ALLOCHTHONOUS WOODY INPUT INTO A TROPICAL SHALLOW MARINE LAGOON AND ITS EFFECT ON BIODIVERSITY

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Abstract. I investigated the role of sunken wood in contributing to a shallow lagoon's ability to harbor life. Woodfalls from the lagoons of Moorea, French Polynesia were characterized and run through a program of exhaustive identification. 53 visually distinct species were found in 16 wood samples, and 27 were found in 15 sediment samples. Wood was projected to harbor a total of 75 visually distinct species, and sediment was projected to harbor 42. Dicot trees were found to harbor a greater richness of life. These results suggest a need to incorporate allochthony in the nutritive modeling of systems, and support the importance of structural complexity in harboring invertebrate life.

Key words: allochthony; lagoons; morphotypes; oligotrophy; rarefaction; Moorea, French Polynesia; woodfalls

INTRODUCTION

matter Biotic imported from one to another, referred to as ecosystem allochthonous input, can create new habitats and enrich existing ones. The past several decades have seen an increased interest in these facets of ecosystems (Stockton and DeLaca 1982, Polis et al. 1996, Lastra et al. 2008. Winterbourn 2010. Błażewicz-Paszkowycz et al. 2014), as they increase the complexity of ecological problems by turning habitats into open systems. Oligotrophic zones such as freshwater streams, the deep sea, and shallow tropical marine sediments are especially dependent on allochthonous organic input, and in many cases may depend on this imported matter to sustain the majority of their biota (Stockton and DeLaca 1982, Mackie et al. 2005, Winterbourn 2010). Allochthony in shallow lagoon environments has received very little study, in comparison with the well-studied deep sea and freshwater ecosystems. Woody matter has been observed to be the most abundant allochthonous input into the former habitats, and the nature of wood as a substrate for invertebrate life is the subject of the present study.

As a substrate, sunken wood in marine environments (woodfalls) has been found to support mostly molluscs, polychaetes, and peracarids, the superorder which contains amphipods, isopods, and talitrids (Evans 1999, Samadi et al. 2010). This diversity is found to differ strikingly from that of sediment assemblages in the deep sea (Pailleret et al. 2007, Samadi et al. 2010, Fagervold et al. 2012), but whether this difference holds true in more shallow environments is understudied. The benefit to organisms living on woodfalls is generally attributed to the nutritional benefit provided by the decaying wood and the microbes found on it (Fagervold et al. 2012, Dittmar and Boetius 2013), but structural benefits may also affect invertebrate assemblages (Dover and Berg 1988).

Tropical islands, while not the only place fit for the study of shallow marine woodfalls, are ideal for several reasons. Islands have an area which is relatively small compared to the length of their shoreline, which emphasizes terrestrial-marine exchange and the importance of the coastal and lagoon zones to the island's ecology. Furthermore, the warm waters of the tropics are especially conducive to the putrefaction of organic material. The shallow lagoons of Moorea, French Polynesia are exemplary of this habitat. Observations also suggest that wood in this habitat may offer a significant boost to habitability through rotting and enriching the sediment.

Species assemblages, measured using presence and absence due to the infeasibility of abundance comparisons, were examined for woodfalls and sediment found in the shallow lagoons fringing Cook's Bay in Moorea. It was hypothesized that woodfalls should harbor a more species-rich assemblage than unassociated sediment, due to the nutritive and structural augmentation they bring to the oligotrophic lagoon. In addition, sediment associated with woodfall rot should have a greater richness than unassociated sediment.

METHODS

Woodfall sampling

All sampling took place on Moorea, French Polynesia. Woodfall sites were located and sampled in Cook's Bay in October and November 2014 (Fig. 1). At each site, samples were taken from the substrate beneath the woodfall, from substrate of similar composition outside of the woodfall's rot influence (1-2 m away), and from the woodfall itself. This vielded subsites of three types, hereafter referred to as 'wood,' 'close substrate,' and 'far substrate.' At each of these "subsites," at least three samples of substrate or wood were taken to properly represent the habitat's diversity. Samples were placed into



FIG. 1. Orange dots indicate woodfall sites sampled between October and November 2014. Blue square indicates UC Berkeley Gump Station.

Ziploc bags and brought to the Gump Station laboratory for closer inspection.

In addition, salient conditions at each woodfall were recorded, including algal cover, decay category, substrate type, location (GPS), woodfall volume, and wood type. Volume was estimated through a decomposition of the woodfall into cylinders, triangular prisms, etc. Most other parameters recorded were categorical or ordinal - decay category, for example, was assigned a value from 1 to 5 based on rot permeation, wood disassociation, and softness. Wood from the coastal trees Casuarina equisetifolia (ironwood), Hibiscus tiliaceus (hibiscus), and Cocos nucifera (coconut) was sampled (note that coconut trees do not produce true wood).

Identification of associated invertebrates

Due to the great volume of invertebrates processed and the abundance of cryptic species in the sample pool, organisms found in samples were identified by morphotype (MT). MTs served as 'bins' for organisms which were not dissimilar enough to differentiate - MT43 (Fig. 2), for example, describes an amphipod with enlarged coxae, but in truth may encompass several species whose differentiation might require intense scrutiny or genetic analysis. When a specimen's affinity to an MT was uncertain, that specimen was always binned in that MT to prevent the undue proliferation of MTs. Each morphotype is accompanied by a preserved specimen and photo identification, and is identified to the lowest possible taxonomic level. Samples were placed in fresh



FIG. 2. Picture accompanying morphotype 43, which shows an amphipod under magnification.

water and macroinvertebrates were identified under a dissection microscope. After wood and sediment was inspected thoroughly, associated water was examined. Identification of a sample was deemed complete when 5 consecutive water samples yielded no morphotypes new to that subsite, or when 45 minutes had elapsed since subsite examination began. This time limit was chosen to expedite identification.

Analyses

A series of statistical tests were performed in an attempt to parse out relationships between site characteristics (woodfall volume, etc.) and site richness and diversity. Woodfall volume and decay category were regressed separately against morphotype richness, and wood type was analyzed against richness using a one-sided t-test.

Richness was assessed using rarefaction curves, which plot the total number of unique specimens (Y axis) against the number of samples taken (X axis). Two critical aspects of these graphs are the asymptote they approach, which represents the number of unique specimens that can be found in a system (species richness), and the fidelity with which the graph resembles a logarithmic function. A graph which curves less, or which resembles a straight line, reflects a system in which unique species are being found at a constant rate. Its effectiveness is in direct proportion to its curvature.

Rarefaction curves were plotted for all three subsite types (wood, close substrate, and far substrate). Chao estimators (Basualdo 2011), which extrapolate total richness using



FIG. 3. Box plot for the morphotype counts of 8 dicot and 8 coconut woodfall samples.

repeated findings in samples, were used for all three subsite types. These data were estimated using the EstimateS program (Colwell 2013).

In order to aid with data visualization, a program was written in Python to generate a "smoothed rarefaction curve." This program generates a large number of rarefaction curves using repeatedly shuffled sampling orders, removing the bias of the study's non-random sampling order. All of these curves are then averaged into one smoothed curve, with all of the morphotype count values for each point on the X axis represented by a mean and a standard deviation.

RESULTS

Woodfall sampling and identification

16 woodfall sites in total were sampled. 8 of these originated from coconut trees, and 8 from dicots (hibiscus and ironwood). Only the wood subsite of the site 16 was sampled.

77 morphotypes (MTs) were found across 46 subsites. 53 morphotypes were found in wood, 30 were found in woodfall-associated sediment, and 27 were found in sediment collected outside of the range of the woodfalls studied.

Analysis

Several of the statistical tests run on site characteristics yielded significant data. Dicot woodfalls (Fig. 3) were found to harbor an average of 11.875 MTs, while their coconut counterparts harbored an average of 7.625 MTs. The former wood type was found to support a higher richness with a p-value of 0.0648.

Dicot woodfalls also tended to be shot through with the holes of boring organisms



FIG. 4. The bored condition.

(Fig. 4). This characteristic was found in all 8 dicot samples bore this characteristic and only 1 of 8 coconut woodfalls.

Other tests yielded insignificant results. Morphotype count was regressed against decay category with a p-value of 0.187, and volume was regressed in the same way with a p-value of 0.7187.

Too few sites of different sediment type were found to make meaningful comparisons between sediments as habitats.

Smoothed rarefaction curves were constructed for the three sample types collected (Fig. 5). Extrapolated species richness (Chao 1987, Colwell and Coddington 1994, Colwell 2013) was 75 for woodfalls, 77 for close sediment samples and 42 for far sediment samples.

Woodfall and far sediment curves approximated the logarithmic function, while the close sediment curve appeared as more of a straight line.

DISCUSSION

Analysis of characteristics

My results indicate that dicots harbor higher morphotype richness than coconuts. This can be attributed to a number of factors, but structural complexity stands out as the most salient. Every dicot sampled was shot through with boring holes – as much as half or more of the total volume could be taken up by these tunnels. This contrasts sharply with coconut's fibrous, tightly-packed structure; the issue may simply be one of space.

Morphotype richness

The community harbored by sunken wood appears to be much richer than that found in unassociated sediment. This assumption can be made safely to the degree to which the two related rarefaction curves (Fig. 5) can be said to flatten out. We can therefore put a good deal of credence in the extrapolated estimate for total richness of these two subsites. The curve for close (associated) sediment, however, is puzzling. Comparable morphotype richness was found in far and close sediment, but it appears that if





collection continued, associated sediment numbers would take a much longer time to level out. While the estimate of 77 total morphotypes is a very rough one, there is a feasible explanation for a total richness this high. Woodfall-associated sediment is more nutrient-rich than unassociated sediment, so the habitat may have faculties of woodfalls unassociated sediment. Further and investigation of this question should investigate overlap habitats, and the interplay of both "parent" habitats in the mixed habitat.

Averaging several or many rarefaction curves into one smoother curve appears to be a safe and helpful way to simplify data, especially for low-resolution datasets like the one used in this study. Although rarefaction curves assembled using hundreds or thousands of samples may more closely approximate the logarithmic function, I recommend rarefaction curve smoothing as a viable option for future studies of small sample size.

These data suggest a universality of allochthony, which stands in contrast to the volume of literature on the subject. The deep sea, freshwater systems, and the land-sea interface have been thoroughly studied in this context, due to their excessively low level of primary productivity (Stockton and DeLaca 1982, Polis et al. 1996, Winterbourn 2010, Marshall 2014). These data suggest the importance of incorporating outside input into any ecosystem model. No system is closed, and even an ecosystem as rich as the tropical coral reef can receive a significant boost to its capacity for life from outside.

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