-	1	1	15	11	18	43	44	21	14	95	3	180	118	26	-
<i>Spiroloculina antillarum</i>	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-	-	1	-	-
<i>Spiroloculina cf. S. communis</i>	-	-	-	-	-	-	-	-	-	-	1	-	-	9	-	-	-	2	-	-
<i>Spiroloculina sp. A</i>	-	-	-	-	-	-	-	-	2	4	3	8	2	15	17	1	22	-	5	-
<i>Spirophthalmidium elegantissimum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-
<i>Spirophthalmidium sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-
<i>Streblodes sp.*</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
<i>Textularia sp. A†</i>	-	-	-	-	-	-	1	1	-	-	-	-	-	2	1	-	-	-	-	-
<i>Textularia sp. B†</i>	-	-	-	-	-	-	-	20	-	-	3	1	-	-	-	-	2	4	-	-
<i>Tretomphalus sp.*</i>	3	-	2	-	-	-	-	1	-	-	1	2	2	2	5	-	3	5	-	-
<i>Trichohyalus aquayoi</i>	1	-	-	17	1	-	309	141	17	3	25	68	90	4	22	1	-	4	-	-
<i>Triloculina asymmetrica</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	-	42	-	-	-	-	-
<i>Triloculina cf. T. tricarinata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	1	-	-
<i>Triloculina sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	3	1	-
<i>Triloculina subgranulata</i>	22	133	47	10	18	42	-	-	5	-	3	7	5	25	3	6	-	61	20	-
<i>Triloculina tricarinata</i>	-	-	-	-	-	-	-	-	1	-	-	4	-	-	-	-	-	4	1	-
<i>Triloculina trigonula</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	15	-	-
<i>Triloculinella parisa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	1	-	25	-	-
<i>Triloculinella pseudoblonga</i>	-																			

two fields. *Hibiscus/Paspalum* and lagoonal mud/sand assemblages have roughly equal amounts of miliolid and hyaline specimens. The assemblages of both environments, however, differ strongly in the composition of species. Mangrove samples, in turn, are characterized by commonly higher percentages of agglutinated and hyaline specimens and lower numbers of miliolids.

DISCUSSION

The foraminiferal species found in this study occur generally in mangrove, marsh and mud environments elsewhere in the world. Two species, *Miliammina fusca* and *Arenoparrella mexicana*, are not present in our samples. *M. fusca* does occur on Moorea in an extensive mudflat/microbial mat environment at Tamae (Hayward and Lipps, personal observations) on the NE end of the island. Here the mud is exposed for very long times (days) with minimum daily inundation only along tidal channels. At our collecting localities, exposed mudflats do not exist simply because of the low tidal ranges (<.33m) and lack of flat areas. Hence the usual habitat for this species is not present along the generally narrow margins of the island-lagoon interface. *A. mexicana* has never been observed at Moorea, although it is common in mangrove-marsh-mud habitats elsewhere. While its habitat could also be limited as in *M. fusca* or it is very rare, it may have never been present at Moorea, like the mangroves themselves. If so, it is absent from the introduced mangroves in our study because it is not a member of the species pool from which the foraminiferal fauna of the mangroves was constituted.

Our results yield species-level faunal comparisons over the mangrove and associated habitats indicating that foraminiferal assemblages intermingle continuously from the shore towards the lagoon (and vice versa). Not a single foraminiferal species can be considered to be exclusively restricted to the mangrove environment. These results contrast with independent evidence showing that the modern foraminiferal fauna in the introduced mangrove environments differs from the faunas living in the associated habitats. Numerical and statistical evidence for this observation stems from cluster and diversity analysis in addition to abundance and percentage data from individual species or species groups. The question, therefore, arises as to what degree the foraminiferal fauna in introduced mangroves environments at Moorea represents a unique biological entity and, if so, which form of unity do the newly established foraminiferal species have?

Cluster analyses of foraminiferal abundance data distinguished three major assemblages of which the mangrove samples constitute a numerically separate entity (text-fig. 3, Cluster B). In addition, the mangrove faunal assemblage differs in composition (text-fig. 4) and diversity (text-figs. 5 and 6) from both the nearshore *Hibiscus/Paspalum* (Cluster A) and the shallow-water lagoon faunas (Cluster C). Abundance comparisons from the three habitat cluster assemblages also show that individual foraminiferal abundance and percentage data exhibit increases of certain species (e.g. *Ammonia* cf. *A. tepida*, *Brizalina striatula*, *Rheophax* cf. *R. bacillaris*, *Siphonaperta* cf. *S. pittensis*, *Paratrochammina stoeni*, *Hauerina pacifica*; table 1) and species groups (miliolids, hyaline and agglutinated foraminifera; text-fig. 4). Thus, the data clearly show that the abundance shifts recorded for those species represent a distinct trend over the habitats sampled and do not result from patchy foraminiferal distribution or postmortem change as seen elsewhere (Debenay, Guiral and Parra 2004; Catia et al., 2005)

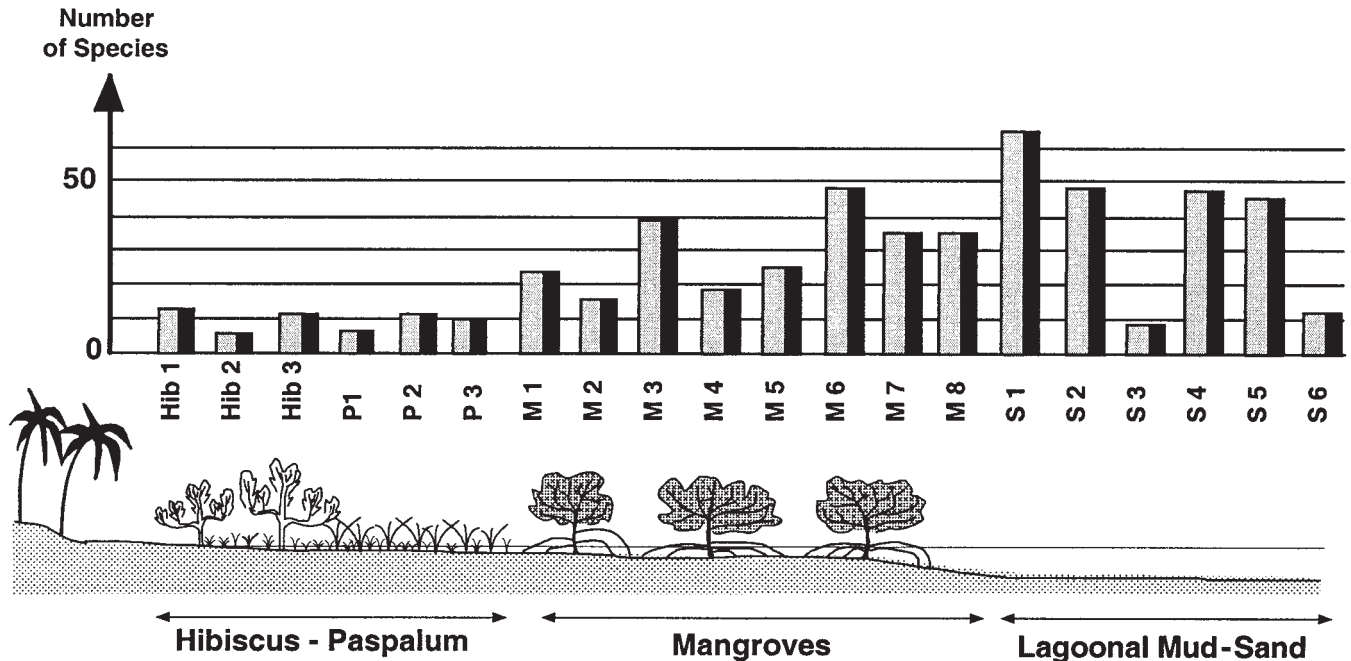
probably because of the limited extent of the habitats along the Moorea lagoon/land interface. The most obvious trend is the general increase in foraminiferal species diversity from the shore (*Hibiscus/Paspalum*) towards the lagoon (text-fig. 5). This trend is probably best explained by lagoonwards increase in depth and decreasing environmental constraints imposing limitations on the existence of foraminifera (salinity variations, low-oxygen content, organic-rich sediments; see Langer and Lipps 2003). Mangrove foraminiferal assemblages exhibit intermediate diversity between the adjacent environments (text-fig. 5).

Detailed species-level comparisons among the three habitats analyzed indicate that not a single species is strictly confined to the mangrove environment but that all mangrove foraminifera are also either present in the lagoon samples or in the *Hibiscus/Paspalum* habitat. This indicates that the modern foraminiferal assemblage present in the introduced mangrove habitats is composed of an admixture of lagoon and nearshore species that have been recruited from the associated habitats. They were not transported to Moorea with the mangroves, as the propagules were most likely collected from the living trees above the water. We therefore conclude that, although the mangrove cluster assemblage represents a separate numerical entity (Cluster B), the foraminiferal mangrove community has no taxon-specific unity, but represents an amalgamation of species assembled from other nearshore habitats.

The results of the species level analyses (table 1) also show that the foraminiferal fauna from mangrove and associated habitats at Moorea have compositional similarities with other mangrove, marsh and shallow lagoonal faunas in the world (compare Saunders 1958; Zaninetti et al. 1979; Steinker and Butcher, 1981; Brönnimann et al. 1981; Rouvillois 1982; Ausseil-Bade 1983; Halicz et al. 1984; Boltovskoy 1984; Brönnimann 1986; Brönnimann and Keij 1986; Debenay 1988; Culver 1990; Brönnimann et al. 1992, Debenay, Guiral and Parra, 2002, 2004; Javaux and Scott, 2003; Catia et al 2005; among others). Since the precise timing of the introduction of the Moorean mangroves is known (Taylor 1979; Cavaloc 1988), the assembly of the mangrove foraminiferal community provides some insight on how communities develop and change over short times geologically.

The status of the mangrove foraminifera, 67 years after the introduction of the trees, shows that the foraminiferal community constitutes a statistically separate entity. The techniques used to separate communities commonly will subdivide gradients in species compositions, and the communities so distinguished are not isolated but continuous with others in the analysis (Bambach and Bennington 1996). The lack of indicator foraminiferal taxa specifically restricted to or particularly dominant within the newly established mangrove environment indicates that this community or assemblage fully interacts with, and recruits and exports its species to and from closely associated habitats. A slight elevational gradient and very low tidal range exists across the higher marsh, through the mangroves to the mud, and this may account for the mixing of species yet slight separation of foraminiferal clusters.

The recruitment and establishment of the foraminifera in the mangroves occurred in less than 50 years or so. We surmise that as soon as mangroves grew large enough to trap sediment, they were recruiting foraminifera. Elsewhere in these kinds of environments, foraminifera colonize areas very quickly, even sea-



TEXT-FIGURE 5

Assemblage diversity of benthic foraminifera in mangrove and associated habitats at Moorea (number of species). Note the gradual increase of taxa from nearshore *Hibiscus* towards lagoonal environments with largest numbers at the interface between mangrove and lagoonal habitats.

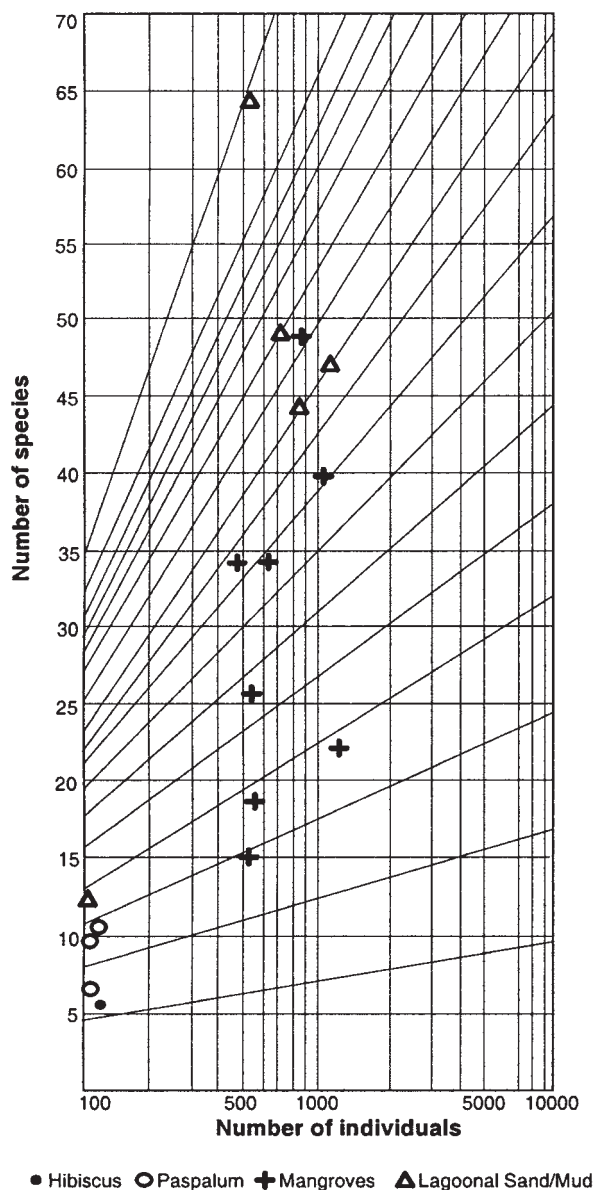
sonally (Debenay, Guiral and Parra 2002), and they likely did at Moorea as well. At Moorea they may be easily dispersed from the other shallow-water habitats to the mangroves in several ways. The mangroves obviously invade the mud and the *Paspalum* marshes and grow in front of the *Hibiscus* stands along the shore. The foraminifera present in those invaded habitats may simply continue to exist, but in different proportions under new but similar environmental conditions. Currents and wave action as well as floating debris in the lagoon transport living foraminifera throughout shallow water areas (Lipps, personal observations at Moorea, 1994-2003). These mechanisms include floating marine vegetation mats, from a few small branches to huge rafts, all carrying living foraminifera, which are deposited where the rafts ground. Live foraminifera are also carried in foam generated by breaking waves in the lagoon. Even areas that are fairly high above mean tidal level at Moorea can be submerged and subject to inoculation of foraminifera when large swells or surge (particularly from the south) fill the lagoon to overflowing. Such mechanisms can move a large number of foraminifera within a few days from one place to another where they become established as reproducing populations. Transport by fish is also possible (Daniels and Lipps 1978; Lipps 1988), if they move from one area to another in their feeding and defecating activities. Birds are known to carry live foraminifera (Lessard 1980) on their feet and feathers for very long distances. Thus, maintaining a mix of live individuals of foraminiferal species from one habitat to another within the lagoon would likely be easy for benthic foraminifera even if they do not have long-range dispersal mechanisms in their life histories. Indeed, the similarity of foraminiferal species from these environments worldwide indicate a mixing of faunas over much wider regional scales. Apparently, if live foraminifera

can get to a suitable environment, they can grow, reproduce and establish viable populations very quickly. The mangrove foraminiferal cluster would appear as a numerically distinct entity in the fossil record geologically instantaneously, were these environments preserved.

The short evolutionary time frame (60+ years) of the introduced mangroves, however, has not yet promoted the evolution of new taxa in this habitat. Given the mixing of species from one place to another, evolution of new species in the mangroves may never occur. Indeed, if our observations on the introduced mangroves are applicable to shallow-water tropical habitats around the world, then widespread mangrove and other habitats may well act in concert to provide selection for new species. Isolation in any of these environments, given the ease of dispersal of foraminifera, is unlikely, thus thwarting whatever differential selection may occur in each area.

On the other hand, mangroves constitute a true environmental barrier for a number of foraminiferal taxa. Larger symbiont-bearing foraminifera (*Sorites*, *Peneroplis*) that are present in reef and lagoonal environments at Moorea and that are also transported between habitats, are largely absent from the mangroves, indicating that certain environmental constraints prevent those species from colonizing the mangrove, *Hibiscus* or salt grass habitats. Inversely, two species (*Quinqueloculina* cf. *Q. incisa* and *Rheophax* cf. *R. bacillaris*) are restricted to most nearshore *Hibiscus*, *Paspalum* and mangrove habitats, and do not cross the mangrove barrier into the lagoon.

Although the modern Moorean mangrove habitat represents a true transitional zone between the limited nearshore *Hibiscus* and *Paspalum* and the shallow-water lagoon habitats, our data



TEXT-FIGURE 6

Fisher's diversity index graph for foraminiferal samples from Moorea indicating a gradual increase in diversity from *Hibiscus/Paspalum*, towards the lagoon.

demonstrate that this newly established habitat constrains the assembly of foraminiferal communities. Such constraints for the assembly and composition of benthic foraminiferal communities may include sedimentologic (grain size, sedimentation rate), elevational, as well as microhabitat-specific changes associated with the establishment of the mangroves (trapping of organic-rich sediments, creation of oxygen-depleted microhabitats, modifications of the trophic structure, etc.). Abundance maxima, for example, of *Paratrochammina stoeni*, *Rheophax* cf. *R. bacillaris*, *Quinqueloculina latidentella*, or *Elphidium* cf. *E. craticulatum* show that some species appear to flourish particularly well within the mangrove environment. However, these species were also found in the associated *Hibis-*

cus and *Paspalum* or the lagoon habitats, indicating that they were endemic species of the associated environments before the mangroves were introduced to Moorea. The logical conclusion, therefore, is that all species have migrated from the associated habitats into the newly-established and environmentally-modified mangrove environment. This change is accompanied by shifts in the abundance of taxa and by the specific composition of benthic foraminiferal assemblages. To date, these changes have created a statistically identifiable mangrove assemblage. This assemblage is, however, devoid of specific indicator taxa, and is subject to a continuous process of community amalgamation. This process of community assembly will not continue forever, because the mangroves are closely linked to populations in the lagoon that represent a particular number of species. That number in *Paspalum*, *Hibiscus* and mud habitats will eventually limit the number of species in the mangroves.

These observations suggest that foraminiferal communities of any kind may not be biologically integrated, that all are chiefly constructed through migration into available habitats or ecological opportunities, and that community assembly takes place very quickly, faster than the geological history of these environments can be recorded. This could even be more general; for example the coral reef communities of the Huon Peninsula, Papua New Guinea, experienced nine rather short periods of reassembly during Pleistocene sea level and tectonic changes, yet the species composition remained constant, except in areas where particular environmental perturbations limited the species present (Pandolfi, 1996, 1999). In this case, as with the Moorean foraminifera, the constant input of larvae and migrants from essentially the same species pool over the 95,000 year period kept the communities closely similar. The similarity of foraminiferal and other marine faunas over long time spans, then, may result from a species pool located nearby with members that can tolerate the new and similar ecologic conditions.

The mixing of benthic, non-self-dispersing foraminiferal species over a few decades from older habitats to newly created ones suggests that community formation on the reefs might likewise have been instantaneous in geological time. In the Californian Pleistocene record, rocky shore faunas are similarly constant over time, in spite of significant sea temperature, sea level, upwelling, and nutrient supply changes (Lindberg and Lipps, 1996). In this case, the plasticity of the biota was considered the important factor, although it could also be due to the breadth of tolerance of the species pool from which successive faunas were derived. In addition, communities seem resistant over the long term to all kinds of changes—the introduction of new species, extinction of a few old ones, temperature, nutrient and sea level fluctuations, and catastrophic damage from hurricanes, seismic activity, temperature extremes, predatory invasions, and similar events. After such events, the associations commonly reconstitute themselves in a manner similar to previous ones because the species available are the same and they tolerate the renewed conditions in a similar manner. While we may see these changes as detrimental on the timescale of human life spans, the changes are ameliorated rapidly in geologic time. This has significant implications for conservation biology, which is mostly based on short-term observations.

Perhaps, in spite of wonderful historical records, the fossil record is not a good place to test the hypothesis of community unity after all, because community formation occurs over very short times rather than evolutionary or geologic time. What these studies do indicate is that communities do not evolve over

geologic time, as Bambach and Bennington (1996) concluded, but are assembled from potentially evolving species pools involving a wider variety of habitats. If those species do not change, then the assembled communities cannot change either.

CONCLUSIONS

The mangroves, *Rhizophora stylosa*, were introduced to Moorea, French Polynesia, in 1937. Since then a community or assemblage of foraminiferal species has developed, most likely starting as soon as the trees began to trap finer sediment and organic materials. The foraminiferal fauna is typical of similar environments elsewhere with the exception of two missing characteristic species. One, *Miliammina fusca*, is present in more extensive mudflats elsewhere on Moorea but the other, *Arenoparrella mexicana*, appears to be absent from Moorea. This community forms an identifiable cluster in numerical analyses, and it intergrades between other shallow-water lagoon habitats of *Hibiscus* trees, *Paspalum* marshes, and mud found elsewhere in the lagoon. Thus we conclude that the mangrove foraminiferal community is undergoing continual mixing of populations, replenishing the assemblage constantly and quickly, from these other habitats by means of several mechanisms. It is not an Eltonian integrated community, but rather a Gleasonian, although not unlimited, assemblage of species that simply tolerate the mangrove environment. Although reef communities seem to have limited membership while other foraminiferal communities do not over geological time, our results suggest that marine communities in general are assembled fast because of the mobility of their included species. Possibly, even reef communities, appearing coherent over geological times, are assembled so fast and so completely on those time scales that they only appear to maintain coherency, as do temperate rocky shore communities. All of these communities or associations, in fact, may be interacting with more broadly distributed species pools in a manner similar to that of the foraminiferal assemblage in recently introduced mangroves at Moorea, French Polynesia. This model should be further examined in other situations.

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APPENDIX 1

List of foraminiferal species in alphabetical order:

Allasoida virgula (Brady 1879)
Ammoastuta salsa (Cushman and Brönnimann 1948)
Ammonia cf. *A. tepida* (Cushman 1958)
Ammonia convexa (Collins 1958)
Ammonia tepida (Cushman 1958)
Ammotium sp.
Amphistegina sp.
Anomalinaella rostrata Cushman 1927
Anomalinoidea sp.
Articulina alticostata Cushman 1944
Brizalina cf. *B. subspathulata* Boomgaart 1949
Brizalina sp.
Brizalina striatula (Cushman 1922)
Cibicides pseudolobatus (Perelis und Reiss 1975)
Cibicides sp.
Clavulinoides sp.
Cornuspira planorbis (Schultze 1854)
Cycloforina cf. *C. carinata* (Albani 1974)
Cycloforina cf. *C. granulocostata* (Germeeraad 1946)
Cymbaloporeta bermudezi (Sellier de Civrieux 1976)
Cymbaloporeta sp.
Discorbinella sp. A
Discorbinella cf. *D. mira* Cushman 1922
Edentostomina cultrata (Brady 1881)
Elphidium cf. *E. articulatum* (d'Orbigny 1839)
Elphidium craticulatum (Fichtel and Moll 1798)
Elphidium williamsoni (Haynes 1973)
Eponides repandus (Fichtel and Moll 1798)
Fissurina sp.
Fursenkoina sp.
Globocassidulina sp.
Gypsina vesicularis Parker and Jones 1860
Hauerina pacifica (Cushman 1917)
Heterostegina sp.
Lachlanella barnardi (Rasheed 1971)
Lachlanella corrugata (Collins 1958)
Lituotuba minuta
Lituotuba sp.
Loxostomina cf. *L. africana* (Smutter 1955)
Miliolinella cf. *M. oceanica* (Cushman 1932)
Miliolinella heligmateira Loeblich and Tappan 1994
Miliolinella sp. A
Miliolinella sp. B
Miliolinella sp. C
Millettiana milletti (Heron-Allen and Earland 1915)
Neoconorbina albida McCulloch 1977
Nonion sp. A
Nonion sp. B
Paratrochammina simplissima (Cushman and McCulloch 1939)

Paratrochammina stoeni Brönnimann and Zaninetti 1979
Parrelina milletti (Heron-Allen and Earland 1915)
Pitella haigi Langer 1992
Pitella transversistriata (Brady 1884)
Planogypsina acervalis (Brady 1884)
Poreponoides lateralis (Terquem 1878)
Pseudomassilina sp.
Pyrgo oblonga (d'Orbigny 1839)
Pyrgo sp. A
Pyrgo striolata (Brady 1884)
Quinqueloculina bicarinata d'Orbigny 1826
Quinqueloculina cf. *Q. incisa* Vella 1957
Quinqueloculina latidentella Loeblich and Tappan 1994
Quinqueloculina sp.
Rectoglandulina sp.
Reophax cf. *R. bacillaris* Brady 1881
Rosalina bradyi (Cushman 1936)
Rosalina sp. A
Sigmohauerina bradyi (Collins 1958)
Siphonogenerina sp. A
Siphonaperta cf. *S. pittensis* (Albani 1974)
Siphonaperta wiesneri (Parr 1950)
Sorites orbiculus Ehrenberg 1839
Spirillina cf. *S. sigillata* McCulloch 1977
Spirillina sp. A
Spirolina arietina (Batsch 1791)
Spirolucina antillarum d'Orbigny 1839
Spirolucina cf. *S. communis* (Cushman and Todd 1944)
Spirolucina sp. A
Spirothamnidium elegantissimum (Said 1949)
Spirothamnidium sp.
Strebloides sp.
Textularia sp. A
Textularia sp. B
Tretomphalus sp.
Triloculina asymmetrica Said 1949
Triloculina cf. *T. tricarinata* (d'Orbigny 1839)
Triloculina sp.
Triloculina subgranulata (Cushman 1918)
Triloculina tricarinata (d'Orbigny 1839)
Triloculina trigonula Lamarck 1804
Triloculinella parisa Loeblich and Tappan 1994
Triloculinella pseudooblonga (Zheng 1980)
Trochammina inflata (Montagu 1808)
Trichohyalus aquayoi (Bermudez 1935)
Vertebrulina striata d'Orbigny 1826
Wiesnerella auriculata (Egger 1839)